

**STRATEGIES FOR REHABILITATION OF
LAKE TROUT IN THE GREAT LAKES:
PROCEEDINGS OF A CONFERENCE ON
LAKE TROUT RESEARCH, AUGUST 1983**



Great Lakes Fishery Commission

TECHNICAL REPORT NO. 40

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ON LAKE TROUT RESEARCH, AUGUST 1983

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TECHNICAL REPORT NO. 40

Great Lakes Fishery Commission
1451 Green Road
Ann Arbor, Michigan 48105

August 1984



Dedicated to Kenneth H. Loftus in recognition of his many years of service to the Great Lakes Fishery Commission and of his encouragement and support for fishery research in the Great Lakes.

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INTRODUCTION

Native stocks of lake trout (*Salvelinus namaycush*) were severely depleted in much of Lake Superior and became virtually extinct in Lakes Michigan, Huron, Erie, and Ontario during the 1940-1950s, due to the combined effects of intense predation by the sea lamprey (*Petromyzon marinus*) and overfishing (Smith 1968; Lawrie and Rahrer 1972; Christie 1974; Pycha and King 1975; Walters et al. 1980). A massive program to suppress sea lamprey populations with selective toxicants and to plant hatchery-reared lake trout was begun in the late 1950s (Smith and Tibbles 1980). In Lake Superior, the only lake to retain significant stocks of native lake trout, lakewide plantings began in 1958, concurrently with the first application of lampricides. In Lakes Michigan, Huron, and Ontario, sea lamprey populations were greatly reduced with the toxicants before major plantings of lake trout were started, respectively, in 1965, 1973, and 1973. The goal of these plantings was to reestablish self-sustaining stocks of lake trout in each lake. However, the goal of sustained reproduction has at best been partially achieved in only Lake Superior, even though over 100 million lake trout have been stocked in the Great Lakes since 1958 (Anonymous 1981) and sea lamprey populations are considered to be less than 10% of their peak abundance in Lake Superior (Smith and Tibbles 1980).

The effectiveness of the existing strategy for reestablishing self-sustaining lake trout populations in the Great Lakes has not been demonstrated. Although the successful reproduction in Lake Superior is encouraging, evaluation of the contribution of hatchery fish to the recovery is confounded by the presence of residual native stocks (Lawrie 1978), which may have influenced the recovery. Swanson and Swedburg (1980) showed that very small numbers of native spawning lake trout effected a recovery of an offshore lake trout stock in Lake Superior. Therefore, 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 (two very small native stocks persist in Georgian Bay (Berst and Spangler 1973)). In fact, the lack of lake trout reproduction in Lake Michigan after 17 years of stocking indicates that the current approach needs to be critically examined. For instance, Clark and Bin Huang (1983) believed that reproduction should have been evident by now in parts of Lake Michigan, and Dorr et al. (1981) and Wagner (1981) have shown that egg densities on spawning reefs are very low or that survival to the fry stage is minimal.

Notwithstanding the need for a proven model to guide the task of restoring lake trout in the Great Lakes, the rehabilitation effort has not been conducted on an experimental basis (Pycha 1982). This deficiency impeded the development of new science and technology which could enhance the rehabilitation efforts. Although lake trout rehabilitation was initially conceived as an experiment (Anonymous 1957), it soon evolved to a stage where a few strains of lake trout, reared to a common life stage under similar hatchery regimes, were planted within a narrow range of densities at most planting sites. Large scale manipulations of the system (experimental management) designed to measure the effects of stocking, fishing, and sea lamprey predation on a controlled basis were never undertaken. Thus, there exists considerable room for experimentation within the lake trout rehabilitation program, and a better coupling of research and management is warranted.

The problem of developing self-sustaining lake trout populations has been the subject of research efforts in both the United States and Canada. However, this work has been independently pursued by various agencies and a more structured and coordinated approach based on an established set of priorities has not taken place since the mid-1960s, when the last such assessment was undertaken (Anonymous 1964). To remedy this absence, the Great Lakes Fishery Commission sponsored the Conference on Lake Trout Research (CLAR) on August 23-26, 1983 at Goderich, Ontario. The goal of CLAR was to recommend priorities for lake trout research, identify hypotheses to be tested, outline the associated experimental designs, and encourage a sharing of the tasks among the appropriate agencies and institutions.

To make the task of identifying research needs more manageable, the CLAR Steering Committee divided the overall problem into seven disciplines and established a working session composed of 3-6 researchers and a management representative for each discipline. Linkage among the sessions and overview were the responsibility of an integrative group and the steering committee (see conference organization).

Research needs for the lake trout rehabilitation program were established by having each working session produce draft research recommendations before the conference started. During the conference, the draft recommendations were improved upon and then subjected to a peer review conducted by dividing the conference participants into three groups and by having each group review and comment on all recommendations. These recommendations were then revised by the working sessions in accordance with the peer reviews. Information transfer among the participants was enhanced by having each research recommendation written in a standard format (this was done from the start) consisting of an issue statement, a hypothesis section (which provided background information and stated the central and alternative hypotheses), and a methodology section that suggested experimental designs, including potential sites.

This report provides a summarization of the research recommendations developed by each working session at CLAR and an overview or integration **of** these recommendations. Each working session report begins with a discussion of relevant issues in that discipline. After the issue discussion, research needs are listed in order of priority and are identified by the appropriate central hypothesis, which is underlined. Experimental designs follow each central hypothesis. Full descriptions of the CLAR session reports may be obtained from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

POPULATION DYNAMICS
AND SPECIES INTERACTIONS^{1,2}

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We examined factors that may be slowing lake trout rehabilitation by limiting the reproductive capacity of the stocks. Attention was focused on mortality and species interactions, particularly predation and competition. Major issues that may be impediments to rehabilitation of lake trout are: (1) measurement and control of lamprey-induced mortality; (2) competition with other salmonids; (3) unknown post-planting mortality and mortality among juveniles too small to be fully vulnerable to sampling gears; (4) inadequate numbers of spawners; and (5) changes in the forage base.

SPECIES INTERACTIONS

The relation between sea lamprey wounding and lake trout mortality is neither well defined nor fully understood. Most of the evidence linking sea lamprey attack marks to lake trout mortality is circumstantial because lake trout killed by lampreys are seldom found and little is known about lake trout survival after the lamprey detaches. Wounding levels may not reflect the same mortality from year to year

1 Leader, R. W. Hatch; Discussants: L. B. Crowder, B. G. H. Johnson, E. L. King, Jr., R. W. Rybicki, C. P. Schneider, and J. H. Selgeby.

²Contribution 617 of the Great Lakes Fishery Laboratory, Ann Arbor, Michigan 48105.

if the fraction surviving attack is some function of time, or of size of fish or of lamprey (Youngs 1980). More precise estimates of lamprey-induced mortality require information on the relation between lamprey wounds and their lethality.

The selection of optimal strategies for rehabilitating lake trout is hindered by our inability to predict the magnitude of reduction of lamprey-induced mortality on lake trout that results from a given increase in sea lamprey control effort. Sea lamprey populations in the upper Great Lakes have been reduced to less than 10% of their peak abundance of the late 1950s through the use of chemical control (Smith and Tibbles 1980). Although the present level of control appears adequate to allow restoration of some important stocks of fish (e.g. lake whitefish (*Coregonus clupeaformis*) and bloaters (*Coregonus hoyi*), significant natural reproduction of lake trout has been limited to Lake Superior. Many biologists attribute this failure to a lack of significant multi-age stocks resulting from exploitation and predation by residual sea lampreys. The degree to which survival of lake trout might be increased by intensified lamprey control (or, conversely, how much survival would decrease if lamprey control efforts were lessened) is not known.

Competition with introduced salmonids may reduce lake trout growth. Fast growing fish are vulnerable to size-dependent mortality sooner, but slow growing lake trout may experience delayed sexual maturity, reduced fecundity, and increased size-dependent mortality. Although lake trout do not consume a substantial portion of the alewife (*Alosa pseudoharengus*) forage available in Lake Michigan (Stewart et al. 1983), the salmonid assemblage as a whole may do so (Stewart et al. 1981). Available data on the food of lake trout and chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) suggest a high degree of diet overlap; furthermore, as judged by thermal preferences, habitat overlap may also be high. The potential for competition is high, particularly if recently reported declines in alewife abundance (Wells and Hatch 1983) continue. The first indications of increased competition probably will be found in decreasing condition factors and increasing diet diversity. Because both age at first spawning and fecundity

are size dependent, a reduction in growth rate resulting from competition may also lead to reduced egg deposition and thus further delay rehabilitation.

POPULATION DYNAMICS

Stock assessment could be substantially improved if known recruitment of planted lake trout could be projected to the adult population. Post-planting survival rates are unknown, and natural mortality rates for fish ranging from yearlings to the age of complete vulnerability to sampling gears have not been adequately established. Accurate estimates of survival rates for these juvenile age groups are central to the estimation of standing stocks of spawning lake trout derived from hatchery-produced fish, and thus to determining stocking rates needed to achieve rehabilitation.

Estimates of adult annual mortality ranging from 32 to 85% in western Lake Superior (Swanson and Swedberg 1980), 50 to 60% in eastern Lake Superior after 1974 (Pycha 1980), 22 to 65% in Green Bay (Moore and Lychwick 1980), and 48 to 71% in eastern Lake Michigan (Rybicki 1983) are of concern relative to Healey's (1978) observation that "lake trout populations...showing annual mortality rates in excess of 50% are all in serious trouble" and unable to sustain themselves by natural reproduction. Attempts to separate total annual mortality into components (fishing, lamprey-induced, and other; e.g. see Pycha 1980) have been frustrated by incomplete knowledge of total harvest, especially the illegal catch, which is believed to be substantial. Although sport fishery harvests are poorly documented, adequate measurement techniques exist and further research in this area is unnecessary.

Neither the abundance nor the structure of spawning stocks appear to be sufficient to produce enough progeny to create an exponential increase in naturally produced lake trout. In most parts of Lake Superior, total mortality is so high that relatively few hatchery-origin lake trout reach sexual maturity and fewer still spawn more than once (Pycha 1982). In Lake Michigan, lake-produced adult lake trout form an insignificant component of the small proportion of the stock reaching sexual maturity, even after 17 years of

stocking. Hatchery-origin spawners may be relatively inefficient in reproducing (Walters et al. 1980), and their abundance may be insufficient to offset the environmental pressures that are impeding population increase; that is, a "critical mass" has not been achieved.

Reduced growth of lake trout in Lake Superior, resulting from a changing forage base, increases age at maturity, decreases average fecundity at a given age, exposes the fish to increased mortality, and reduces potential production from its former level. Since the early 1960s, lake herring (*Coregonus artedii*) have been relatively scarce and have been replaced in the lake trout's diet by rainbow smelt (*Osmerus mordax*). Smelt are found mainly along the periphery of the lake and its nearshore islands, rather than in the pelagic zone throughout the lake as were lake herring. Lake trout distribution appears to have become associated with that of smelt, thus reducing the productive potential of the population compared with earlier years when the whole lake was used. Rainbow smelt populations began to decline sharply in Lake Superior in the late 1970s, and by 1982 the estimated smelt biomass averaged only 7% of that of 1978. Samples of lake trout taken in Wisconsin waters of Lake Superior in fall 1982 and spring 1983 exhibited poor condition and reduced growth (J. H. Selgeby pers. Comm.).

HYPOTHESES - EXPERIMENTAL DESIGNS ³

Lethality of single sea lamprey attacks on individual lake trout is a function of size of the host, its physiological condition, and the attack site. A laboratory derived relationship between wounding rate and mortality rate can be used to determine lamprey-induced mortality in the wild, given a measure of wounding rate in the wild.

³Full descriptions available from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

In the first phase of the research individual lake trout of three size categories would be confined with a single parasitic-stage sea lamprey in laboratory tanks. Sea lampreys would be allowed to remain attached until they either kill the fish or detach. The experiment would be continued through the entire feeding cycle. In the second phase the effects of multiple attacks would be studied. Survival (as evidenced by healing wounds) would then be related to mortality by lake trout size category.

Changes in sea lamprey-induced mortality of lake trout resulting from changes in sea lamprey control effort can be estimated. A relation between mortality and degree of control can be established to determine the cost effectiveness of various control levels.

Testing this hypothesis would require that the predator-prey ratio be altered in a given area of the Great Lakes by changing the number of parasitic-phase sea lampreys while lake trout abundance is held constant (or vice versa) or by selecting sites where sea lamprey abundance is known to be the only major variable. Relative lamprey abundance, prey density, lamprey wounding rate, and lamprey-induced mortality in lake trout and alternate prey would be measured. The experiment could also be carried out in an inland lake where numbers of predators and prey could be controlled directly.

Significant unknown natural mortality between time of planting and size at full vulnerability prevents accurate estimation of standing stocks.

Experimental fishing carried out to determine size-specific -mortality from planting through full vulnerability would be conducted for several years during the 2-3 weeks immediately after the annual spring planting. Large trawls calibrated for area or volume swept and gillnets calibrated for size selectivity would be used to estimate abundance. Size-specific estimates would be converted to age-specific estimates annually by applying stock-specific size-at-age determinations.

Competition with non-native salmonids may reduce growth rates of lake trout, and thus increase the time that lake trout are vulnerable to size-selective mortality.

This research would rely on existing data sets that contrast lake trout populations under high and low levels of inter-species competition. Growth rates and condition factors in lake trout and exotic salmonids, age at maturity in lake trout, and diet diversity in all salmonids would be compared.

Growth of lake trout in the Great Lakes is related to a few key forage species. For example, lake trout growth in Lake Superior is directly related to the abundance of rainbow smelt.

Present abundance and biomass production of rainbow smelt would be estimated. Smelt consumption would be determined by using a lake trout bioenergetics model (Stewart et al. 1983) and compared with estimated production. Current growth of lake trout would be compared with historical rates and with rates during periods of high smelt abundance.

Existing spawning stocks of lake trout produce too few eggs to significantly increase lake trout abundance at current rates of natural and fishing mortality.

Develop spawner-recruit relations from the historical records and for present day wild and hatchery stocks in the Great Lakes and inland Canadian lakes. Larger stockings or improved adult survival would provide the high end of the stock-recruitment relationship for hatchery stocks.

STOCKING PRACTICES¹

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The establishment of reproducing lake trout stocks in the Great Lakes is the goal of the rehabilitation program. Thus, we focused on factors that would increase the number of eggs deposited by hatchery origin spawners on sites thought to be suitable for reproduction. The major issues we discussed follow:

- are the conventional stocking rates well below the optimal stocking rates needed for lake trout rehabilitation?
- will the stocking of very early life stages of lake trout on historically used spawning reefs produce spawners that are reproductively more efficient than spawners resulting from stocked yearlings?
- are egg incubation devices effective in reducing overwinter mortality of eggs stocked on spawning reefs?
- can spawning reefs be conditioned to attract spawners of hatchery origin?

Hatchery origin spawners may not reproduce successfully because stocking densities in the Great Lakes produce inadequate numbers of spawning adults. Low stocking densities coupled with high mortality rates and a possibility that hatchery origin spawners are inefficient compared with native spawners (Walters et al. 1980) may act in concert to inhibit reproduction. In some parts of Lake

¹ Leader, F. P. Binkowski; Discussants: W. H. Horns, W. R. MacCallum, J. W. Peck, B. L. Swanson, and L. C. Wubbels.

Superior the mortality rate is sufficiently high that few fish reach sexual maturity (Pycha 1982). This mortality combined with potential problems of homing and locating suitable spawning substrate (Horrall 1981) may result in either production of an insufficient number of eggs or in excessive egg and fry mortalities.

A stocking strategy that concentrates large numbers of lake trout in a few areas may be more effective than one in which low rates are employed over a larger area. For instance, over 2 million lake trout were planted annually in Michigan's waters of Lake Superior during the late 1960s and early 1970s. This high planting rate appeared to be responsible for a pronounced increase in spawners and reproduction in areas where residual native spawning stocks were scarce (Pycha pers. Comm.). When the numbers planted were reduced to 1 million in the mid-1970s, reproduction from the survivors of the smaller planting leveled off and may even have declined slightly. Therefore, optimal stocking densities may be very high, much higher than the conventional stocking rates.

Stocking green eggs or sac fry on ancestral spawning reefs might result in survivors that are imprinted and that can home to the stocking site for spawning. Selection of spawning areas by lake trout may involve homing guided by early experience, and perhaps this experience involves chemical imprinting (Horrall 1981). If lake trout depend on such cues, hatchery rearing followed by transplantation may confuse the site selection mechanism. Hatchery rearing might have other disadvantages, including selection for inappropriate genetic traits (Ihssen 1984) and diminished fitness (Foster 1984). Therefore, the stocking of very early life stages should be incorporated as part of an experimental management approach to rehabilitation. However, because supplies of eggs for seeding experiments are low and survivors from egg seeding would probably be few in number, yearlings would also have to be stocked to provide alternative prey for sea lampreys, which otherwise would decimate the survivors from egg seeding.

Swanson (1982A) has shown that very low egg mortality can be achieved for eggs incubated in protective enclosures anchored on lake trout spawning grounds. This **success** raises

the possibility of large-scale planting of eggs in protective incubators for stock rehabilitation. Advantages of the egg stocking approach compared with yearling stocking are reduced hatchery costs and the avoidance of hatchery conditioning effects. Several questions remain regarding the utility of large-scale stocking of eggs in incubation devices: Can egg stocking methods be improved? What proportion of the fry that emerge from shelters will survive to maturity? What is the cost per surviving spawner for egg stocking methods? Will surviving adults return to the natal site and spawn? Will returning spawners reproduce successfully?

Small numbers of wild spawners on spawning reefs may attract hatchery origin spawners to the site and enhance their ability to reproduce. Swanson (1982B) reported that hatchery origin spawners were most common on those offshore spawning reefs in the Wisconsin waters of Lake Superior that already supported wild stocks. Consequently, a few wild spawners produced by direct egg seeding or by the use of incubation devices could have an impact on reproduction well beyond the contribution of their own progeny.

HYPOTHESES - EXPERIMENTAL DESIGNS²

Optimal stocking densities for lake trout rehabilitation are substantially above the conventional stocking rates.

Shoreline stocking zones separated by at least 70-80 km and containing historically used spawning sites will be chosen for study. One zone will be stocked at the conventional rate (50-100,000 yearlings per site per year) and the other at three times the conventional rate until the age distribution of the spawning stock approaches equilibrium. Ideally, yearling lake trout of one genetic strain raised in a single hatchery would be stocked. If it is necessary to use a second hatchery source, the fish from each hatchery should be planted in equal proportions in each zone. Fishing would have to be

²Full descriptions available from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

eliminated or reduced to an equal intensity in each area. The experiment will be evaluated by assessing the amount of natural reproduction in each zone. Lake trout and forage stocks should be evaluated before conducting the experiment. Variables to be measured for lake trout include survival, growth, lamprey marking, spawner abundance, distribution, and recruitment. A food study should be conducted during the experiment to estimate forage utilization and cannibalism; forage abundance should also be monitored. This experimental design would be improved by the addition of replicate zones with other stocking rates, for example, at 2 or 4 times the conventional or control stocking rate.

In situ incubation devices are an effective method for stocking eggs on historically used spawning reefs.

Newly fertilized eggs would be stocked in artificial turf sandwiches (Swanson 1982A) anchored to offshore spawning shoals not now used by lake trout. Short-term survival of fry and long-term survival of adults and their spawning success would be assessed. Egg stocking techniques can be enhanced by further research that measures the relative survival of recently fertilized eggs versus that of eyed eggs and by comparing different strains of lake trout. Genetically marked eggs would help isolate these experiments from the confounding effects of naturally spawned eggs or of the presence of other unmarked lake trout in assessment samples. Research should also explore alternative methods for construction and deployment of egg enclosures.

Stockings of eggs and/or fry on historically used spawning reefs is a cost-effective method of establishing reproductive lake trout stocks.

Various early life stages would be stocked on spawning reefs and their subsequent return to the stocking site would be assessed. If genetically marked fish (Ihssen 1984) were not available, each life stage would be stocked on a separate reef.

Small numbers of wild spawners will attract hatchery origin spawners to spawning sites.

This attraction experiment could be tested with the incubation or early-life stage experiments discussed above by selecting experimental sites that are accessible to hatchery

origin spawners. An experimental effect would be quantified by measuring differences in catch per unit of effort for hatchery origin spawners at treated and nearby untreated sites.

GENETICS¹

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Historical evidence indicates that the lake trout populations of the Great Lakes were subdivided into discrete spawning stocks (Brown et al. 1981; Goodier 1981). These stocks utilized different spawning habitats such as deep and shallow shoals, as well as rivers. Some of these stocks have survived to the present, and evidence is available indicating that these stocks are genetically differentiated (Dehring et al. 1981; Ihssen unpublished data). It is believed that this genetic differentiation is associated with adaptation to different habitats. This is not to say that the genetic differences observed are directly related to fitness differences, but that they reflect genetic isolation of these stocks and, hence, very probably adaptation to local environments. Our overall understanding of the genetic differentiation among the remaining lake trout stocks is very limited. Better understanding is required to protect the remaining stocks, to choose stocks intelligently for the rehabilitation program, to provide base-line data for the study of natal homing and colonization of stocks, and to provide techniques for marking early life stages of stocks.

Lake trout rehabilitation usually involves transplanting donor stocks into non-native habitats. Frequently, such transplantations have resulted in lower fitness of the donor stock in the non-native environment (Plosila 1977); hence, the need for matching stocks to their receiving habitats. Transplantation raises two major questions associated with

1 Leader, P. E. Ihssen; Discussants, J. A. Driver, L. C. Jacobson, C. C. Krueger, T. N. Todd.

rehabilitation: firstly, how much genetic differentiation is there among the lake trout stocks involved in the rehabilitation program, and secondly, how should we apply our limited understanding of lake trout genetic differentiation to the rehabilitation program? An answer to the first question will refine the rehabilitation effort in the long-term, whereas answers to the second question are required in the short-term to expedite the program.

Little is known about the adaptation of lake trout stocks to their native habitats. Variation in stock characters, such as seasonal spawning time, growth rate, age of maturity, choice of spawning site or substrate, and seasonal depth distribution cannot be easily related to fitness. It is not generally known whether such character differences represent adaptation to local environmental conditions, or whether they are different responses of the same genotype to different environments. Although in the long-term it is important to study the adaptive significance of individual character variation in detail, in the short-term it is more expedient, in our view, to employ an empirical approach involving a suite of characters. The approach we are suggesting involves matching habitat characters of the donor stock to the receiving habitat.

The phenotypic expression of a single life history, physiological, or behavioral character may be an overriding determinant for reestablishing a lake trout stock. Variation in such characters among stocks has been demonstrated to be associated with differences in adaptation to local environments (e.g. Schaffer and Elson 1975; Powers et al. 1983). For instance, lake trout in Cayuga Lake, New York, coexist with sea lamprey, and despite high wounding rates, sea lamprey induced mortality is very low (Youngs 1980). If Cayuga Lake lake trout show resistance to sea lamprey predation outside of their home waters, this character could be valuable in the Great Lakes where sea lamprey predation is a major problem. Genetic differences for physiological characters have been established for lake trout stocks (Ihssen and Tait 1974). Also, evidence is accumulating that different genetic stocks of lake trout planted into the same habitat perform differently in terms of survival and behavior (Horrall 1982; Schneider 1982). The converse, namely, that the same

genetic stock performs differently in growth and survival in different habitats, is the rule rather than the exception. In the long term, detailed genetic studies that separate environmental from genetic effects and measure environmental and genetic interactions should provide information useful for matching stocks to specific environments.

It is inherently difficult to carry out comparative studies that relate genetic differences to character differences of obvious adaptive significance. Previous studies are primarily of two types: (1) those that have measured genetic variation directly by using gel electrophoresis (Dehring et al. 1981) and, also, more recently, chromosome banding polymorphisms (Phillips and Ihssen 1983); and (2) those that have measured characters related to fitness, such as deep diving ability (Ihssen and Tait 1974), survival, growth, and movement (Plosila 1977; MacLean et al. 1981). Since the linkage between the two types of studies has been rarely made (DiMichele and Powers 1982; Allendorf et al. 1983; Leary et al. 1983), both kinds of variation need to be studied to obtain a realistic picture of the genetic differentiation of lake trout stocks.

Many lake trout stocks have disappeared from the Great Lakes during the last two or three decades. Consequently, a considerable erosion of the total lake trout genetic resource of the Great Lakes area has undoubtedly occurred. The remaining genetic diversity represented by stocks occupying different habitats needs to be protected because a variety of genetic stocks will be required to restore lake trout to different habitats. It is uncertain whether the remnant Great Lakes stocks have the genetic potential to develop into self-sustaining populations in a reasonable time in the major habitats formerly occupied by lake trout. This caveat applies particularly to habitats heavily impacted by man. It may be necessary to develop new genetic stocks to reestablish lake trout in degraded habitats. For example, it may be desirable to produce an early maturing lake trout strain. This could be accomplished by either selecting lake trout for early maturity or hybridizing lake trout with an earlier maturing species such as brook trout (*Salvelinus fontinalis*), and backcrossing to lake trout (Tait 1970; Berst et al. 1980).

Another approach to overcome poor success with standard hatchery production has been suggested by Krueger et al. (1981). Intraspecific, interstock hybrids frequently show hybrid vigor in the first generation and greater genetic variability in the second generation, because of segregation of parental alleles. The receiving environment would select genotypes of the highest fitness from the hybrid strains. Such an approach would be long term, however, because several generations of selection would probably be required before any appreciable change in fitness occurs.

Genetically marked lake trout are needed to address a variety of research problems related to lake trout rehabilitation. It has been suggested that the hatchery rearing environments used for salmon and trout may impose irreversible physiological and behavioral changes that have a detrimental impact on survival and reproduction in the wild (Vincent 1960; Ihssen 1976; Bilton 1978; Barns 1979). However, the effectiveness of early life history plants has been difficult to assess, because very small fish and eggs cannot be marked by traditional methods. Also, marks such as fin clips, tags, and brands are usually only identifiable for part of the life cycle, and are not passed on to succeeding generations. Genetic markers introduced at fertilization (Ihssen et al. 1981), on the other hand, can be read not only through the ontogeny of one generation but indefinitely into succeeding generations. These markers could be isozyme or chromosome variants. Before genetic marking can be applied routinely, however, the practicality of breeding fish with genetic marks and the fitness of such fish need to be assessed. Some stocks carry natural marks that can be used for assessing the genetic interaction of wild populations. Generally, however, sufficient genetic differentiation for natural markers may not be present. Further research is needed to uncover more of this naturally occurring genetic differentiation among lake trout stocks.

HYPOTHESES - EXPERIMENTAL DESIGNS'

A significant proportion of the total genetic variation of lake trout in the Great Lakes is among stocks occupying different habitats.

The initial choice of stocks for this study should be from those that occupy discrete spawning habitats, and possibly from those which vary in other ecological, behavioral, or physiological characters. Samples should be collected during the spawning period when stocks are segregated. Electrophoresis has recently been the preferred method for the study of genetic differentiation of stocks (Ihssen et al. 1981). For lake trout, preliminary indications are that the levels of heterozygosity for enzyme systems studied routinely for fish are comparatively low, making electrophoresis a somewhat imprecise tool for stock differentiation. Cytogenetic methods, such as Q banding and NOR markers, may provide additional markers for stock differentiation (Phillips and Zajiak 1982; Phillips and Ihssen 1983). In the future, recombinant DNA techniques may prove useful for discriminating among lake trout stocks. Morphological and physiological methods are useful for measuring genetic differentiation of lake trout if environmental and genetic effects can be separated (Ihssen and Tait 1974).

Rehabilitation of lake trout stocks will be facilitated by matching characteristics of the donor stock, and the donor stocks' environment to the receiving environment.

A data base on naturally reproducing stocks of lake trout should be developed. Each stock should be described for as many characters as possible such as spawning time, age of maturity, seasonal depth distribution, and growth. Similarly, the corresponding native habitat of each stock should be described for water quality, temperature regime, species composition, spawning habitat, etc. In the short-term, stocks

²Full descriptions available from the Great Lakes Fishery Commission by requesting **Special Publication 84-2**.

could be matched to receiving habitats by using non-statistical methods on a few characters. Matched planting, on the basis of a few characters, should involve as many stocks as possible in one area. As the data base becomes sufficiently large (10 or so stocks, 10 or so stock characters, 20 or so environmental characters), multivariate techniques such as canonical correlation analysis can be employed to match a stock to a particular environment. This procedure would involve paring down the character sets (stock, habitat) to those that give the most significant relationships. Using the functional relationship between stock and habitat variables, one can choose the stock that gives the highest correlation between its variables and the variables of the receiving habitat. The stock of choice should be tested against a control stock in a matched planting experiment to validate or refute the matching procedure.

Lake trout stocks are genetically differentiated for life history, physiological, or behavioral characters that affect their fitness in the wild.

Methodology would involve testing lake trout stocks for genetic differences of physiological and life history characters under field and laboratory conditions. To measure genetic vs. environmental components of variation, full and half sib families should be compared under the same environmental conditions. If genetic differences are found, comparisons should be made over a variety of environmental conditions to measure possible environmental-genetic interactions (Ayles 197 5).

Selectively bred interstock or interspecific hybrids are better suited for the rehabilitation program in lake trout habitats which have been heavily impacted by man.

The methodology would involve determining characters that are necessary for successful introduction into specific environments. Subsequently, a strain possessing such characters can be developed in a breeding program involving selection or hybridization. Several lines could be developed for specific characters. To take advantage of hybrid vigor, strain hybrids could be produced and field tested in a matched planting experiment. For such breeding programs, control stocks should be maintained to assess genetic changes and the performance of newly developed strains in the wild.

It is practical to produce genetically marked lake trout stocks.

Lake trout stocks used in the rehabilitation program would be screened for isozyme and chromosome variants useful for genetic marking. Electrophoretic markers for brood stocks can be identified from biopsy samples. Chromosome markers are most easily screened for in progeny tests since these markers can be readily identified in embryos. Phillips and Ihssen (1983) found that haploids can be employed to identify chromosome markers in lake trout females and that lake trout x brook trout hybrids can be used to identify markers in male lake trout. Those individuals that carry electrophoretic or chromosome variants useful for marking would be selected from the brood stock and either bred to produce a second generation for further selection or used to produce progeny for field testing.

PHYSIOLOGY AND BEHAVIOR^{1,2}

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Spawning populations of hatchery origin lake trout are expected to substitute for the wild populations formerly abundant in the Great Lakes in bringing about a recovery of the stocks. However, the difficulties experienced in reestablishing self-reproducing stocks of lake trout in the Great Lakes (Pycha 1982) suggest that hatchery origin spawners may be deficient in comparison to native spawners (Swanson 1982B). We therefore concentrated on issues and research that identified those physiological or behavioral processes that may be disrupted by hatchery rearing and thereby diminish the reproductive potential of hatchery origin stocks. In particular we focused on how hatchery rearing might interfere with homing and spawning mechanisms of lake trout and how hatchery conditioning could affect the ability of stocked fish to survive and reproduce. We also identified certain aspects of the early life history of lake trout as being important for future work.

The physiological and behavioral processes that control homing and spawning in lake trout are presumably similar to those in other salmonid species (Horrall 1981; Groot 1982; Hasler and Scholz 1983), with olfaction playing a primary role in the homing migration. Martin (1955) suggested that spawning grounds used by native lake trout had "some

1 Leader, R. M. Horrall; Discussants: J. M. Casselman, N. R. Foster, and D. L. G. Noakes.

²Contribution 619 of the Great Lakes Fishery Laboratory, Ann Arbor, Michigan 48105.

characteristic odor” that attracted spawners. Laboratory studies have shown that adult lake trout provided with a choice of experimental reefs in a large indoor pool preferentially spawned at reefs artificially scented with feces and sloughed mucus from fry hatched in the previous spring (Great Lakes Fishery Laboratory, unpublished). Behavioral and electrophysiological experiments on Arctic char (*Salvelinus alpinus*), a close relative of lake trout, demonstrated that certain bile acid derivatives act as powerful attractants to adult char, that these substances (pheromones) are present in intestinal contents of smolts, and that adult char can detect them at a concentration of 2×10^{-10} M (Selset and Døving 1980, Døving et al. 1980). If there were such a pheromonal mechanism of attraction of native lake trout to spawning grounds in the Great Lakes, then one would predict: (1) some difficulty in inducing planted lake trout to use historically known spawning sites where pheromonal odors had long since dissipated; and (2) spawning by hatchery origin lake trout in the immediate vicinity of successful egg and sac fry plants, at spawning sites used by existing native stocks, and at sites where planted adults had reproduced successfully.

Data from gillnet catches suggest some differences in prespawning behavior between adults of hatchery origin in western Lake Michigan and native adults at Gull Island Shoal in western Lake Superior (Swanson 1982B; R. M. Horrall, pers. comm.). For example, the breeding aggregation of planted fish in western Lake Michigan consists of 95 to 99% ripe males, whereas the breeding aggregation at Gull Island Shoal seems more typically structured, with 75 to 80% males. Overnight catches per unit of effort of gillnet may be as high as 200 fish in western Lake Michigan, but only 60 to 80 at Gull Island Shoal. Detailed behavioral studies on Great Lakes lake trout might clarify the function of substrate cleaning behavior performed by male lake trout (Merriman 1935; Royce 1951). Such cleaning activity is performed by descendants of a river-spawning stock from Lake Superior (C. H. Olver, pers. comm.) and by domestic lake trout of the Lake Superior lean strain (Great Lakes Fishery Laboratory, unpublished).

Artificial imprinting of lake trout to synthetic chemicals (Scholz et al. 1975) during hatchery rearing might be used to decoy previously imprinted fish to suitable but currently unused spawning sites. Such research is currently under way in Lake Michigan. Two groups of hatchery reared lake trout have been imprinted to phenethyl alcohol-one group during the period from eyed egg until early fingerling stage, and another group at the yearling stage 1 month before stocking in Lake Michigan (Horrall 1981). Two objectives of these studies are to determine the critical period for olfactory imprinting and to assess the relative importance of natural vs. synthetic odors in decoy experiments.

Because of the many ways in which the hatchery environment differs from the lake environment, hatchery rearing may permanently affect certain aspects of the physiology and behavior of planted fish and thereby reduce their ability to survive and reproduce. For example, the temperature of spring or well water sources at lake trout hatcheries fluctuates relatively little, averaging between 7 and 9°C. In the natural environment, lake trout have been recorded at seasonally varying temperatures that range from -0.8°C at a (brackish) coastal locality northwest of Hudson's Bay to 18°C in Ontario lakes (Martin and Olver 1980). Daytime light levels in rearing troughs and raceways are many times brighter than those at depths where the species dwells in the lake environment, and it has been observed that lake trout reared in covered raceways sought significantly greater depths following planting than did those reared in uncovered raceways (J. M. Casselman, unpublished). The photoperiod regime under which fish are reared might cause some subsequent off-season maturation and spawning in the lake, as demonstrated in pink salmon (*Oncorhynchus gorbuscha*) by MacQuarrie et al. (1979). The high densities of hatchery reared fish may modify their social or feeding behavior, as reported in Atlantic salmon (*Salmo salar*) by Fenderson and Carpenter (1971). In addition, flow velocities in the hatchery are relatively high and food is abundant and regularly available. Rapid growth at elevated temperatures may reduce the longevity of planted fish. Slower growth, later maturity, and greater longevity typical of lake produced fish are probably more desirable in terms of overall reproductive potential.

Although substantial descriptive and experimental work on developmental, physiological, and behavioral aspects of the early life history of lake trout has been carried out (Garside 1959; Tait 1960; Balon 1980, Horns 1983, Ferguson et al. 1983), there still remain substantial knowledge voids in two major areas: (1) the relation between year-class success and the timing of various early life events in native lake trout populations and of limnological events, such as at the onset of the production cycle and thermal stratification; and (2) geographic (interstock) variation in the timing of early life history events. We formulated hypotheses and research approaches to address these issues, but these were similar in many respects to those drafted by other working groups (Sly 1984; Ihssen 1984) and hence are omitted.

HYPOTHESES - EXPERIMENTAL DESIGNS³

Lake trout stocked at sizes or ages beyond some identifiable period in their life cycle will not exhibit an appropriate homing response; however, life stages stocked before this key size or age will imprint to precise locations and mature fish from such plantings will home to those locations to spawn.

This hypothesis can be tested by stocking a series of early life stages from green egg to yearling and establishing which stages are most successful in producing fish that return to the stocking site at maturity. If the earliest life stages (eggs) can be differentiated by genetic markers (Ihssen 1984), then all stages should be stocked at the same locality. An approach using a common site is preferred because variables associated with different localities are avoided and replication would be logistically simpler. However, if the early stages cannot be distinctively marked, each life stage would have to be planted at sites separated by a distance at least as great as the normal home range (about 32 km) of

³Full descriptions available from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

planted lake trout (Rybicki and Keller 1978). In either situation, remote offshore locations should be used as stocking sites to make it less likely that subsequent recoveries would be taken because of random effects in movement patterns.

Adult lake trout use odors as orientation cues in homing to breeding areas.

Two approaches are suggested. Spawners from native stocks from Gull Island Shoals in Lake Superior, for instance, would be captured on the spawning grounds, marked with sonic tags, and transplanted. Half of the transplants would be olfactorily blocked and the other half would serve as controls. Differential ability to return to the spawning grounds would be a measure of the relative significance of olfaction as a homing mechanism. In the other experiment chemical compounds such as morpholine or phenethyl alcohol would be used to decoy hatchery origin spawners. Lake trout would be exposed to such artificial imprintants (Horrall 1981) at appropriate life stages in the hatchery. When the planted fish matured, homing to a site scented with the artificial imprintant would be compared for imprinted and control lots of lake trout.

Adult lake trout use conspecific odors (pheromones) emanating from specific areas of substrate in selecting spawning sites.

At a study area with a self-reproducing stock and used and unused (but potentially usable) spawning sites, fertilized eggs would be obtained from adults; fry would be reared and fry odor source materials (fry feces and sloughed mucus) would be collected and frozen; or, some waste products from lake trout hatcheries could be used as an alternative odor source. In fall of the second year, sampling stations would be established at (1) traditional spawning sites, (2) fry odor-scented sites, and (3) control sites. Egg pails (Stauffer 1981) would be buried in the substrate at each site. Catch per unit of effort of spawners and deposition of fertilized eggs in egg pails would be measured at scented and unscented sites. Control and treatment sites would be switched in alternate years.

Lake trout reared under normal hatchery conditions have reduced longevity compared to those reared in hatcheries under simulated lake conditions.

In this experiment longevity of paired plants of otherwise identical sublots of lake trout reared under conditions typical of hatchery and lake environments would be compared. Effects of the following rearing conditions would be assessed: (1) high light vs. low light levels; (2) relatively constant, elevated temperature vs. ambient lake temperature; (3) high flow vs. low flow velocities; (4) high densities vs. low densities; and (5) flat substrate vs. natural substrate.

Most hatchery produced lake trout in the Great Lakes do not spawn on sites appropriate for reproduction.

The distribution of wild and hatchery origin adults would be monitored during the spawning season by experimental fishing. Distributions of wild and hatchery origin spawners would be compared in relation to the availability of spawning substrate.

CONTAMINANTS^{1,2}

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We identified five research issues or questions associated with contaminants and their relation to lake trout rehabilitation efforts in the Great Lakes. These questions should be addressed in a sequential order (i.e., the answer to the first question should be affirmative or demonstrate a need for further studies before research should proceed to the next question). The five questions are listed below and a discussion of each follows. (1) Are existing contaminant levels in any of the Great Lakes (or in parts of individual lakes) sufficient to impede rehabilitation of lake trout? (2) How are lake trout being affected or their rehabilitation being impeded? (3) Which lakes, or parts of lakes, are being impacted? (4) Are Other fish species in impacted areas affected? (5) What is the fate of the various contaminants in the aquatic ecosystem?

Considerable indirect and circumstantial evidence exists regarding the question of whether lake trout rehabilitation is being impeded by existing contaminant levels in the lakes. There is a documented lack of significant recruitment in four of the lakes (Michigan, Huron, Erie, and Ontario) and measured concentrations of several toxic substances in adults and eggs are, or have been, at levels

1 Leader, W. A. Willford; Discussants, J. E. Breck, V. W. Cairns, G. R. Craig, and F. L. Mayer.

²Contribution 618 of the Great Lakes Fishery Laboratory, Ann Arbor, Michigan 48105.

shown in laboratory studies to cause physiological or toxic effects. Substances tested on lake trout and shown to cause such effects at levels measured in the Great Lakes include DDT (Burdick et al. 1964), PCBs and DDE (Berlin et al. 1981), and toxaphene (Mayer et al. 1975). There is also a growing body of evidence that liver enzymes (mixed function oxidases) associated with metabolism of environmental contaminants such as polynuclear aromatic hydrocarbons are significantly elevated in lake trout from southern Lake Michigan (J. J. Leach, pers. Comm.) and western Lake Ontario (V. W. Cairns, pers. Comm.). In addition, laboratory incubation studies indicate that the survival rate of fry hatched from eggs of lake trout from southern Lake Michigan is significantly lower than that of fry hatched from eggs originating from Lakes Superior and Huron, or from hatchery broodstock, regardless of the water quality in which they are reared (Willford 1982). Finally, contaminant concentrations in lake trout from several areas of the lakes exceed established guidelines for human consumption, thereby adversely affecting use of the fish and continuation of the associated fisheries. We concluded that the available evidence is therefore sufficient to suggest with a high degree of probability that contaminants have previously, and currently are, impeding lake trout rehabilitation in some areas of the Great Lakes. Although more direct evidence would be helpful, the information already available is sufficient to elicit an affirmative answer to the first question.

We found no evidence that contaminants are adversely influencing the survival of stocked fish during the period between the planting of yearlings and the attainment of sexual maturity. Available information indicates, however, that contaminant impacts are probably being manifested in early life stages. However, more direct evidence is needed. Therefore, the first major research need identified was that of determining the stages of reproduction and development that are being adversely affected by contaminants. To address this need, researchers need to investigate the following three sub-topics. Are contaminants affecting the ability of adults to produce viable gametes? Are contaminants transferred from the adult to eggs or sperm adversely affecting the development and survival of embryos

and fry? Are contaminants in the environment affecting development and survival of embryos and fry?

As further evidence of the need for research on reproductive effects in lake trout, we note that laboratory studies have demonstrated effects of contaminants in other fish species on gamete development (e.g. vitellogenesis, spermatogenesis, and steroidogenesis) and on embryological development (i.e., effects on subsequent development of contaminants transferred from parents to eggs and sperm); also demonstrated are effects of several environmental contaminants on the fry of other species (Helder 1981; Lesniak and Ruby 1982; Niimi 1983).

Discussion regarding which lakes, or parts of lakes, are being affected centered on the need for improved monitoring programs. The discussion was divided into the two most commonly used monitoring approaches-chemical and biological. Existing chemical monitoring programs need to incorporate the routine use of ancillary variables associated with the fish (e.g. fish age, weight, percent lipid) when residue levels are reported. Although this is not a research need per se, the availability of such information would allow improved interpretation of residue data and lead to a better understanding of contaminant dynamics.

Another need identified, but not requiring a specific research recommendation, was the improved application of chemical detection and screening systems. Chemical scanning techniques provide a qualitative and frequently semi-quantitative evaluation of the array of chemicals representing potential contaminants of fish, thus providing an early warning of possible contaminant problems of the future and, equally important, enhanced interpretation of residue effects in the fish. Analysis of individual contaminants in fish does not adequately take into account, or allow interpretation of, the combined effects of the numerous contaminants present in **the environment and biota.**

A facet of monitoring requiring extensive research, however, is the demonstration of the biological effects and significance of chemical residues in fish, and the development of cross-linkages between paired chemical and biological monitoring programs. The identification of where and how lake trout are being impacted by contaminants will ultimately

require, the development of baseline information describing the "health" of fish and fish populations in several areas of the lakes and correlations between that information and chemical residues in the fish. Unfortunately, much of the clinical methodology needed for such a biological monitoring program is still under development. Thus, the second major research need identified was the development of clinical and other measurements of contaminant effects in lake trout, and the application of resulting procedures in a systematic program to detect and monitor these effects.

For such a biological monitoring program to be useful, it is necessary to determine experimentally: (a) whether whole-body residues in lake trout are correlated with biological effects, or whether specific tissues such as liver or gonads should be sampled instead; (b) how and to what degree the fate and behavior of contaminants in lake trout influence the biological effects; and (c) whether clinical measures of individual lake trout health are quantitatively related to population effects. These issues were identified as specific research needs in support of biological monitoring.

The question of why or whether lake trout might be the principal species affected by contaminants in the Great Lakes was then examined. The apparent failure of lake trout to reproduce adequately in most regions of the Great Lakes is in contradiction to the successful reproduction and performance of other species in the lakes. If contaminants are responsible for reproductive failure (i.e., questions 1-3 are answered in the affirmative), is it because lake trout are inherently more sensitive to contaminants than other species of salmonids and other families of fishes, or is it because the long life span, the high trophic status, and the high lipid content (and associated accumulation potential for lipophilic compounds) combine to essentially result in a "higher exposure" of lake trout than of other species to contaminants? Further, if lake trout are more sensitive than other species, are there more tolerant strains of lake trout that could be planted in the Great Lakes? Alternatively, if lake trout are not more sensitive than other fishes, are forage species and other higher trophic species also being affected? Answers to these questions would allow improved understanding and integration of water quality issues into rehabilitation plans and help

identify other species in the lake that may be threatened by contaminants. The issue of differential species sensitivity was therefore identified as another topic requiring research.

We concluded that although information concerning the fate of various contaminants in the aquatic ecosystem was extremely important for understanding the relation between the sources, distribution, sinks, and likely duration of specific contaminant problems, research in these areas by fishery agencies in support of lake trout rehabilitation was questionable. The need for research on the fate and behavior of contaminants in lake trout was previously identified in support of biological monitoring programs and the determination of the likely effects of contaminants of lake trout. Improved understanding of the dynamics and fate of contaminants in the ecosystem would undoubtedly be useful to fishery agencies in a general sense and to water quality agencies in a specific sense. We were unable, however, to develop a consensus on additional priority research needs within this issue that would have immediate and direct application to lake trout rehabilitation.

HYPOTHESES - EXPERIMENTAL DESIGNS³

Contaminants in spawned products, as a result of parental transfer, impair embryo-larval development and survival.

Feed hatchery adults with forage fish collected from a "clean" source (e.g. Lake Superior) and a "contaminated" source (e.g. Lake Michigan) to provide groups with "low" and "high" contamination; this procedure would enable comparison of embryo-larval development and survival, isolated from other potential confounding factors present in lake stocks. Intermediate exposure regimes would allow estimation of threshold effect concentrations. Alternatively, raise eggs

³Full descriptions available from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

from hatchery and planted stocks in incubation devices placed on clean and contaminated shoals (in situ) and in the laboratory to determine effects of parental transfer of contaminants and of environmental exposures to contaminants on embryo-larval development and survival.

Methods are available for routine biological monitoring to assess individual fish health and differentiate between biological and chemical stressors.

Select a number of potential individual (e.g. clinical) and population estimators of lake trout health; apply them in a pilot scale biological monitoring program at locations with differing amounts and types of contaminants; and identify the procedures and estimates that enable detection and differentiation of stress in fish populations and that then can be used in routine, basinwide programs.

Whole-body contaminant residues in lake trout are correlated to biological effects.

Develop cross-linkage with biological monitoring programs to test correlations of effects with whole-body residues and accumulable chemicals in fish. Continue current experimental work on the relation between residues of specific chemicals (dose) and observed effects in lake trout. Develop improved chemical detection and screening systems that provide rapid and economical scanning techniques for contaminant residues in lake trout for use in early hazard assessments.

Information on contaminant fate and behavior in lake trout is essential to understanding contaminant effects.

Review the literature on contaminant dynamics in fish (including uptake, deposition, metabolism, and transfer to spawned products) and the major factors influencing these processes (e.g. body size, lipid level, temperature, octanol-water partitioning coefficient). Conduct appropriate studies to develop needed information that is not available on lake trout. Determine the effects of lipid mobilization on the fate and behavior of contaminants, including changes in metabolites, excretion, and lipid redistribution.

Clinical measures of individual health are quantitatively related to growth, reproduction, and survival within lake trout populations.

Identify and test biochemical, physiological, and pathological measures of individual fish health that have obvious quantifiable consequences on individual survival, reproduction, growth, or behavior. Develop several population models describing how each of these factors measured in individuals (growth, reproduction, etc.) influences population success.

Differential species sensitivity accounts for the greater effect of contaminants on reproduction and survival in lake trout than in other species.

Compile, through a review of toxicology literature, the acute and chronic toxicity data for lake trout and other fish species with the aim of quantifying the relative sensitivity of lake trout compared with that of other Great Lakes fishes. Compile the available data on contaminant concentrations in eggs and fry of Great Lakes fish species and compare these "exposures" with corresponding toxicity compiled from the literature review.

HABITAT¹

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Lake trout planted in the Great Lakes (usually as yearlings) survive to maturity, but, with the exception of Lake Superior, only a few naturally reproduced fish age I and older have been found. We concluded that natural recruitment was failing because of a breakdown in the life cycle somewhere between spawning and the advanced fry stage. Therefore, we emphasized those habitat concerns that relate to these stages. Two major issues were identified. The first is whether degradation of nearshore lake trout spawning and nursery habitat seriously inhibits lake trout rehabilitation. The second is the lack of specific information on the physical, chemical, and biological habitat characteristics that limit lake trout reproduction. The second issue is closely linked with the first because when the spawning and nursery habitat requirements of lake trout are defined, our ability to measure habitat degradation will be greatly improved. At present we cannot identify those areas where lake trout reproduction is inhibited because of habitat degradation nor can we detail the water quality requirements for this very important fish in the Great Lakes.

Severe degradation (e.g. low dissolved oxygen and toxic levels of ammonia or hydrogen sulfide due to the decomposition of organic matter) of lake trout spawning sites in the Great Lakes may be a cause of early mortality among the progeny of planted lake trout. Unfortunately, there are very few data available to support or refute this hypothesis.

1 Leader, P. G. Sly; Discussants: D. O. Evans, D. J. Jude, J. P. Keillor, and R. A. Ryder.

Studies on lake trout spawning grounds in Cayuga and Seneca Lakes, New York, have indicated that increased siltation may have played a major role in preventing reproduction of lake trout in these lakes (Rayner 1941; Webster et al. 1959; Sly and Widmer 1984). Recent studies in Lake Michigan also indicated that differential survival of lake trout eggs and fry at several sites may be due to reduced habitat quality (Dorr et al. 1981; Wagner 1981). Research is needed to compare habitat quality (in terms of physical, chemical, and biological characteristics) at presently productive spawning and nursery sites in the Great Lakes with unproductive sites used by spawning lake trout and thought to be degraded.

The physical habitat requirements (or limiting factors) for successful lake trout spawning in the Great Lakes are only generally known. In most areas of the Great Lakes, spawning is expected to occur in shallow water (a few meters deep) during September through November, but historic deep water spawning sites (to depths of 30 m and greater) and early spawning (June) have been reported for Lake Superior (Martin and Olver 1980). Recent accounts of lake trout spawning in the Great Lakes are somewhat scarce. Those which do exist (Dorr et al. 1981; Stauffer 1981; Wagner 1981; Peck 1982; Sly and Schneider 1984; Nester and Poe 1984) often describe spawning on artificial substrates (gravels trapped by new shoreline structures or construction materials). Documents that describe spawning at historic sites are usually based on catch records which indicate areas where ripe fish were taken during the spawning period (Goodyear et al. 1982). The capture of ripe fish, however, does not necessarily imply that spawning actually took place at the capture site; it may well occur at some other location. Because of the high spatial variability of substrate types in the narrow littoral zone of the Great Lakes or because of the very large areas of some offshore shoals (as in Lake Superior), it is often impossible to identify specifically where native lake trout used to spawn. Similarly, it is very difficult to predict locations where hatchery fish will spawn. Records of lake trout reproduction in inland lakes tend to be more specific about the spawning location and its physical characteristics (Merriman 1935; Royce 1951; Martin 1957). However, we do not know how useful inland lake records are for comparison with the Great

Lakes where wave action, currents, and ice movement are considerably more pronounced, and thus more of a potential threat to incubating eggs or to recently hatched fry.

Chemical characteristics of the sediment/water interface of lake trout spawning and nursery habitat are generally unknown, although some information on dissolved oxygen requirements is available from laboratory studies (Garside 1959). High contaminant levels could also limit survival of lake trout eggs or fry (Willford 1984).

Biological factors such as food resources for fry, invertebrate and fish predators, and fungal or bacterial infections may have an important bearing on survival of lake trout eggs and fry. Very little is known of the food habits of lake trout fry in the Great Lakes, with the exception of a study by Eschmeyer (1956) and a recent study by Swedberg and Peck (in press); the latter reported that the first food of lake trout (as small as 22 mm) included a wide variety of organisms and suggested that young-of-the-year lake trout may be opportunistic feeders. Further studies are needed to determine if food type and abundance is adequate for newly hatched lake trout. A lack of synchrony between fry emergence and early spring plankton pulses or a change in food quality due to size selective predation by exotic planktivores (Wells 1970) could result in extremely high mortality of early life stages. Predation on lake trout eggs and fry may also limit lake trout reproductive success. Many fish species and crayfish in the Great Lakes eat lake trout eggs and fry (Stauffer and Wagner 1979; Horns and Magnuson 1981; Dorr et al. 1981). Recent information (G. Eck, Great Lakes Fishery Lab, pers. Comm.) also suggests that newly planted lake trout (yearlings) in Lake Michigan are eaten by adult lake trout, despite the presence of several other abundant forage species. Likewise, earlier life stages may be eaten. Fungal or bacterial infection may also cause high mortality of eggs or sac fry. In Ontario lakes the fungus, *Saprolegnia*, was considered to be a prime factor in egg mortality (Martin 1957).

HYPOTHESES - EXPERIMENTAL DESIGNS²

Inadequate reproduction by stocked lake trout in many areas of the Great Lakes is due to physical and chemical degradation of spawning habitat.

Comparative site data should be collected to quantify differences between degraded and non-degraded historical spawning and nursery habitats. A historical site used successfully for reproduction by hatchery lake trout would serve as the control site and other historically used spawning sites in degraded areas such as in Green Bay, outer Saginaw Bay, and in Lake Ontario would serve as the treatment sites (the eastern basin of Lake Erie might also serve as a treatment site if recent climatological changes (Sly and Widmer 1984) are taken into consideration). Data to be collected include: particle-size, shape, depth, structure, and geological origin of substrate; contour, slope, currents, and water depth; shoal orientation, wind fetch, ice formation, and sedimentation (both organic and inorganic); and water quality (as defined by dissolved oxygen, temperature regime, major ions, nutrients, selected contaminants, and decomposition of organic material). Habitat degradation will be quantified by site differences in egg and fry survival. Survival would be assessed either for seeded eggs or for eggs placed in incubation devices within the spawning reefs.

Lake trout rehabilitation is impeded by inadequate knowledge of the physical and chemical factors that limit reproduction.

Those water quality factors that appear to be implicated in low egg and fry survival, in the above field studies, should be assessed under controlled laboratory conditions. Laboratory studies would aim at identifying the value or point at which the suspected factor limits reproduction. Results from the laboratory studies would then be validated by comparisons of the distribution of the limiting

²Full descriptions available from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

factor(s) with that of the known distribution of successful reproduction.

Predation by fish and invertebrates on lake trout eggs or fry is significantly limiting survival of lake trout.

Estimate the abundance of lake trout eggs, fry, and of their potential predators on and near reefs where there is natural reproduction. Numbers of eggs and fry consumed by predators would be determined by the usual frequency of occurrence and digestion rate methods.

An inadequate food supply during the early fry stage is limiting survival of lake trout.

Food availability and consumption would be quantified at sites where reproduction is successful and at sites where lake trout are known to deposit fertilized eggs but very limited or no production of fry occurs. Differences in food availability and diet among the sites would be used to assess whether food scarcity has potential to be a serious impediment to rehabilitation.

SOCIO-ECONOMICS¹

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Studies are needed to distinguish between the specific interests and values of sport and commercial fishermen for lake trout from those related to Great Lakes salmonids in general. There is considerable evidence that lake trout constitute an integral part of Great Lakes fisheries values. The sport fisheries component of the fishery, estimated to have an annual net economic value of \$525 million in 1979, compares with a value of \$12 million per year for commercial fisheries (Talhelm et al. 1979). Over 42% of the 1979 trout and salmon derby anglers in Lake Superior indicated that lake trout were their first or second most sought species (Fleischman et al. 1981). A revitalized lake trout fishery in the eastern basin of Lake Ontario has been credited as the primary factor associated with increases of 73% in resident and 248% in nonresident fishing licenses in that area during 1977-83 (N.Y. Dep. Environ. Conserv., pers. Comm.).

Rehabilitation of lake trout in the Great Lakes will in all likelihood include additional fishery regulations. The regulation of commercial fishing activities may include the use of licensing, fees, and the restriction of fishing techniques. The sport and charter anglers may be affected by further regulation of daily catch limits. Angling may also be affected by regulations which restrict fishing in specific areas. The regulation of angling activities can be expected to have effects on anglers, agencies and organizations involved in lake trout rehabilitation activities, communities along the regulated lakes, and others who have an interest in the waters

¹ Leader, T. L. Brown; Discussant: W. A. Fleischman.

in which regulations apply. Related to these audience groups, four broad issues statements have been developed for which research needs have been identified:

1. Further regulation of angling in conjunction with lake trout rehabilitation will have varying effects on overall angler effort, satisfaction, and the reactions of Great Lakes sport angling organizations.
2. The activities and processes associated with lake trout rehabilitation involve conditions and principles that have values beyond that of the fishery. Suitable water quality for survival, growth, and reproduction is necessary to effect rehabilitation. Natural reproduction of lake trout may be negatively affected by contaminants in water and fish. In addition, certain water quality variables affect the marketing and consumption of lake trout. Lake trout policy affects not only anglers, but also the general public, private enterprise, and numerous governmental agencies.
3. Agencies whose activities include and are directly related to lake trout rehabilitation will incur widely varying costs, and receive varying economic benefits from lake trout rehabilitation. The costs and benefits will also be realized over somewhat different time periods. These costs and benefits should be carefully assessed.
4. The taking of fish for market and the provision of guide or charter boat services are the major Great Lakes commercial fishing enterprises. In some instances these activities involve fishing specifically for lake trout. In others, the fishing activities are more indiscriminant or involve the "incidental" taking of lake trout. The degree of commercial dependence on lake trout by geographic area, and the degree to which alternative species are available to guide/charter and commercial fishermen should be assessed.

HYPOTHESES - EXPERIMENTAL DESIGNS²

Certain groups of Great Lakes anglers (beginning salmonid anglers, "meat" versus "sport" anglers, and others wanting the option to catch lake trout) will be adversely affected by more restrictive regulations and will more strongly oppose them.

We need to understand the attitudes of anglers who prefer to fish for lake trout. We know that in some areas where other salmonids are not abundant, anglers depend very heavily on lake trout stocks. The proportion of anglers preferring lake trout and estimates of the value of lake trout to these anglers should be assessed before further regulations are implemented. The methods for this assessment would include further analysis of the 1980 United States Fish and Wildlife Service survey and other available angler surveys supplemented by in-depth studies of anglers and angling organizations in areas (e.g. eastern Lake Ontario) most dependent on lake trout.

The degree of support or opposition of non-angling groups to rehabilitation strategies will depend heavily on group perceptions of impacts on local economies and group understanding of the primary issues and factors related to lake trout rehabilitation.

Two types of studies are needed. The first is a public opinion survey of non-angling groups potentially impacted by or having an interest in rehabilitation (e.g. business people, environmental groups). These surveys would measure not only perceptions and concerns, but also knowledge about lake trout rehabilitation. The second study would estimate the actual socio-economic impacts of changes in regulations on affected communities. Results from these studies would be available for input into larger benefit/cost models that encompass values to anglers (both sport and commercial) as well as to non-anglers.

²Full descriptions available from the Great Lakes Fishery Commission by requesting Special Publication 84-2.

Long-term social and economic benefits realized from stable, productive, and self-sustaining lake trout stocks and their harvest can be attributed to rehabilitation.

To test this hypothesis cost analyses are needed to quantify long-term benefits of rehabilitated lake trout stocks against short-term advantages of put-grow-take fisheries. Estimates of other social benefits such as extra-market values (Talhelm 1983) should be obtained for input into a broad, overall cost/benefit analysis. This research should incorporate sensitivity analysis of several conversion rates for policies that seek rehabilitation versus policies that seek put-grow-take fisheries.

Charter businesses fishing specifically for lake trout and commercial fisheries for other species that experience severe bycatches of lake trout may be forced out of business or reduced to part-time status by regulations related to rehabilitation.

Decisions about rehabilitation strategies should be made with consideration given to those whose livelihoods will be affected. These strategies should provide an appropriate amount of lead time for implementing regulations found to be in the larger public interest, but that also have significant negative impacts on particular groups. Studies of business operations and profitability of commercial fishermen, charter captains, and guides are needed. These studies should include detailed investigations on the role of lake trout in the operation of the business, and on the feasibility of shifting to substitute species or gears.

OVERVIEW¹

The purpose of this section is to establish a sense of urgency and order for the research proposed by the conference working sessions and to identify some field experiments which because of their scale require support from fishery management agencies. It is not our intention to critique the product from each working session. Extensive peer reviews were conducted at the conference, and each session report is an entity for its respective discipline. We will, however, attempt to organize the research into a logical framework so that the individual pieces are rationalized, complementary, and in the aggregate, comprehensive. Thus, our task is to frame an overall research strategy that could preclude a failure of the lake trout rehabilitation program because of inadequate science.

Because the rehabilitation effort has required increasingly restrictive fishing policies, and the planting of over 100 million lake trout is not known to have produced a rehabilitated stock in the Great Lakes (see Introduction), public acceptance of the program could decline and preempt its continuation before a predictable strategy for producing self-sustaining lake trout stocks is developed. Accordingly, we recommend that key research be undertaken on a concurrent rather than a progressive basis. The most fundamental or first order research will be that concerned with producing detectable recruitment from spawners of hatchery origin. It is recognized that to achieve rehabilitation, lake trout at some life stage will have to be planted because significant native stocks are absent in four of the Great Lakes. In contrast, second order research is concerned with enhancement of recruitment from hatchery origin spawners. Both categories of research are necessary,

¹ Discussants: R. L. Eshenroder, J. F. Kitchell, C. H. Olver, T. P. Poe, and G. R. Spangler.

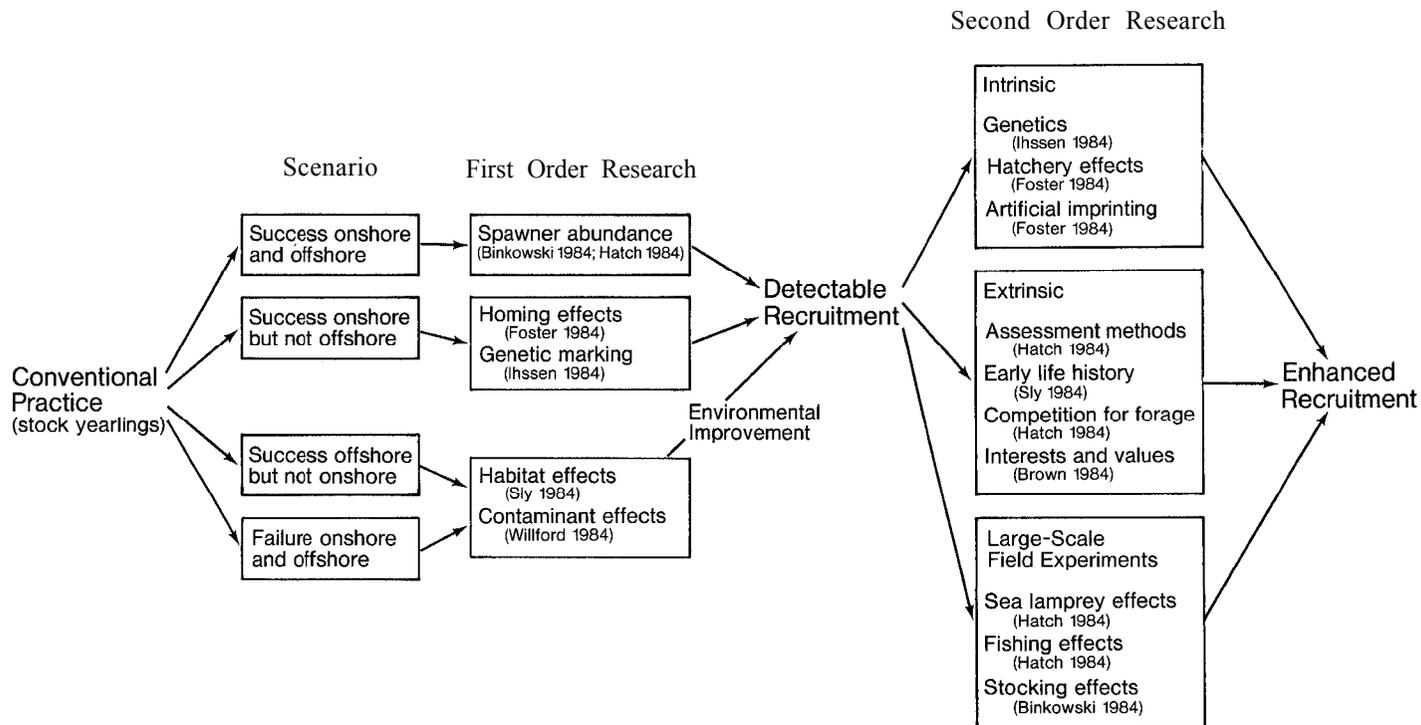
but the distinction between the two orders establishes urgency and dependency.

We believe that research is obligated to thoroughly assess the existing management strategy, and use it as a benchmark against which other approaches are measured. Agencies are geared for planting yearling-sized lake trout and a strategy that uses these facilities would be far easier to implement than would an approach requiring new investment in facilities and skills. Nonetheless, other methods must be tested, and a better understanding of the reproductive biology of lake trout may dictate major changes in the conduct of the program.

The general types of research recommended by the working sessions at the conference will be placed into a framework which distinguishes between the two orders of research and which employs the yearling stocking strategy as a benchmark. Research will be fit into this framework based on the issues that are most relevant to a series of alternative assumptions (scenarios) regarding the probability of success for two stocking strategies. Inasmuch as we have urged concurrent implementation of key research needs, the issues raised by the alternative assumptions would also be resolved on a concurrent basis to ensure that the most critical issues, which remain unknown, are addressed by a swamping effect. In the following, we will discuss the alternative assumptions and the related issues and research that are important. A schematic of the results is given in Figure 1.

FIRST ORDER RESEARCH

The first of the alternative assumptions, that the current stocking strategy will produce a detectable level of recruitment at onshore and offshore sites, suggests that in the past most stocking densities have been too low (Binkowski 1984) or that mortalities have been too high (Hatch 1984). The associated issue would be a scarcity of spawners in most areas, and first order research would focus on spawner biomass effects. Implicit in this scenario is the supposition that lake trout cultured to yearling size will utilize inshore and offshore spawning reefs located in the areas of planting.



1. Rationalization schematic for priority research identified at the Conference on Lake Trout Research held at Goderich, Ontario in 1983.

The second scenario implies that there is some factor that encourages spawners of hatchery origin (planted as yearlings) to reproduce on inshore sites, but inhibits offshore reproduction. This phenomenon is reasonably consistent with field reports from the Great Lakes (Anonymous 1980; Pycha 1982; Swanson 1982B; Rybicki 1983; and Argyle 1984). Foster (1984) suggested that hatchery rearing interferes with the proper establishment of homing mechanisms (imprinting), and results in a tendency of hatchery origin spawners to move inshore when ripe and widely broadcast eggs over areas that are often inappropriate for incubation. If quality spawning sites are common inshore, a low level of reproduction is possible due to random effects. However, offshore sites are infrequently used even though hatchery-reared yearlings are stocked there. The issue(s) involved in this scenario relates in general to our poor understanding of how lake trout select spawning sites, how stocking practices affect this selection (Binkowski 1984), and how much of the historical recruitment resulted from offshore spawnings. Foster and Binkowski suggest two lines of research. In the first, natal homing would be assumed and a variety of life stages would be stocked, preferably offshore, with the goal of determining the most advanced stage that would subsequently home. In the second, a variety of field and laboratory experiments would be designed to identify the homing mechanism (Foster 1984). Both lines of research would be enhanced by the development of techniques (Ihssen 1984) for marking very early life stages.

The third scenario or alternative assumption, that reproductive success occurs offshore but not inshore, is inconsistent with field observations (see citations under second scenario). If this phenomenon were observed, the most likely explanation would be a water quality effect in nearshore areas, which are more impacted by land use than are offshore areas. Research in this scenario would focus on habitat (Sly 1984) and contaminant concerns (Willford 1984).

Water quality effects also appear to be the most likely issue associated with reproductive failures at both onshore and offshore sites (the fourth scenario), because lake trout stocked as yearlings are capable of reproduction at least on a limited basis (Rybicki 1983; Argyle 1984). Many areas

(southern Lake Michigan, outer Saginaw Bay, eastern Lake Erie, etc.) formerly occupied by lake trout have been degraded since the inception of the rehabilitation program, and it is important to establish which of these areas remain suitable for reproduction. Lake trout are being planted over almost all of their former range in the Great Lakes, and some of this effort might be wasteful because of water quality constraints. Furthermore, a quantification of water quality effects on lake trout reproduction would be valuable for linking fishery and water quality goals in the Great Lakes. The issue here is similar to that outlined in the preceding scenario, and first order research would address habitat (Sly 1984) and contaminant (Willford 1984) effects.

SECOND ORDER RESEARCH

We have divided second order research into two broad categories. The first pertains to research that would intrinsically improve the reproductive potential of hatchery-origin stocks. The second involves assessment and descriptive work, which would extrinsically favor the development of spawning stocks by allowing more calculated and responsive management. Some of the assessment work involves large-scale field experiments that require considerable management cooperation, and these are reviewed separately. In the following discussion we provide a brief rationale for the research elements within each category.

Research in genetics (Ihssen 1984), hatchery effects (Foster 1984), and artificial imprinting (Foster 1984) has much potential to improve the fitness of hatchery origin spawning stocks. Various strains of lake trout are stocked in the Great Lakes (Brown et al. 1981), and it is important to know which strains are best adapted. Research is also needed to develop methods to genetically identify the progeny from mixed strain, hatchery origin spawners and to distinguish hybridization rates between hatchery and wild stocks. Hatchery rearing may diminish the fitness of planted lake trout (Foster 1984), and research that seeks to identify methods for minimizing this unintended effect is desirable. Hatchery-reared lake trout experience different diets, substrates, depths, currents, and temperatures than do wild

trout, and these anomalies may impose some liability on planted fish. The substantial differences in year-class strengths of planted lake trout reported by Pycha and King (1967) should not be accepted as being inevitable. Improvements in hatchery and stocking practices could make the weaker year-classes uncommon. The use of attractants or artificial "imprintants" (Binkowski 1984; Foster 1984) to influence the distribution of hatchery origin spawners is also appealing. Such techniques, if efficacious, appear to be practical in application. They could profoundly affect the reproductive potential of hatchery stocks, and they should be investigated.

The need for improved assessments was indicated by several of the conference working sessions, and those considered most important are identified here. Foster (1984), Hatch (1984), and Sly (1984) believe that better estimates of population characteristics or more knowledge of the life history requirements for early life stages are required. They note that improved sampling and enumeration techniques for these stages are also needed. Hatch also suggested that severe competition between lake trout and other salmonids for forage fish could impact lake trout growth, maturity, and fecundity. Delays in maturation may increase a lake trout's period of vulnerability to sea lamprey attack. Reductions in growth as Eck and Wells (1983) report for Lake Michigan likely influence allowable catches. Therefore, interactions between lake trout, other piscivores, and forage fish, particularly alewife and smelt, are of great concern and should be closely monitored. So&-economic studies (Brown 1984) that distinguish the interests and values of both participants and non-participants in the lake trout fishery are very relevant to the conduct of the rehabilitation program. The need to control lake trout catch and bycatch is the cause of some of the most restrictive fishing policies on the Great Lakes, and public concerns should be addressed if political support for the program is to continue.

LARGE-SCALE FIELD EXPERIMENTS

We recommend that the major issues relating to sea lamprey, fishing, and stocking (density) effects on lake trout

reproduction be addressed empirically through large-scale field experiments. Designs employing refuges to eliminate fishing as a variable are desired. As for sea lamprey effects (Hatch 1984), refuges should be established in contrasting areas of sea lamprey abundance, conventional stocking rates would be utilized, and differences in lake trout longevity would be taken as measures of mortality caused by sea lamprey. In the second experiment quantification of fishing effects (Hatch 1984) would be assessed by stocking in refuges at the conventional rate, and comparing longevity in the refuges with longevity in areas under various fishing regimes. In the third experiment high stocking rates, at least three times greater than the conventional rate, would be made in refuges to determine density effects (Binkowski 1984), and to provide the upper end of the stock-recruitment relationship (Hatch 1984) for hatchery lake trout. Comparisons of reproduction and spawner abundance in heavily stocked refuges with that in conventionally stocked refuges and non-refuges should provide a sufficient range of values to establish the relationship.

The three field experiments discussed above are complementary in that the control for the sea lamprey experiment can serve as the fishing control and also provide contrast for the density effect experiment. For efficiency, these studies should be coordinated among the lakes so that replication can be achieved. In addition, precautions regarding emigration and the elimination of unwanted variables such as lot differences in planting stock need to be observed. Ideally, these experiments would be incorporated into the management plan of each lake so that quality control, assessment, and reporting become a routine concern of the cooperating agencies and institutions.

ACKNOWLEDGEMENTS

We thank N. R. Kevern and A. H. Lawrie who worked on the steering committee during the planning phase of the project but were unable to attend the conference. We also are grateful to Dick Pycha for his thorough review of the conference proceedings.

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