

Density-Independent Survival of Wild Lake Trout in the Apostle Islands Area of Lake Superior

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ABSTRACT. The lake trout (*Salvelinus namaycush*) stock at Gull Island Shoal in western Lake Superior was one of only a few stocks of lean lake trout in the Great Lakes that survived overfishing and predation by the sea lamprey (*Petromyzon marinus*). Since the mid 1960s, the abundance of wild recruits measured at age 0 and the number of age-7 to -11 wild fish recruited to the fishable stock have increased. We used the Varley-Gradwell method to test for density-dependent survival between these life stages. Survival from age-0 to ages 7–11 was not affected by increasing density, which suggests that further increases in recruitment and stock size are still possible. We suggest that testing for the existence of density-dependent survival can be used to indicate when lake trout populations are rehabilitated.

INDEX WORDS: Lake Trout, recruitment, survival, Lake Superior.

INTRODUCTION

Lake trout (*Salvelinus namaycush*) living near and spawning on Gull Island Shoal, a complex of several reefs in western Lake Superior (Fig. 1, described by Bronte *et al.* 1995b), were one of the few stocks of lean lake trout in the Great Lakes that survived overfishing and predation by the sea lamprey (*Petromyzon marinus*) (Dryer and King 1968, Swanson and Swedberg 1980). In response to chemical control of the lamprey and to restrictions on the fisheries, spawner numbers at this site increased from about 3,000 fish in 1967 to about 18,000 fish in 1992 (Swanson and Swedberg 1980; Wisconsin Department of Natural Resources, Bayfield, WI, unpublished data). Since 1976, this stock has been protected from sport and commercial fishing year-round by the 70,000 ha Gull Island Refuge which was established through executive order by the state of Wisconsin (Fig. 1), and this protection appears to have aided lake trout recovery at this site (Schram *et al.* 1995). Spawner abundance at this site increased due to an increase in the numbers of wild (lake-produced) fish even though the abundance of hatchery-reared lake trout was increasing rapidly in nearby areas (Schram *et al.* 1995). Since the 1950s when stocking was begun, wild lake trout have historically made up a majority of the spawners at Gull Island Shoal (Schram *et al.* 1995), in contrast to most other spawning areas among the Apostle Islands which were, and continue to be, occupied mostly by hatchery-reared spawners (Krueger *et al.* 1986). Hatchery-reared lake trout have contributed little to recruitment of wild fish in the Apostle Islands (Krueger *et al.* 1986, Hansen

et al. 1995, and Schram *et al.* 1995) in contrast to their contributions in other areas of Lake Superior (Hansen *et al.* 1995).

In the 1960s, exploratory bottom trawling by the U. S. Fish and Wildlife Service¹ discovered age-0 wild lake trout near Michigan Island (Fig. 1), approximately 11 km southwest of Gull Island Shoal proper, which indicated that some natural reproduction had continued in this area in spite of severe declines in lake trout abundance. These fish were assumed to be the progeny of wild fish that spawn at Gull Island Shoal, and Bronte *et al.* (1995b) confirmed that lake trout hatched on Gull Island Shoal migrate to the nursery area near Michigan Island (Fig. 1) where they spend their first summer and fall. The nursery area was systematically sampled with bottom trawls from 1973 through 1992 to provide a time-series of the density (strength) of each year class. Exploratory trawling adjacent to other spawning sites in the Apostle Islands located one additional concentration of age-0 lake trout, but the density at that location was much lower than at Michigan Island. The minimal contribution of hatchery-reared lake trout to recruitment and the failure to detect significant concentrations of age-0 fish at areas other than Michigan Island indicate to us that wild spawners at Gull Island Shoal provide most of the natural recruitment in the Apostle Islands area of Lake Superior.

¹In late 1993, most research laboratories of the U.S. Fish and Wildlife Service were transferred to a new agency, the National Biological Service.

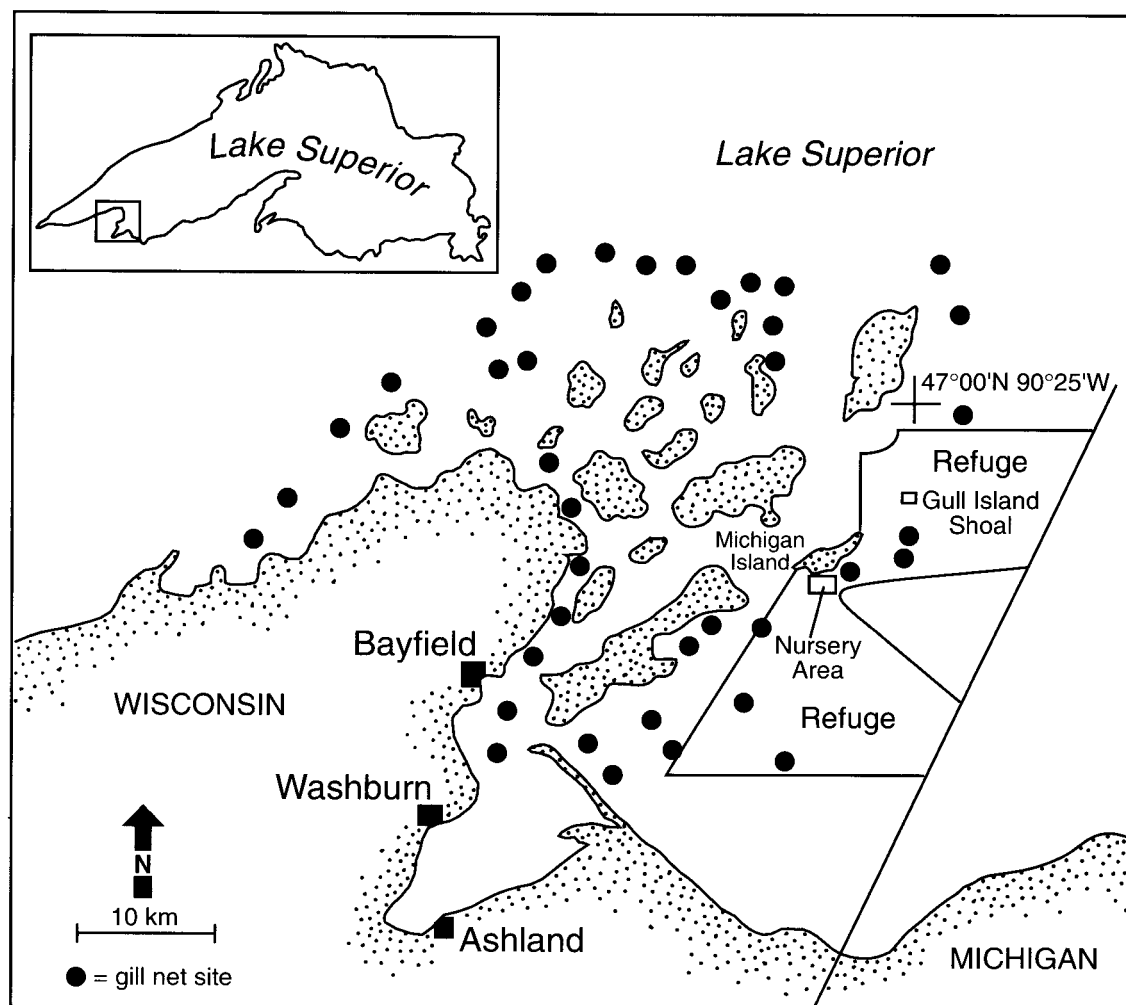


FIG. 1. Location of spring gill-net index stations for large juvenile and adult lake trout (the recruits) in the Apostle Islands area, and bottom trawling location at the Michigan Island nursery area for age-0 lake trout, western Lake Superior.

As the abundance of wild spawners has increased at Gull Island Shoal so has the density of age-0 recruits at Michigan Island. A positive linear relationship between the abundance of wild female lake trout on Gull Island Shoal in the fall and the abundance of age-0 lake trout (ages 2-3 month, Bronte *et al.* 1995b) the following late summer and fall at Michigan Island in 1964-1992 (Schram *et al.* 1995) indicated that lake trout survival between egg deposition and the first few months after hatching was unrelated to increasing density. Density-dependent survival is characterized by a decline in survival as density or stock size increases, and implies limitations of available resources (i.e., food, space) or higher probabilities of the spread of parasites or diseases that reduce survival (Hillborn and Walters 1992).

Hansen *et al.* (1995) analyzed spring gill net assessment data and showed that the relative abundance of

adult-sized wild lake trout (generally ages 6-12 years) in the Apostle Islands area gradually increased from 1959 to 1993. If the age-0 wild lake trout at Michigan Island are the major component of total wild recruitment, a relation should exist between the density of age-0 fish at Michigan Island and the relative abundance of the same wild year classes measured as large juveniles and adults in the assessment fishery in later years. The primary objective of this paper is to determine if the survival of wild lake trout between age 0 and ages 7-11, when they recruit to the fishery, is density-dependent or density-independent. The characteristics of this relationship should provide a general indication of the status of recovery of this lake trout stock. The existence of density-dependent survival between these life stages would indicate that the maximum stock size had been reached and that further stock increases may not produce additional recruits.

Density-independent survival would indicate that further increases in stock size should provide more recruits. The secondary objective of this paper is to forecast the abundance of recruits into the late-1990s.

METHODS

Data Sources

Densities of age-0 wild lake trout were obtained from sampling and estimation techniques presented in Schram *et al.* (1995). The estimates are based on trawling done at the Michigan Island nursery area in August and September, 1973–1992. The age-specific relative abundance of the same year classes at ages 7–11 was measured by standardized gillnetting in the spring in 1978–1993 at established index stations (Fig. 1) in the Apostle Islands area. The number of index stations sampled each year ranged from 14 to 40 in 1978–1986 and was consistently 31 in 1987–1993. Each year from 305 to 3,048 m of 114-mm stretch-measure gillnet were set and lifted at each index station. All lake trout captured were counted and their origins (hatchery-reared or wild) determined. Scales or sagittal otoliths were aged from a length-stratified subsample of the catch of wild fish each year, and these data were used to construct length-age keys for each year. The age composition of wild fish from each gillnet was estimated by applying the appropriate length-age key to the length frequency for each lift. The catch-per-unit-effort (CPUE; number of fish/100,000 m net/night) of each age group in each year was estimated by 1) adjusting numbers captured for net length and nights out, 2) applying a $\text{Log}_e (x + 1)$ transformation to normalize the distribution and stabilize the variances, and 3) calculating the least squares mean (LSM) of the transformed values across all lifts to compensate for unequal sampling effort among years.

Statistical Analysis

We tested for density-dependent survival of wild lake trout from age 0 to recruitment at ages 7–11 for the 1973–1986 year classes (those recruited by 1993) by the method of Varley and Gradwell (1963, 1968), as presented in Peterman (1978). This procedure uses geometric mean regression and involves fitting the following relations to the data:

$$\begin{aligned}\text{Log}_e R_t &= \text{Log}_e c + k_{YX} \text{Log}_e S \\ \text{Log}_e S &= \text{Log}_e c + k_{XY} \text{Log}_e R_t\end{aligned}$$

where R_t = LSM CPUE of wild lake trout at age t captured in the spring assessment fishery in the Apostle Islands (the recruits);
 S = LSM density of age-0 fish of the same year classes in R_t as measured by bottom trawls at Michigan Island;
 c = the y-intercept of the relations; and
 k_{YX} and k_{XY} = the slopes of each relation.

A geometric mean regression was used because measurement error exists in both the independent and dependent variables, which can cause an underestimation of the value of the slope when ordinary least squares regressions are employed. The slopes of the geometric mean regressions provide an estimate of the curvature of the relationship between age-0 fish and their subsequent recruitment. The null hypothesis (H_0) of no density-dependent survival is accepted if both k_{YX} and k_{XY} are not significantly < 1 , as determined by one-tailed t -tests, and if these regression lines lie on opposite sides of the line with $k_{YX} = 1$ when all are plotted on the same axis. Conversely, if both k_{YX} and k_{XY} are significantly < 1 and lie on the same side of a line with $k_{YX} = 1$, the true relation lies somewhere between lines k_{YX} and k_{XY} and density dependence is assumed. Graphical depictions of these relationships on the same axis require calculations of the line $k_{YX} = 1$ where

$$\text{Log}_e R_t = \text{Log}_e c + (1) \text{Log}_e S,$$

and the value of $\text{Log}_e c$ is estimated, and similarly the line k_{XY}

$$\text{Log}_e R_t = \text{Log}_e c + 1/k_{XY} \text{Log}_e S.$$

Statistical power was calculated for all analyses where H_0 was not rejected as recommended by Peterman (1989, 1990). Power is defined as the value $1 - \beta$, where β is the probability of a Type II error, or simply the probability of accepting H_0 when H_0 is not true (Zar 1974). Peterman (1990) recommended that power should be > 0.80 ($\beta < 0.20$) before accepting H_0 . We estimated β using the "Sample Size" routine in STATGRAPHICS Plus version 6 (Manugistics, Inc. 1992), in which inputs were the values of k_{YX} and k_{XY} and their standard errors, sample size (i.e., number of year classes), $\alpha = 0.05$, and appropriate statements about H_0 and H_A .

We used the linear relations of the k_{YX} lines and the density of age-0 lake trout of the 1987–1992 year classes to forecast future recruitment in 1994–1999. Because age-7 and -8 lake trout make up about 50% of the fish captured in the assessment fishery in the Apostle Islands (Wisconsin Department of Natural Resources, Bayfield, WI, unpublished data) we restricted our forecasts of abundance to those two age groups.

RESULTS

Values of k_{YX} at ages 7–11 ranged from 0.59 to 0.78, and all but k_{YX} for age-8 recruits were not significantly < 1 (Table 1). Statistical power was high (> 0.79) for testing the significance of k_{YX} for recruitment to ages 7, 9, and 11, which means that there was a 13–21% chance of accepting the null hypothesis when it was actually false (Type II error). Power was less (0.57) for testing the significance of k_{XY} for recruitment to age 10. Values of k_{XY} at ages 7, 9, 10, and 11 were lower than those for k_{YX} (0.30 to 0.49) and were all significantly < 1 (all

TABLE 1. Statistical results of the application of the Varley-Gradwell method to test for density-dependent survival between age 0 and aged 7–11 wild lake trout in the Apostle Islands area of Lake Superior. The parameters k_{YX} and k_{XY} are the slopes of the relations $\text{Log}_e R_t = \text{Log}_e c + k_{YX} \text{Log}_e S$ and $\text{Log}_e S = \text{Log}_e c + k_{XY} \text{Log}_e R_t$, where R_t is a measure of the relative abundance of age -7 to -11 fish and S is a measure of the density of the same year classes at age-0. P-values were determined by one-tailed t-tests. Statistical power ($1 - \beta$) was calculated for all statistical analyses where H_0 was not rejected, where β is the probability of a Type II error.

Age of recruits (t)	N	r	$\text{Log}_e R_t = \text{Log}_e c + k_{YX} \text{Log}_e S$				$\text{Log}_e S = \text{Log}_e c + k_{XY} \text{Log}_e R_t$			
			k_{YX}	SE	P-value $H_0: k_{YX} = 1$	Power ($1 - \beta$)	k_{XY}	SE	P-value $H_0: k_{XY} = 1$	Power ($1 - \beta$)
7	14	0.62	0.79	0.29	0.23	0.87	0.49	0.18	< 0.001	—
8	13	0.78	0.59	0.14	< 0.002	—	1.02	0.25	0.53	0.05
9	12	0.50	0.72	0.40	0.24	0.79	0.34	0.19	< 0.001	—
10	11	0.47	0.74	0.47	0.29	0.57	0.30	0.19	< 0.001	—
11	10	0.44	0.64	0.46	0.21	0.81	0.31	0.22	< 0.001	—

$P < 0.001$). Calculated value of k_{XY} at age 8 was 1.02 and was not significantly < 1 ($P = 0.53$), but power was low. All k_{YX} and k_{XY} lines, except for age 8, were on opposite sides of the $k_{YX} = 1$ line (Fig. 2), which, coupled with the fact that most age specific-values of k_{YX} were not significantly < 1 , suggests that survival from age 0 to ages 7–11 years is not density-dependent over the densities of year classes analyzed.

Correlation coefficients were highest for recruits at age 7 ($r = 0.62$) and age 8 ($r = 0.78$), and declined at higher ages. Forecasted CPUEs indicated that the abundance of age 7 fish will decline in 1994–1995, but will increase thereafter to a level similar to that in 1980 (Fig. 3). Similarly, the abundance of age-8 fish is also expected to decline but will increase and stabilize after 1996.

DISCUSSION

Our analysis indicates that survival of wild lake trout in the Apostle Islands area is independent of initial density, and this finding is consistent with the results of Schram *et al.* (1995), who described a significant positive linear relationship between the CPUE of wild female spawners at Gull Island Shoal and the abundance of their progeny. We applied the Varley-Gradwell method to those data and estimated that $k_{YX} = 0.76$ (not significantly < 1), with a 0 % chance of a Type II error ($\beta = 0$). The estimate of k_{XY} was significantly < 1 , but the k_{YX} and k_{XY} lines appeared on opposite sides of the $k = 1$ line (Fig. 4). Based on our results and those of Schram *et al.* (1995), we conclude that we have no evidence of density-dependent survival in the life cycle of wild lake trout in this area of Lake Superior. These findings are symptomatic of a stock whose density is still below the level at which compensatory population regulatory mechanisms such as intraspecific competition for food

and habitat, or increased transmission of pathogenic or parasitic agents operates. Thus, further increases in recruitment can be expected with increases in stock size.

Cannibalism (MacLean *et al.* 1981, Evans and Willox 1991) and reduced fecundity (Walters *et al.* 1980) have been suggested as mechanisms that would cause density-dependent declines in recruitment of lake trout. Hilborn and Walters (1992) suggested that predation can be a limiting factor only if the predators concentrate at the same time and place as the juveniles, or if predators respond to increasing juvenile densities. Neither of these mechanisms have been adequately investigated for lake trout in Lake Superior and their potential to cause compensation at increased stock sizes cannot be completely ruled out. However, empirical evidence of predation on juvenile lake trout in Lake Superior is limited to the occurrence of hatchery-reared yearling lake trout found in stomachs of both hatchery-reared and wild adults captured in the spring near stocking sites (Bronte *et al.* 1995a). Extensive cannibalism on wild lake trout has not been reported in Lake Superior (Dryer *et al.* 1965, Conner *et al.* 1993, Gallinat 1993). Concentration of larger lake trout and other predators does not occur at the Michigan Island nursery area where high densities of age-0 lake trout are found. Catches of older lake trout, burbot (*Lota lota*), rainbow smelt (*Osmerus mordax*), and exotic salmonines (*Oncorhynchus* spp.) were very low in our trawl samples from the nursery area. For these reasons, we infer that predation may have little potential for population regulation at Gull Island Shoal.

Density-dependent changes in fecundity cannot be accurately assessed because of the lack of historical data for this population. Eschmeyer (1955) described fecundity of lake trout in the early 1950s from central Lake Superior during a period of declining lake trout abundance (Pycha and King 1975), and Schram (1993) described fecundity of Gull Island Shoal lake trout in

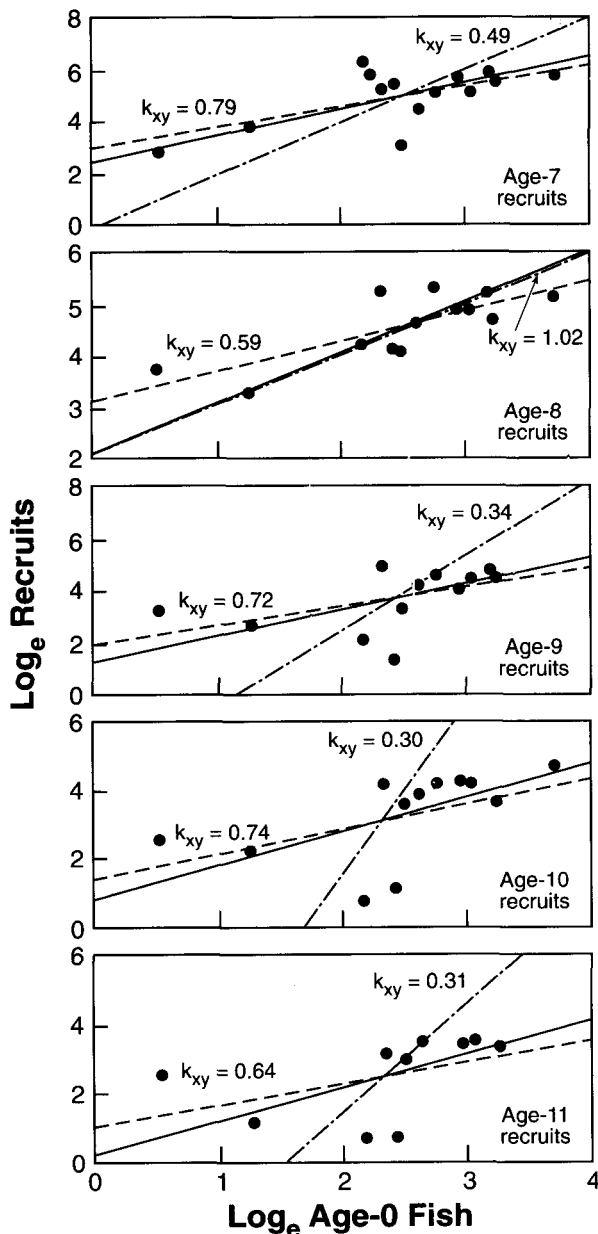


FIG. 2. Graphical depictions of age-0 and ages 7–11 lake trout abundance used in the Varley-Gradwell method of testing for density-dependent survival. The null hypothesis of no density-dependence can only be rejected if the values of k_{YX} and k_{XY} are significantly < 1 (see Table 1), and lie on the same side of the line $k_{YX} = 1$ when plotted on the same axis. Log_e Recruits is the least squares mean (LSM) of the $\text{Log}_e (x + 1)$ number of wild lake trout/100,000 m net/night captured in the spring assessment fishery in the Apostle Islands. Log_e age-0 Fish is the LSM $\text{Log}_e (x + 1)$ density (no/ha) of the age-0 fish of the same year classes in Log_e Recruits as measured by bottom trawls at Michigan Island and fully recruited by the assessment fishery.

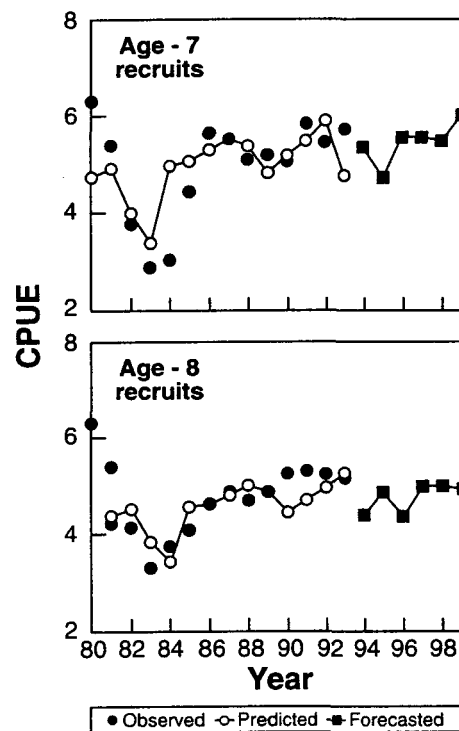


FIG. 3. Observed, predicted, and forecasted catch-per-unit effort (CPUE) of age-7 and age-8 wild lake trout in the Apostle Islands area of Lake Superior 1980–1999. Predicted values are derived from the linear regressions of observed CPUE at ages 7 and 8 and the density of the same years classes at age-0. Forecasted CPUEs are derived from the densities of the 1987–1992 year classes used in the age-specific linear regressions.

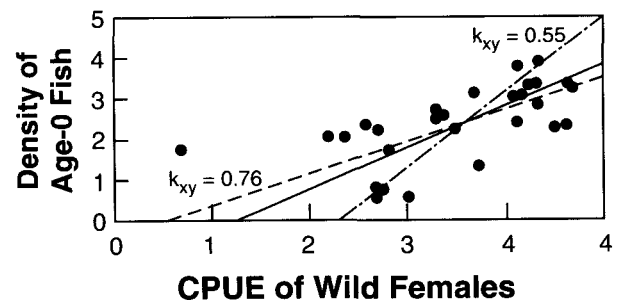


FIG. 4. Graphical depiction of Log_e – Log_e relations of female spawner abundance and age-0 recruits used in the Varley-Gradwell method of testing for density-dependent survival. Data from Schram et al. (1995).

1985-1988. As total stock size in this area increases, we would expect growth rates to decline, and declining growth would probably reduce fecundity of this, as well as all other stocks (Walters *et al.* 1980).

When density-dependent survival does appear in the Gull Island Shoal population, we speculate that the limiting factor will be the availability of suitable spawning habitat. Eshenroder *et al.* (1995) speculated that lake trout recruitment in the Great Lakes may ultimately be limited by physical processes, such as waves and water currents, which reduce the amount of habitat suitable for egg incubation.

MANAGEMENT IMPLICATIONS

We believe that this study provides important information to managers responsible for assessing the status of lake trout recovery in the Great Lakes. In Lake Superior, most stocks are now supported by natural reproduction rather than by hatchery-reared fish (Hansen *et al.* 1994). The goal of lake trout restoration in Lake Superior is to develop self-sustaining populations that can yield the annual harvest of 2.0 million kg that was realized during the 1929-1943 pre-sea lamprey period (Busiahn 1990). Measurements of goal attainment must, however, rely on stock-assessment statistics (i.e., CPUE) comparable with those from historical periods (see Hansen *et al.* in press) because it is unlikely that the fisheries will be allowed the liberty required to test for long-term yield sustainability. Though Hansen *et al.* provide a practical way to measure restoration by linking historical and contemporary CPUE time series, this procedure does not incorporate possibly biasing changes that have occurred in the physical and biological characteristics of Lake Superior since the pre-sea lamprey period. For instance, even with aggressive mechanical-and chemical-control efforts, sea-lampreys will continue to kill some lake trout. The forage base of Lake Superior (Lawrie and Rahrer 1973, MacCallum and Selgeby 1987) and forage used by lake trout (Dryer *et al.* 1965, Conner *et al.* 1993) have been altered, probably irreversibly, and some forage production is now also used by other salmonines. In addition, much of the original genetic diversity that contributed to historical lake trout production has been lost through extinction of discrete stocks that were well-adapted to specific environments (Burnham-Curtis *et al.* 1995, Krueger and Ihssen 1995). Any or all of these factors may have reduced the biological potential of lake trout to reach historical stock sizes. The recruitment dynamics of the stock itself may therefore provide a better indication of the status of recovery than would progress toward attaining historical levels of production. When stock sizes are large enough to cause saturation of the better spawning habitat on Gull Island Shoal, a decline in recruitment can then be expected. Until then, we recommend that the Gull Island Refuge be maintained to provide continued protection for this stock.

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