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Factors Affecting Recruitment of Walleyes in Escanaba Lake, Wisconsin, 1958–1996

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Abstract.—We modeled recruitment variation of age-0 walleyes *Stizostedion vitreum* in Escanaba Lake, Vilas County, Wisconsin, to determine factors regulating their abundance. Abundance of age-5 and older walleyes (spawning population), variation in May water temperatures, and abundance of 152.4-mm total length and longer yellow perch *Perca flavescens* explained 89% of annual variation of age-0 walleye abundance from 1958 through 1995. Abundance of age-5 and older spawners accounted for 32% of the recruitment variation and indicated that maximum numbers of age-0 recruits were produced at low numbers of spawners (fewer than 1,000 individuals). The coefficient of variation of May water temperatures improved the model fit to 56% of recruitment variation and indicated that increased variation of May water temperatures greatly reduced recruitment. The abundance of yellow perch 152.4 mm and longer further improved the model fit to 78% of recruitment variation and also reduced recruitment, though not as much as variation in May water temperatures. The interaction between May temperature variation and yellow perch abundance improved the model to explain 89% of walleye recruitment variation. We interpret the results of the model to mean that walleye recruitment in Escanaba Lake is regulated by competition with or cannibalism by walleyes, variation in May water temperatures, and competition with or predation by adult yellow perch.

The relationship between stock and recruitment is one of the most important biological questions for fishery managers and one of the most difficult to quantify (Hilborn and Walters 1992). Recruitment may vary as a result of some factors, such as spawner abundance, that are density dependent and others, such as the environment, that are density independent (Sissenwine et al. 1988). Density-independent environmental factors often determine survival of fish species and obscure density-dependent stock–recruit relations (Cushing 1988). In such situations, fishery biologists may conclude that no relation between spawner and recruit abundance exists, which can lead to underestimation of the risk of recruitment overfishing (Hilborn and Walters 1992).

Recruitment of walleyes *Stizostedion vitreum* has been studied in lakes that range widely in size, such as Lake Erie (Busch et al. 1975; Madenjian et al. 1996), Oneida Lake (Chevalier 1973; Forney 1976, 1980), and Escanaba Lake (Serns 1982a, 1982b). In western Lake Erie, walleye recruitment was modeled as a function of spawner density, the spring warming rate, and the density of gizzard shad *Dorosoma cepedianum* (Madenjian et al. 1996). Rapid spring warming in western Lake Erie favored rapid development of walleye embryos, thereby shortening the period of vulnerability to spring storms (Busch et al. 1975). High densities of gizzard shad, a major prey source in western Lake Erie, favored gonadal development of female walleyes in the autumn and led to greater egg deposition the following spring (Madenjian et al. 1996). The full model explained 92% of recruitment variation, and spring warming rate explained 20% of the recruitment variation.

Walleye recruitment in Oneida Lake, New York, is regulated by adult cannibalism, as mediated by

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first-year growth (Chevalier 1973; Forney 1976, 1980). In years of rapid growth, cannibalism was less than in years of slower growth, so recruitment was directly related to growth rate (Forney 1976, 1980). Cannibalism was high in winters following seasons of slow growth and was observed as size-selective overwinter mortality (Chevalier 1973). Such density dependence in the stock–recruitment relation conforms with expectations of cannibalism as the underlying process of the Ricker stock–recruitment model (Ricker 1975).

Walleye recruitment in Escanaba Lake, Wisconsin, was thought to be influenced by fecundity, egg size, and water temperatures in spring (Serns 1982a, 1982b). The average numbers of eggs produced by female walleyes was directly related to their condition (plumpness), which was thought to be determined by feeding conditions the previous summer (Serns 1982b). Survival of age-0 walleyes was positively related to egg size, but the cause of larger egg size was not determined (Serns 1982b). Survival of walleyes from egg until fall was inversely related to variability of water temperatures in May, and the growth of age-0 walleyes from spring to fall was positively related to average water temperatures in June (Serns 1982a).

We modeled recruitment variation in Escanaba Lake walleyes to determine the relative importance of density-dependent and density-independent factors. We hoped to determine whether recruitment of age-0 walleyes in Escanaba Lake was predictable from knowledge of density-dependent factors, such as spawner density, and density-independent factors, such as spring temperature variation, as has been found in Oneida Lake (Forney 1980) and Lake Erie (Madenjian et al. 1996).

Methods

Study area.—Escanaba Lake is a 119-ha drainage lake in the northern highlands of Vilas County, Wisconsin (46°04′ latitude, 89°35′ longitude; Kempinger and Carline 1977). The shoreline is 8.2 km, the maximum depth is 8 m, and the mean depth is 4.3 m. The shoreline has a substrate of rock and cobble along the steeper north shore and islands and sand and silt in bays and shallow areas. Temperature stratification usually occurs only briefly in summer, so dissolved oxygen falls below 5 mg/L only briefly at depths greater than 6 m. Ice cover generally extends from late November through late April, but winterkill has not occurred since 1946, when studies were initiated to determine the effects of angling on the fish community.

The fishes of Escanaba Lake have been the basis of long-term research to determine effects of angling on the fish community (Patterson 1953; Churchill 1957; Kempinger and Churchill 1972; Kempinger et al. 1975; Kempinger and Carline 1977; Serns and Kempinger 1981; Serns 1982a, 1982b, 1986a, 1986b, 1987). Walleyes and northern pike *Esox lucius* were introduced in the lake during 1933–1945. Walleyes were firmly established in the lake by 1948 and northern pike by 1958. Other common species are muskellunge *Esox masquinongy*, yellow perch *Perca flavescens*, and white sucker *Catostomus commersoni*. Pumpkinseed *Lepomis gibbosus* were abundant during 1955–1963 but declined to negligible numbers by 1966. Smallmouth bass *Micropterus dolomieu* were also abundant until walleyes became established in the lake.

Escanaba Lake data.—We provide a summary of methods, previously described, that were used to obtain data on the Escanaba Lake fishery (Patterson 1953; Churchill 1957; Kempinger and Churchill 1972; Kempinger and Carline 1977; Serns and Kempinger 1981; Serns 1982, 1986). Age-0 walleye abundance was estimated in mid-September to mid-October during 1958–1996. Age-0 walleyes were caught at night with a 230-V AC electroshocking boat, measured (total length, $N = 100$), marked with a unique fin clip, and released. Age-0 walleyes were separated from age-1 fish by length-frequency and annuli on scales. Abundance of age-0 walleyes (±95% confidence intervals, CI) was estimated by the Schnabel mark–recapture method from catches in 3–5 nights of sampling (Ricker 1975). Standard deviations of the population estimates averaged 85% of the mean from 1958 to 1980 (Serns 1982a).

Abundance of adult walleyes was estimated during spring spawning during 1958–1996. Adult walleyes were caught in 19-mm- or 25-mm-square-mesh fyke nets, tagged with Monel metal jaw tags, fin-clipped, and released. A compulsory creel census allowed inspection of all fish caught by anglers for tags and fin clips. Ages were estimated from scales or spines (Serns 1986b). Abundance of each age-group (±95% CI) was estimated by the modified Peterson mark–recapture method (Ricker 1975). Abundance of age-groups for which no tagged fish were examined (±95% CI) was estimated by the Bailey modification of the Peterson method (Ricker 1975). Standard deviations of the population estimates averaged 10% of the mean from 1959 to 1991 (Carpenter et al. 1994). The majority of female walleyes did not mature until age-5 (Serns 1982b), so we modeled three different adult age-groups (age 3 and older, age 4 and older, age 5 and older).

Cohort analysis was used to estimate adult walleye numbers in 1973, 1975–1976, and 1978, when mark–recapture estimates were not obtained. Numbers of each age-group in these years (N_t) were estimated from numbers of each age-group in the next year (N_{t+1}), catches of each age-group in these years (C_t), and an estimate of the instantaneous rate of natural mortality (Pope 1972):

$$N_t = N_{t+1}e^{M} + C_t e^{M/2}.$$

To estimate the instantaneous natural mortality rate, M, we first estimated the instantaneous total mortality rate ($Z = 0.6117$) from a catch curve of the average population age frequency from 1958 to 1995 (Ricker 1975). We then estimated the instantaneous fishing mortality rate as follows: $F = Z \times u/A = 0.3955$, where A = annual mortality rate ($A = e^{-Z} = 0.4576$) and u = annual exploitation rate during 1958–1996 (u = recaptures/marks = 0.2958). The instantaneous natural mortality rate was then estimated by difference ($M = Z - F = 0.2162$).

Abundance of adult (≥152.4 mm total length) yellow perch was estimated during spring spawning in 1958–1966, 1969, 1977, and 1981–1996. Abundance of yellow perch was not estimated in other years because too few fish were marked and recaptured. Adult yellow perch were caught in 19-mm- or 25-mm-square-mesh fyke nets, marked by removal of a fin, and released. Pectoral and pelvic fins were used in a 4-year rotation to differentiate years of marking. A compulsory creel census allowed inspection of all fish caught by anglers for fin clips. Abundance of adult yellow perch (±95% CI) was estimated by the modified Peterson mark–recapture method, based on the number marked in the spring and the ratio of marked to unmarked fish observed in the creel census through mid-June. Standard deviations of the population estimates averaged 23% of the mean from 1969 to 1996 (S. Newman, Wisconsin Department of Natural Resources, unpublished data).

Water temperature in Escanaba Lake was recorded twice daily during the open-water season during 1958–1996. Surface temperature was measured to 0.5°C with a hand-held thermometer at 0800 and 1800 hours (Central Daylight Time) in a bay on the south end of the lake near the entry. Mean, standard deviation, coefficient of variation (CV = SD/mean), and warming rate (°C/d) of morning temperature readings in May and June were used to describe lake temperatures. The CV of morning surface temperatures in the bay was correlated with both the CV of evening surface temperatures in the bay ($r = 0.931$; df = 6; $P < 0.001$; Serns 1982a) and the CV of temperatures measured on one of the major walleye spawning reefs ($r = 0.852$; df = 21; $P < 0.001$; Serns 1982a). We therefore assumed that morning bay temperatures reflected the pattern of temperature fluctuations in the lake.

Recruitment model.—We used a Ricker (1975) stock–recruitment model to test for the effects of spawner abundance, spring water temperatures, yellow perch abundance, and age-0 walleye growth on age-0 walleye abundance in Escanaba Lake:

$$R = Se^{a-bS-cX}.$$

The model describes age-0 walleye abundance (R) as a function of parental abundance (S), background density-independent mortality (a), density-dependent interactions (bS), and other factors such as water temperatures, yellow perch abundance, and age-0 walleye growth (cX). An insignificant b-coefficient would indicate density-independent mortality, a significant negative b-coefficient would indicate compensatory density-dependent mortality, and a significant positive b-coefficient would indicate depensatory density-dependent mortality (Hilborn and Walters 1992).

Model coefficients (a, b, and c) were estimated by multiple regression on the linear form of the model for 1958–1991:

$$\log_e(R/S) = a - bS - cX + \epsilon.$$

The linear form of the model describes the per-capita recruitment rate, $\log_e(R/S)$, as a function of the parental stock size (S), other explanatory variables (X), and residual error (ϵ). Partial correlations between explanatory variables and residuals were tested at each step for entry to ($P \le 0.05$) or exit from ($P > 0.05$) the model, and modeling was stopped when the model was not significantly improved by adding or deleting additional variables (Draper and Smith 1981; SPSS 1997).

The final model was used to predict age-0 walleye abundance in 1992–1996 to test the validity of the model for predicting future year-classes (Draper and Smith 1981). Differences between observed and predicted age-0 abundance (residuals) for 1992–1996 were compared with residuals obtained from the model for 1958–1991. We judged that the model was valid for predicting future year-

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TABLE 1.—Abundance of age-0 walleyes, age-5 and older walleyes, and adult (≥152.4-mm) yellow perch and coefficient of variation (CV) for May water temperature used to model survival of walleyes from spawning in spring to the next fall in Escanaba Lake, Wisconsin, 1958–1996.

Year-class	Number of Age-0 walleye	Number of Age-5 and older walleye	May temperature CV (SD/mean)	Number of yellow perch[a]
1958	4,532	775	0.24125	66,000
1959	22,996	2,310	0.16319	34,000
1960	628	2,990	0.46056	35,000
1961	879	1,400	0.33028	54,000
1962	14,747	1,130	0.22618	68,000
1963	13,205	790	0.20596	37,000
1964	31,793	1,195	0.19229	29,000
1965	10,621	981	0.20363	11,000
1966	22,271	870	0.34520	6,000
1967	8,736	1,104	0.27511	NA
1968	8,761	883	0.10884	NA
1969	18,885	1,421	0.17799	18,410
1970	10,098	1,198	0.21060	NA
1971	3,394	760	0.22098	NA
1972	1,697	1,354	0.39461	NA
1973	25,159	1,308	0.19696	NA
1974	14,093	2,016	0.20992	NA
1975	1,932	962	0.33459	NA
1976	2,292	976	0.24803	NA
1977	17,386	1,062	0.19815	12,274
1978	5,334	1,945	0.32837	NA
1979	6,957	2,073	0.41620	NA
1980	1,036	1,458	0.26409	NA
1981	16,345	946	0.25728	17,174
1982	6,149	1,952	0.27111	36,262
1983	10,366	1,280	0.18882	28,242
1984	16,795	851	0.28661	7,153
1985	14,599	394	0.12269	3,132
1986	15,299	2,121	0.18605	17,690
1987	13,882	452	0.14723	33,869
1988	4,351	369	0.18968	28,101
1989	4,262	603	0.34298	29,653
1990	35,607	735	0.19356	14,480
1991	4,876	1,261	0.32032	23,926
1992	12,331	1,011	0.23614	12,549
1993	19,690	988	0.21200	15,060
1994	30,225	853	0.26766	14,409
1995	4,136	683	0.17347	8,603
1996	1,325	472	0.36654	13,574

[a] NA = not available.

classes if the range of residuals for the model validation years, 1992–1996, was similar to the range of residuals for the model construction years, 1958–1991.

Results

The abundance of age-5 and older walleyes, S (Table 1), explained 32% of recruitment variation, R, in Escanaba Lake ($F = 15.19$; df = 1, 32; $P \leq 0.001$):

$$R = Se^{3.392-0.001176 \times S}.$$

The greatest number of recruits was produced by fewer than 1,000 spawners, and the greatest number of spawners (3,000 individuals) produced the fewest recruits (Figure 1). The abundance of age-4 and older walleyes accounted for only 6% of recruitment variation ($F = 2.14$; df = 1, 32; $P = 0.15$), and the abundance of age-3 and older walleyes accounted for only 13% of recruitment variation ($F = 4.87$; df = 1, 32; $P = 0.035$).

The CV of May water temperatures, T (Table 1), improved the model to explain 56% of recruitment variation ($F = 19.61$; df = 2, 31; $P \leq 0.001$):

$$R = Se^{4.792-0.000730 \times S-7.839 \times T}.$$

The greatest number of recruits was produced when the CV of May temperatures was 0.19, and the fewest recruits were produced when the CV of May temperatures was 0.46, the maximum value observed (Figure 2). May temperature variation reduced recruitment, so that if temperature varied too greatly, fewer recruits were produced regardless of the number of spawners (Figure 3). Other variables of temperature, including the mean, standard deviation, and warming rate for other periods (including the first 30 d after ice-out and the month of June), were less descriptive of walleye recruitment in Escanaba Lake.

Abundance of adult yellow perch, YP (Table 1), improved the model to explain 78% of recruitment variation ($F = 21.11$; df = 3, 18 $P \leq 0.001$):

$$R = Se^{5.716-0.000825 \times S-7.989 \times T-0.000021 \times \mathrm{YP}}.$$

The greatest numbers of age-0 walleyes were produced when adult yellow perch abundance was low, although yellow perch abundance was not significantly related to age-0 walleye abundance (Figure 4). As a factor in the stock–recruit model, adult yellow perch abundance reduced age-0 walleye recruitment, though not as much as May temperature CV (Figure 5). Small to moderate numbers of age-0 walleyes (2,000–15,000 individuals) were estimated to be produced when adult yellow perch abundance was as high as 70,000 individuals.

The interaction between May temperature variation and yellow perch abundance improved the model to explain 89% of recruitment variation, but May temperature variation was deleted from the model in the presence of its interaction with yellow perch abundance ($F = 48.20$; df = 3, 18; $P \leq 0.001$):

$$R = Se^{3.718-0.000714 \times S+0.000057 \times \mathrm{YP}-0.000324 \times (T \times \mathrm{YP})}.$$

The effect of yellow perch abundance on age-0

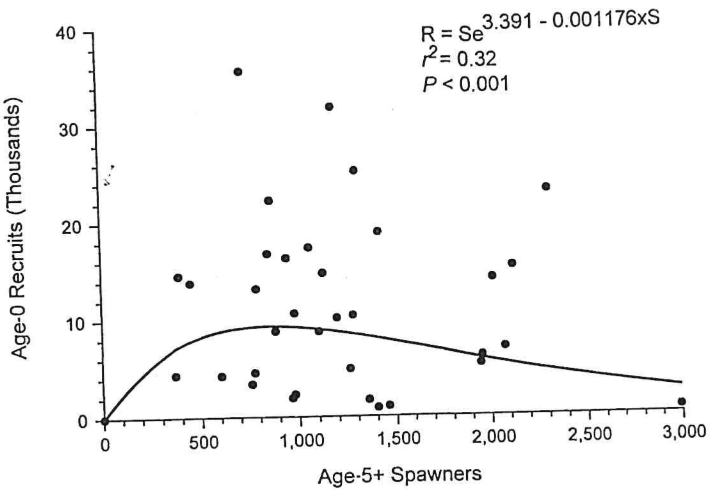

FIGURE 1.—Number of age-0 walleyes in Escanaba Lake, Wisconsin, as a function of the number of age-5 and older walleyes in 1958–1991.

walleye recruitment was not evident at levels of May temperature variation lower than CV = 0.176 but increased at greater May temperature variation (Figure 6). May temperature variation exceeded CV = 0.176 in 34 of 39 years during 1958–1996, so yellow perch suppressed age-0 walleye recruitment in most years during this period.

The full model we developed using data from 1958–1991 was equivocal in its ability to predict abundance of age-0 walleyes in 1992–1996. Predictions of the full model were generally better for low to moderate levels of recruitment, which was common, than for high recruitment, which was rare (Figure 7). The largest recruitment in 1990 (35,607 fish) was underestimated by 56%, whereas the smallest recruitment in 1960 (628 fish) was underestimated by less than 9%. Differences between observed and predicted age-0 abundance (residuals) for 1992–1993 were within the range obtained for 1958–1991, but residuals for 1994–1996 were larger than any obtained for 1958–1991 (Figure 8).

Discussion

The number of age-0 walleyes produced and surviving through their first summer in Escanaba Lake seems to be regulated largely by early mortality associated with cannibalism or intraspecific com-

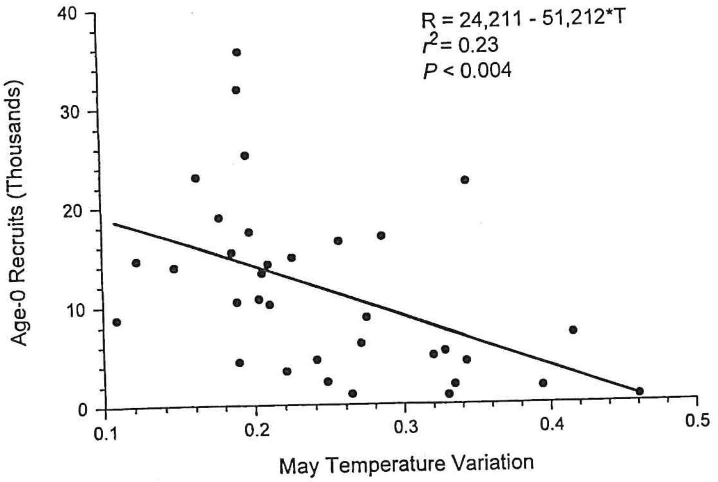

FIGURE 2.—Number of age-0 walleyes in Escanaba Lake, Wisconsin, as a function of the coefficient of variation of May water temperature in 1958–1991.

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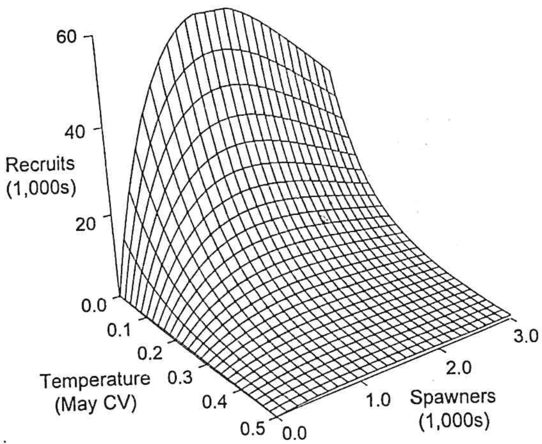


FIGURE 3.—Number of age-0 walleyes in Escanaba Lake, Wisconsin, as a function of the number of age-5 and older walleyes and the coefficient of variation (CV) of May water temperature in 1958–1991.

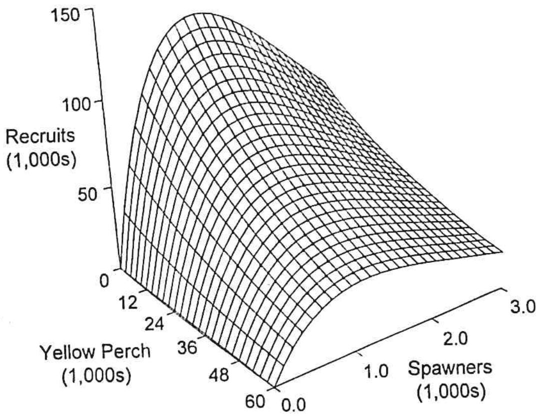


FIGURE 5.—Number of age-0 walleyes in Escanaba Lake, Wisconsin, as a function of the number of age-5 and older walleyes (spawners), the coefficient of variation of May water temperature, and the number of adult yellow perch (152.4 mm and larger) in 1958–1991. The coefficient of variation of May water temperature was set to zero, to show the independent effect of yellow perch abundance on walleye recruitment.

petition with walleyes, temperature variation in May of the year of hatching, and predation by or interspecific competition with adult yellow perch. The negative relation between recruitment of age-0 walleyes and abundance of age-5 and older walleyes agrees with the results of Chevalier (1973) and Forney (1976, 1980) for Oneida Lake. However, our failure to find evidence of an effect of size of age-0 walleyes in the fall on first-year recruitment is in contrast with their findings. Perhaps the nearly two-times higher density of walleyes in Oneida Lake imposes more severe cannibalism on age-0 recruits than in Escanaba Lake, enhancing the importance of first-year growth on survival in Oneida Lake.

The negative relation between variability in May water temperatures and first-year recruitment of walleyes in Escanaba Lake was consistent with laboratory studies that showed sudden temperature changes increased mortality of walleye fry (Koenst and Smith 1976). Serns (1982a) felt that variability in May water temperatures indicated the importance of temperature fluctuations to recent post-hatch fry rather than to incubating eggs, as would

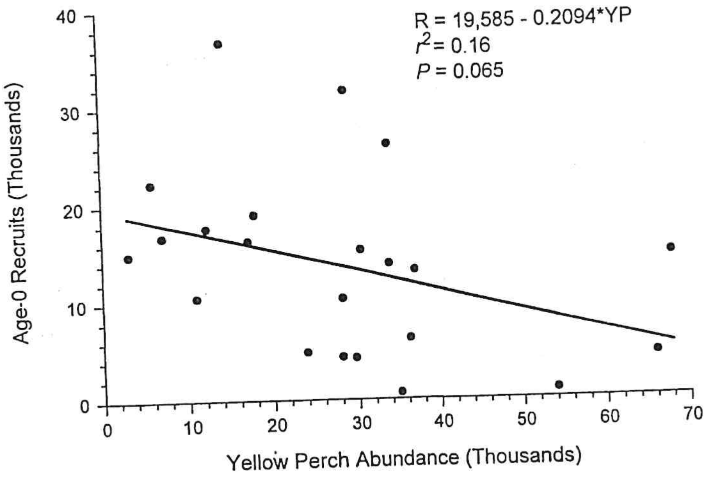


FIGURE 4.—Number of age-0 walleyes in Escanaba Lake, Wisconsin, as a function of the number of adult yellow perch (152.4 mm and larger) in 1958–1991.

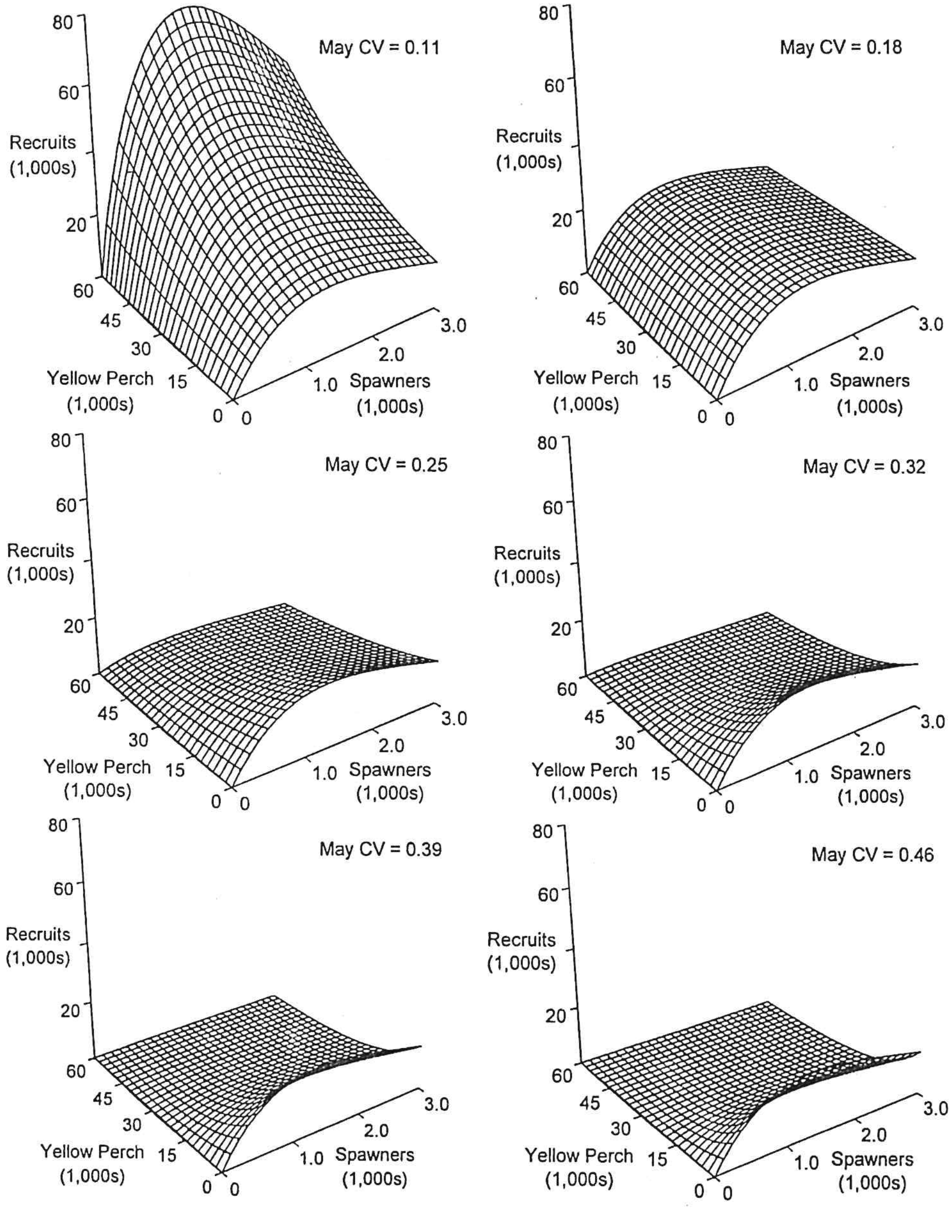
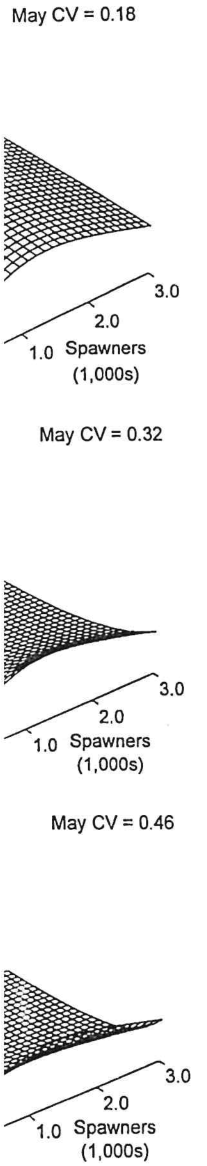


FIGURE 6.—Number of age-0 walleyes in Escanaba Lake, Wisconsin, as a function of the number of age-5 and older walleyes (spawners), the number of adult yellow perch (152.4 mm and larger), and interaction between May water temperature coefficient of variation and number of adult yellow perch in 1958–1991.

be indicated by temperature variability in the first 30 d after ice-out. Koonce et al. (1977) concluded that water temperature was a dominant regulator of year-class strength in percids, based on a review of published studies. Variation in spring temperatures may affect age-0 survival by (1) delaying, interrupting, or terminating spawning of adults (Hokanson 1977); (2) slowing embryological development during incubation (Koonce et al. 1977); (3) altering timing of microcrustacean reproduction needed by age-0 walleyes for initial feeding (Hokanson 1977); (4) causing direct mortality (Koenst and Smith 1976); or (5) reducing growth, which increases vulnerability to predation and reduces the ability to compete with other age-0 fish.

Our failure to find evidence of an effect of spring



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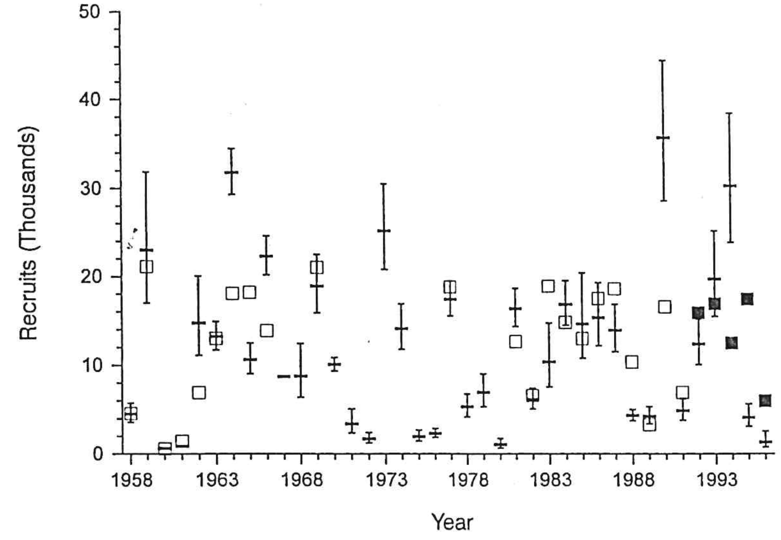

FIGURE 7.—Number of age-0 walleyes estimated by mark–recapture (vertical bars = ±95% confidence interval) and estimated from the number of age-5 and older walleyes, number of adult yellow perch (152.4 mm and larger), and interaction between May water temperature coefficient of variation and yellow perch abundance (squares) in Escanaba Lake, Wisconsin, in 1958–1996. Open squares indicate years used to estimate model coefficients (1958–1991) and filled squares indicate years used to verify the model (1992–1996).

warming rate on first-year recruitment of walleyes, which is in contrast with results for Lake Erie and Oneida Lake, may be related to the relatively small size of Escanaba Lake (119 ha). In Lake Erie (the western basin alone is 327,600 ha), the warming rate in spring enhanced recruitment of age-0 walleyes (Busch et al. 1975; Madenjian et al. 1996), and Busch et al. (1975) thought that the warming rate in spring determined the length of time that walleye eggs were exposed to the effects of storms. In Oneida Lake (20,700 ha), onshore winds and waves were thought to cause most of the mortality of walleye eggs during incubation (Forney 1976). Serns (1982a) felt that wind effects were not important in Escanaba Lake due its short fetch (1.7 km) and heavily forested shoreline.

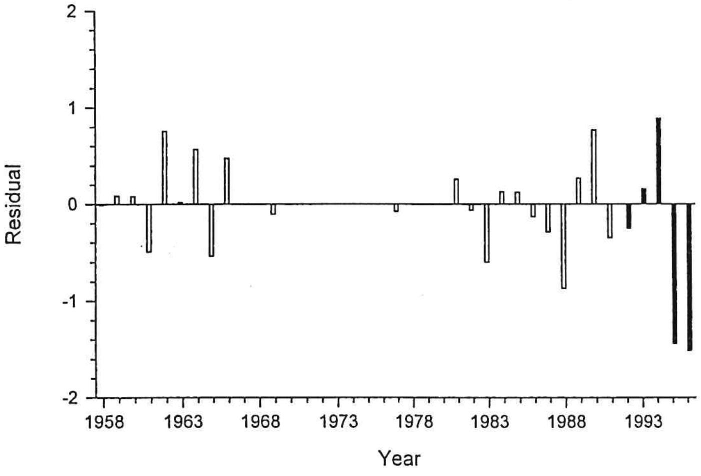

FIGURE 8.—Residuals for age-0 walleye abundance predicted from the number of age-5 and older walleyes, number of adult yellow perch (152.4 mm and larger), and interaction between May water temperature coefficient of variation and adult yellow perch abundance in Escanaba Lake, Wisconsin, in 1958–1996. Open bars indicate years used to estimate model coefficients (1958–1991) and filled bars indicate years used to verify the model (1992–1996).

The small size of Escanaba Lake may also express a greater limitation on food resources for juvenile walleyes than in Oneida Lake and Lake Erie. Our finding that abundance of adult yellow perch in Escanaba Lake reduced walleye recruitment differed from related studies in Oneida Lake and Lake Erie, where yellow perch and gizzard shad appeared to enhance recruitment. Age-0 and age-1 yellow perch in Oneida Lake mitigated the degree to which adult walleyes cannibalized their young by serving as alternate prey (Forney 1974). Age-0 gizzard shad in Lake Erie enhanced gonadal development of female walleyes, thereby enhancing egg deposition and year-class strength the following year (Madenjian et al. 1996). Adult yellow perch in Escanaba Lake may be both predators on small age-0 walleyes early in their first growing season and competitors with large age-0 walleyes later in their first growing season. In either case, yellow perch would negatively affect age-0 walleye abundance in Escanaba Lake.

Poor prediction of the largest recruitments during model development suggests that an important variable may be missing from the model, such as summer temperature or mean length of age-0 walleyes (Serns 1982a), which may favor very high levels of survival of walleyes from egg deposition to fall. We considered June temperatures (mean, SD, and CV) and mean length of age-0 walleyes in autumn, neither of which accounted for significant variation in walleye recruitment in Escanaba Lake. Such factors may be more important for survival through the first winter than through the first growing season, as was found in Oneida Lake (Chevalier 1973; Forney 1976, 1980).

We judged that the model should be used with caution for predicting future year-classes. Although there were periods when residuals were large across several years, residuals for the last three model validation years (1994–1996) were larger than those for any model construction years (1958–1991). The model may not therefore describe forces regulating contemporary recruitment of walleyes in Escanaba Lake. Further study of the factors that are currently regulating walleye recruitment in Escanaba Lake is warranted to determine if recruitment in 1995–1996 was anomolous, if age-0 abundance in 1995–1996 was estimated inaccurately, or if recruitment dynamics have changed over time.

Management Implications

Knowledge of the factors that regulate walleye recruitment would help fishery managers understand the risk of overfishing and, perhaps, permit estimation of walleye abundance with greater precision than at present (Hansen et al. 1991). Walleyes in northern Wisconsin are managed jointly by tribal and state biologists using methods that account for uncertainty in estimated total allowable catch, TAC (Hansen 1989; Staggs et al. 1990; Hansen et al. 1991). Walleye abundance in most lakes is estimated from knowledge of lake size (Hansen 1989) and past abundance in lakes of similar size (Hansen et al. 1991). Because of uncertainty of estimates, a margin for safety is included in the estimates of TAC (Staggs et al. 1990). The safety factors account for the degree of uncertainty in estimated TAC and a 1-in-40 risk of harvesting greater than TAC (Hansen et al. 1991).

Knowledge of factors that contribute to uncertainty in estimates of walleye abundance will improve fishery management in two ways. First, the relative importance of density-independent and density-dependent factors in regulating walleye recruitment will permit evaluation of the risk of recruitment overfishing (Hilborn and Walters 1992). In Escanaba Lake, recruitment of walleyes is likely regulated by a mixture of density-independent and density-dependent factors, which means that fisheries must be managed within the reproductive potential of the spawning stock but that stochastic fluctuations in environmental factors, such as spring temperature, along with coincident fluctuations in biotic factors, such as yellow perch abundance, mediate the number of recruits that are produced by the spawning stock. Obviously, fishery managers can control harvest of spawners but not spring temperature fluctuations. Harvest must be adjusted to achieve stock sizes that maximize or optimize recruitment, within the limits of stochastic environmental variation.

Second, the precision of estimated TACs can be improved if factors regulating recruitment are quantified and are available for use in forecasting future populations (Hansen et al. 1991). Density-independent factors, such as temperature variation in May, can be used to predict recruitment of age-0 walleyes in autumn, even though temperature cannot be manipulated to affect survival of eggs and fry. How these year-classes translate into exploitable adult stocks might be predicted from age-structured population models that can be used to set future regulations to accommodate anticipated adult stocks. Other factors that affect early survival of walleyes, such as density of adult walleyes and yellow perch, can be both manipulated and used for estimating recruitment. The costs of ob-

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taining such data for predicting recruitment must, of course, be weighed against the benefits of the increase in precision of estimated TAC that is attributable to the increased data (Hilborn and Walters 1992).

The cost of measuring factors that may control recruitment of walleyes in Escanaba Lake ranges from relatively inexpensive (May temperature variation) to costly (estimates of adult walleye and yellow perch abundance); the benefit is the value of more walleyes harvested by spearing and angling. These costs and benefits are measurable and should be considered in designing assessment programs for the walleye fishery in northern Wisconsin. In the absence of quantitative knowledge of the factors that regulate survival, margins for safety on allowable harvest levels must be commensurate with levels of uncertainty in management targets, such as population estimates, TAC, or maximum sustainable yield, which are often great (Peterman and Bradford 1987; Hansen et al. 1991; Caddy and McGarvey 1996).

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