Enhancing a walleye population by stocking: effectiveness and constraints on recruitment

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A long term project to evaluate the potential for food web manipulation to improve water quality in Lake Mendota, Wisconsin began in 1987. Intensive walleye *Stizostedion vitreum* stocking and harvest regulations were used to enhance walleye biomass. Over 60 million walleye fry and 2.4 million 50-mm walleye fingerlings were stocked during 1987–1992. Fry survival was negligible; mark-recapture estimates of small (< 275 mm) walleye abundance showed first year survival of stocked fingerlings to be variable but always \leq 10%. Direct (predator consumption) and indirect (prey abundance, predator biomass) evidence suggested predation to be a major constraint to augmenting walleye recruitment by stocking.

1. Introduction

Understanding natural recruitment variability continues to be a perplexing problem in fisheries ecology (Magnuson 1991). Where natural recruitment is lacking or deemed insufficient stocking (the release of cultivated fishes into the wild) can be an important management tool. However, stocking events historically have not been adequately evaluated (Cowx 1994, Wahl *et al.* 1995). As a result, our understanding of the ecological mechanisms underlying variability in recruitment of stocked fishes is perhaps even weaker, and many stocking practices have been ineffective or detrimental (Cowx 1994, White *et al.* 1995).

Recently, fishery biologists have been paying increasing attention to evaluating the success and impacts of stocking programs (Stroud 1986, Ellison & Franzin 1992, Schramm & Piper 1995), but there is much to be learned. With the increasing popularity of the walleye *Stizostedion vitreum* among North American anglers (Quinn 1992) interest in walleye stocking is growing (Ellison & Franzin 1992). However, as with many other species, the success of stocking programs to augment walleye recruitment has been variable at best (Laarman 1978, Ellison & Franzin 1992).

This paper has two goals. The first is to evaluate the effectiveness of a large scale walleye stocking program that was being conducted as part of a food web manipulation. Beginning in 1987 an ambitious walleye stocking program was undertaken to enhance the sport fishery and to test the potential for biomanipulation as a water quality management tool in a large, eutrophic lake (Kitchell 1992). During the first three years of the study this stocking program used a significant proportion of the management agency's entire hatchery production of walleye larvae (38%) and fingerlings (14%). Fingerling stocking continued for three more years at reduced levels. Second, we offer some hypotheses to explain the outcome of the stocking program. While determining factors controlling stocking success was not an *a priori* goal, the fortuity of an intensive food web study and multiple years of data allow us to draw some inferences about factors influencing the survival of stocked walleyes.

2. Study site

Lake Mendota (43°6'N, 89°24'W) is a 3 983 ha eutrophic lake situated at 259 m above sea level in Southcentral Wisconsin, USA. It has a mean depth of 12.7 m and maximum depth of 25 m. The pelagic zone comprises about 75% of the lake's surface area. The lake is dimictic; epilimnetic temperatures in summer are generally 24-27°C and the hypolimnion is anoxic (Lathrop 1992). There are over 30 species in the current fish community; fish biomass is dominated by three planktivores: yellow perch (Perca flavescens), bluegill (Lepomis macrochirus), and cisco (Coregonus artedi) (Johnson et al. 1991). The most common piscine groups are: percids (walleye, yellow perch, logperch Percina caprodes, Iowa darter Etheostoma exile, Johnny darter Etheostoma nigrum), centrarchids (eight spp.), cyprinid (five spp.), and esocids (three spp.). Cisco and white bass (Morone chrysops) are periodically very abundant.

Walleye are believed to be native to the lake, but prior to stocking their abundance was low and largemouth bass and northern pike were the dominant piscivores (Magnuson & Lathrop 1992). The first walleye stocking (of fry) occurred before 1900; fingerlings were stocked sporadically during 1970–1986 and in earnest beginning with this study in 1987. Northern pike were also stocked during 1987– 1989, resulting in a rapid increase in northern pike biomass (Johnson *et al.* 1992). Lake Mendota has been studied extensively; Kitchell (1992) provides a synthesis of historical changes and recent food web research.

3. Materials and methods

3.1. Walleye production and stocking

Walleye eggs were obtained from native or naturalized populations at locations throughout central and northern Wisconsin. The number of walleyes required necessitated using fish from multiple production facilities. Fry (2-d old larvae) were produced at the Spooner and Woodruff State Fish Hatcheries in northern Wisconsin; fingerlings were produced at four hatcheries and 10 ponds across the state. Fingerlings were reared extensively in fishless ponds on zooplankton prey. Ponds were monitored for zooplankton density and walleye size. Zooplankton populations typically crashed when the fingerlings reached about 50 mm total length (*TL*). The fingerlings were then seined into aerated transport trucks for stocking. We were careful to temper transport water with lake water to within 2°C of ambient lake temperature before stocking to minimize thermal stress. Estimated cost to produce fingerlings was 6.7 cents (1995 US currency, CPI inflation adjusted value from Madenjian *et al.* 1991) per fish.

Fry were stocked in midlake regions at 5 000/ha in May 1987–1989 (Table 1). Finglerlings were stocked in the littoral zone at densities of 126–163/ha in early summer 1987–1989 and at 63–74/ha in 1990–1992. A local angling club stocked a total of 164 000 (41/ha) walleye fingerlings in 1985–1986.

3.2. Sampling and assessment

A variety of ichthyoplankton gear was used to sample for larval walleyes. A Miller high-speed sampler was used in May 1987 and 1993; in April–May 1987–1993 a neuston net was used. During May–August 1988–1993 a 1-mm² mesh, 30 m long by 9 m deep purse seine was used throughout the lake to sample small pelagic fishes (Post *et al.* 1992). During July– August 1988–1993 small-mesh mini-fyke nets (Johnson *et al.* 1995) were used at 12–35 littoral zone sites around the lake to sample small inshore fishes, including young-of-year (YOY) walleye. These nets were constructed with a 51 × 51 mm mesh in the throat to exclude large fishes, and were more effective than shoreline seining especially at vegetated sites (Johnson *et al.* 1995). Mean catch of YOY fishes per net-day was used as an index of prey year class strength.

We used shoreline boat electrofishing (300 VDC, 2.5A, 20% duty cycle, 60 Hz) in May to early June, and during September-October 1987-1993 to sample juvenile walleyes (TL < 279 mm), perch and bluegill. All walleyes sampled during electrofishing were marked (tip of a caudal lobe; top in fall, bottom in spring) and released. We took scales in both periods to distinguish age groups. Mark-recapture population estimates (Chapman's modified Petersen estimator, Ricker 1975) of walleye abundance were performed each spring and fall, each requiring approximately 15-20 nights of electrofishing effort. Marking was conducted systematically along shoreline transects that totaled about twice the lake's shoreline length, and recapture sampling occurred at randomly selected transects. We computed 95% confidence intervals using a variance formula (Ricker 1975); differences between fall and spring population estimates were tested using a one-tailed z-test (White et al. 1982). Estimates were computed for walleyes < 279 mm (TL); we computed the abundance of size classes by multiplying the Petersen estimate by the relative length-frequency distribution (in 25mm size classes) of unmarked fish sampled during marking and recapture periods ($N \ge 268$ fish). Abundance of age classes in each season were computed from an unbiased agelength key generated from scale samples in fall or spring.

Based on extensive sampling before fingerlings were stocked, we assumed natural recruitment of walleyes was negligible during the study. Post-stocking survival, *S*, was computed by the formula:

$$S = \left(\frac{\hat{N}_t}{N_0}\right) \times 100 \,(\%) \tag{1}$$

where \hat{N}_t is the estimated number of walleyes at time *t*, and N_0 is the number of walleyes stocked. Fingerling growth was obtained from subsamples measured at stocking and lengths in electrofishing samples of YOY walleye in fall and age-1 walleye in spring. Maximum possible growth occurring between fall and spring samples (15 October–15 May) was predicted using observed Lake Mendota surface temperatures (R. Lathrop, Wisconsin Dept. Natural Resources, unpublished data) and the approach of Larscheid (1995).

YOY yellow perch and bluegill growth were obtained from ichthyoplankton, mini-fyke net and electrofishing samples. We used YOY walleye and prey growth and prey: predator size ratios for walleyes feeding on yellow perch and bluegills to track YOY prey vulnerability to YOY walleye predation. Maximum prey: walleye size ratios were 0.46 for yellow perch and 0.32 for bluegill (Madenjian & Carpenter 1991). Abundance, mortality, growth, and diet of walleyes and northern pike were used in a bioenergetics model (Hewett & Johnson 1992) to estimate consumption by age-2 and older piscivores (Johnson *et al.* 1992). An access point creel survey provided estimates of fishing effort directed at walleyes, and walleye angler catch rates and harvest (Johnson and Staggs 1992).

4. Results

Larval walleyes were extremely rare during the study. Extensive ichthyoplankton sampling during 1987–1993 captured young walleyes only in 1989, when 19 walleyes 10–19 mm *TL* were captured in 36 daytime purse seine hauls (Lars Rudstam, personal communication). Catch rates dropped from 1.1 fish/haul on May 31 to 0.6 fish/haul on June 8 to 0.2 fish/haul on June 12. Estimated abundance of larval walleyes on June 12, 1989 was 141 795 larvae or 35.6 larvae/ha. Assuming these fish arose from fry stocking, survival to June 12 was 0.7%. No larval walleyes were captured in years when fry were not stocked.

Unbiased mark-recapture population estimates were required to evaluate survival of stocked fingerlings. Variance of population estimates of walleyes ≤ 278 mm were high owing to small recapture samples. However, spring abundances were always smaller than estimates from the preceding fall, and in four of the six cases the difference was statistically significant at p < 0.01 (Table 2).

Survival of stocked fingerlings to October (Table 3) was variable (range = 0.2-5.5%, mean = 2.5%), and did not appear to be related to stocking density. Highest survival occurred in 1991, a low density stocking year, and the lowest survival occurred in another low density year (1990). The second highest survival rate was observed in 1987 when the highest number of fingerlings was stocked. We estimated the survival of the 1986 year-class to be 10.4% from numbers stocked and an abundance estimate in spring 1987; however, we did not sample during 1986 and can not be certain no natural reproduction occurred

Table 1. The number, dates, and size of larval (fry) and fingerling (fgl) walleyes were stocked into Lake Mendota, and mean lake temperature at stocking. Mean length of fry is approximate based on time since hatching (Colby *et al.* 1979). Stocking evaluation began in spring 1987.

| Year | Stage | Number stocked | Density (number per ha) | Median stocking date | Range of stocking dates | Mean length (mm) | Mean lake temperature (°C) |
|------|-------|----------------------------|-------------------------------|----------------------------|-------------------------------|------------------------|----------------------------------|
| 1985 | fgl | 106 200 | 26.7 | Jun 13 | _ | 53.3 | 19.4 |
| 1986 | fgl | 57 662 | 14.5 | Jun 16 | Jun 13–Jul 3 | 76.2 | 21.7 |
| 1987 | fry | 20.1×10^{6} | 5 046.4 | Apr 26 | Apr 24–May 5 | 7.0 | 8.9 |
| | fgl | 647 540 | 162.6 | Jun 23 | Jun 8–Jul 9 | 52.2 | 25.6 |
| 1988 | fry | $26.9	imes10^{6}$ | 6 753.7 | May 9 | May 5–May 10 | 7.0 | 13.3 |
| | fgl | 500 986 | 125.8 | Jun 29 | Jun 5–Jul 18 | 59.2 | 24.4 |
| 1989 | fry | $20.0	imes10^{6}$ | 5 021.3 | May 15 | May 1–May 18 | 7.0 | 14.4 |
| | fgl | 500 038 | 125.5 | Jun 28 | Jun 27–Jul 3 | 48.3 | 26.1 |
| 1990 | fgl | 296 175 | 74.4 | Jul 4 | Jun 22–Jul 5 | 44.8 | 23.9 |
| 1991 | fgl | 250 079 | 62.8 | Jun 12 | Jun 11–Jun 25 | 53.8 | 25.6 |
| 1992 | fgl | 251 000 | 63.0 | Jun 11 | Jun 5–Jun 12 | 38.0 | 23.9 |
| | fry | $\Sigma = 67.0 	imes 10^6$ | | | Apr 24–May 18 | | mean = 12.2 |
| | fgl | $\Sigma = 2.61 	imes 10^6$ | | | Jun 5–Jul 18 | | mean = 23.8 |



Fig. 1. Survival rate (\log_{10} scale) of fingerling walleyes from stocking to age-1 as a function of (A) predator biomass (kg/ha of walleye \geq age-3 and northern pike \geq age-2), (B) prey abundance index (mean July–August catch per mini-fyke net set), (C) mean length of age-0 walleye in October, and (D) mean length of walleye fingerlings at stocking.

in 1986. The percentage of walleyes surviving to age-1 (May) during the study years varied (range = 0.04–3.8%, mean = 1.1%), but declined steadily during 1987–1990. Survival to age-1 was highest for the 1991 year class but was low (0.1%) for the 1992 year class. First year survival (log*S*) appeared to be related to predator (walleye and northern pike > 279mm) biomass (Pearson's r = -0.74), index of prey year class strength (r = 0.74), and the mean length of the cohort at stocking (r = 0.70). However, the number of years of data was low ($n \le 7$)

and correlation coefficients were not significant (p > 0.05; Fig. 1). Within the range of sizes observed in 1987–1992 (137–170 mm) survival did not appear to be related to average length of the cohort in fall (r = 0.16, p = 0.768).

Survival to fall was not a good indicator of stocking success because overwinter survival was unrelated to YOY survival (r = 0.28, p > 0.5). First winter mortality was highest for the 1989 year class (96%), was about 80% for 1988 and 1990 year classes, and was about 35% for 1987, 1991, 1992

yearclasses. Size distributions in fall and spring suggested that overwinter mortality was selective for smaller members of a year class (Fig. 2). Mean length of cohorts in their second spring was higher than for the same cohort the previous fall in five of six years (Fig. 2). Growth could not account for the shift in size distributions from fall to spring. Maximum overwinter growth rates, assuming unlimited food availability, accounted for an average of 37% of the increase in mean length of stocked cohorts. The majority of the overwinter size increase is presumably due to higher mortality of smaller members of each cohort. During April 15-June 15, 1989 (the only period with sufficient data to model) cannibalism and predation by northern pike accounted for 49% (205 kg) of the estimated overwinter loss in biomass (416 kg) of walleyes < 229 mm TL.

Because first year survival appeared to be sizedependent we were interested in factors affecting first year growth. On average, walleyes < 152 mm *TL* were YOY in fall and age-1 in spring (all years and seasons combined; Fig. 3). About 97% of 152–174 mm fish were YOY in fall and age-1 in spring and 97% of 229–253 mm were age-1 in fall and age-2 in spring. The 1991 year class had the largest mean length in October (170 mm); the 1988 year class was smallest in October (137 mm). First summer growth appeared to be affected by abiotic and biotic factors. Growth generally increased with length of the growing season (number of days $\geq 10^{\circ}$ C) and prey abundance, but the two factors varied inversely causing univariate correlations to be weak (Fig. 4). The mean length of YOY perch exceeded the maximum size YOY walleye can consume by 5–20 mm throughout the first growing season in all years (Fig. 5). This suggests that the proportion of yellow perch cohorts vulnerable to YOY walleye predation was low. There was overlap between mean length of bluegill cohorts and walleye maximum prey size at the start of each year, but by mid-August bluegill growth reduced their size vulnerability to young walleyes (Fig. 5).

Cost is an important consideration in any stocking program. Our estimate of production costs for the entire stocking program totaled approximately \$164 000 (1995 US\$, exclusive of evaluation costs) during 1987-1992. Given observed survival rates to age 1, the cost per age 1 fish contributed was about \$6 but ranged annually from \$1.78 to \$173.85/fish. The cost per recruit to the fishery is undoubtedly much higher due to mortality after age 1. Angler exploitation rates were high in 1988-90 (Johnson & Staggs 1992, Vogelsang et al. 1993), but catchable walleye (TL > 278 mm) density and biomass increased in response to the stocking program from 1.71 fish/ ha (S.E.: 1.17-2.25) and 1.24 kg/ha (0.96-1.52) in 1987 to 3.80 fish/ha (2.63-4.97) and 4.74 kg/ha (3.77-5.71) in 1993.

Table 2. Mark-recapture population estimates (Chapman's Petersen estimator) of seven length classes of walleyes sampled in Lake Mendota during spring (SP) and fall (FA) 1987–1993. Variance of the estimate is $V(\hat{N})$, and 95% confidence limits on the estimate are computed from $\pm 1.96\sqrt{V(\hat{N})}$. The hypothesis that a fall estimate was greater than spring was tested with a *z*-test; *p* is the one-tailed probability associated with the computed *z*-value.

| | | Ab | undance | per Leng | th Class | (mm) | | | | | |
|--------|-------|-------|---------|----------|----------|--------|-------|-----------|---------|--------------------------|-------------------|
| Period | 102 | 127 | 152 | 178 | 203 | 229 | 254 | \hat{N} | p | <i>V</i> (\hat{N}) 9 | 95 % <i>C.L</i> . |
| SP87 | 0 | 86 | 968 | 3 413 | 1 648 | 128 | 505 | 6 748 | | 2 196 612 | 2 905 |
| FA87 | 1 645 | 5 874 | 8 531 | 3 851 | 610 | 196 | 548 | 21 255 | 0.250 | 11 372 181 | 6 610 |
| SP88 | 938 | 1 487 | 4 238 | 5 594 | 2 263 | 581 | 485 | 15 586 | | 58 988 111 | 15 054 |
| FA88 | 3 601 | 7 944 | 4 344 | 1 279 | 4 432 | 7 566 | 3 944 | 33 110 | 0.004 | 27 634 329 | 10 303 |
| SP89 | 38 | 976 | 1 579 | 1 125 | 1 615 | 3 533 | 4 722 | 13 589 | | 21 503 186 | 9 089 |
| FA89 | 134 | 4 274 | 5 582 | 1 095 | 1 660 | 2 508 | 2 384 | 17 637 | < 0.001 | 11 133 137 | 6 540 |
| SP90 | 0 | 23 | 148 | 311 | 422 | 1 457 | 2 268 | 4 629 | | 2 469 529 | 3 080 |
| FA90 | 0 | 16 | 270 | 794 | 2 349 | 2 349 | 2 159 | 7 937 | 0.123 | 2 349 546 | 3 004 |
| SP91 | 0 | 10 | 167 | 491 | 1 453 | 1 453 | 1 334 | 4 908 | | 4 488 282 | 4 152 |
| FA91 | 16 | 381 | 4 518 | 14 373 | 7 165 | 381 | 16 | 26 850 | 0.010 | 13 379 546 | 7 169 |
| SP92 | 0 | 111 | 879 | 5 914 | 5 179 | 815 | 64 | 12 962 | | 22 851 828 | 9 370 |
| FA92 | 0 | 296 | 296 | 613 | 11 717 | 11 366 | 1 907 | 26 195 | < 0.001 | 9 672 054 | 6 096 |
| SP93 | 0 | 143 | 143 | 295 | 5 631 | 2 283 | 383 | 8 877 | | 2 440 328 | 3 062 |
| FA93 | 0 | 0 | 0 | 66 | 471 | 2 829 | 2 844 | 6 210 | | 5 738 040 | 4 695 |



Fig. 2. Size-frequency (estimated abundance) distributions of stocked young-of-year (shaded) and age-1 (open) walleyes by 51-mm size classes during six years; survival rates (percentages) to fall and spring and mean length of the cohorts in fall and spring are shown below the years.



Fig. 3. Proportions of Lake Mendota walleyes in three age-classes (corrected for population length-frequency) by size class, based on scale sampling in fall and spring, 1987–1993.

5. Discussion

Based on stocking records and age composition at the start of the study, we know that natural recruit-

Table 3. Summary of survival rate (S) estimates for walleye fingerlings stocked in Lake Mendota. Age-0 estimates were computed in fall as number in fall divided by number stocked. Age-1 estimates were computed as the number remaining in the following spring divided by the number stocked the previous year. Abundance data were not available in fall 1986. *S.E.*(*S*) is the standard error of the estimated survival rate.

| Year-class | Age | (%) | S.E.(S) |
|------------|-------|-------|---------|
| 1986 | age-0 | _ | |
| | age-1 | 10.40 | 2.28 |
| 1987 | age-0 | 3.18 | 0.50 |
| | age-1 | 2.02 | 1.00 |
| 1988 | age-0 | 3.64 | 0.58 |
| | age-1 | 0.69 | 0.23 |
| 1989 | age-0 | 2.17 | 0.41 |
| | age-1 | 0.10 | 0.03 |
| 1990 | age-0 | 0.20 | 0.04 |
| | age-1 | 0.04 | 0.02 |
| 1991 | age-0 | 5.53 | 0.75 |
| | age-1 | 3.78 | 1.40 |
| 1992 | age-0 | 0.24 | 0.03 |
| | age-1 | 0.15 | 0.03 |



Fig. 4. Mean length of a stocked walleye cohort in fall (October) as a function of (A) length of growing season (number of days with lake temperature $> 10^{\circ}$ C), and (B) prey abundance index (mean July–August catch per mini-fyke net set), showing years of occurrence.

ment of walleyes is possible in Lake Mendota; however, it appears to be a rare event (Johnson *et al.* 1991, 1995). Using fecundity and hatching success data from an unusually extensive dataset on Oneida Lake, New York, USA (Forney 1976) we estimated that the Lake Mendota walleye population could produce about 17 larvae/ha in 1987 and about 15 larvae/ha in 1989 (Johnson *et al.* 1995). Even if our calculations underestimate potential fry production by an order of magnitude or more, reproductive potential of the Mendota walleye population appeared to be minimal during the late 1980s. In contrast, we stocked about 5 600 larvae/ha/yr in 1987–1989. Still,



Fig. 5. Growth trajectories of young-of-year (A) bluegill and (B) yellow perch during 1987–1992 (solid lines), and the maximum ingestible prey size (dotted line) a young-of-year walleye could consume (Madenjian *et al.* 1991) based on average fingerling growth during 1987–1992.

only a small number of larvae were detected in 1989, and none in any other year, indicating that both natural reproduction and survival of stocked fry was negligible during the study. One of the justifications for the stocking program was to build walleye spawner biomass sufficiently to allow natural reproduction to occur. Walleye biomass was highest in 1993 and no walleye were stocked, but no YOY walleye were observed. Several more years of monitoring the enhanced population in the absence of stocking will be needed to evaluate this objective.

Survival of the fingerlings stocked during this study ranged three orders of magnitude. Survival to age-1 was not predicted by survival to the first fall because overwinter survival was occasionally high. This suggests that: 1) the first winter can be an important survival stanza in the recruitment of walleyes, and 2) stocking evaluations should extend beyond the first fall. Survival was not density-dependent suggesting that intraspecific competition was probably not an important regulatory force. Predation did appear to be important. The negative association of survival and larger piscivore biomass, and positive association with prey abudance suggest that cannibalism and predation were important. We speculate that as the stocking program progressed predator biomass and their consumption of young walleye increased, reducing survival of subsequent stockings. Large prev year classes may have improved survival by buffering walleyes from intraguild predation, a common phenomenon in Oneida Lake (Chevalier 1973, Forney 1976) and noted for pikeperch in the Netherlands (Van Densen & Grimm 1988). These hypotheses are supported by estimates of predator consumption during spring 1989 which showed that about half of the observed overwinter loss in fingerling biomass could be accounted for by predation by previously stocked walleye and northern pike. Native populations of small- and largemouth bass, white bass, and adult yellow perch also consumed young walleye (B. Johnson, personal observation) but this predation could not be quantified.

Predation in fishes is a size-structured interaction (Stein et al. 1988) and smaller members of cohorts are routinely the most vulnerable to predation (Chevalier 1973, Carline et al. 1986, Wahl & Stein 1989). Further, large size going into the first winter confers survival advantages (Forney 1976, Wahl et al. 1995). Thus, it is reasonable to expect that factors which improve first year growth may reduce predatory mortality and increase recruitment to age-1. Average midsummer surface temperatures in Lake Mendota are close to the juvenile walleye's optimum for growth with unlimited food (26°C; Hokanson & Koenst 1986), and the growing season (lake temperatures $> 10^{\circ}$ C) is usually about 180 d long. Growth of stocked YOY walleye in Lake Mendota was comparable to growth in several midwestern U.S. lakes cited by Colby et al. (1979).

While Lake Mendota and Oneida Lake differ in some regards, e.g., the lack of thermal stratification in Oneida, much of our understanding of factors affecting growth and survival of young walleye come from the extensive, careful work of John Forney and others on Oneida Lake. Mean length of Mendota

walleyes in fall (151 mm) was similar to that observed over seven years in Oneida Lake (146 mm; Forney 1966). While first summer growth of walleye in Mendota is similar to Oneida, YOY yellow perch grow about 50% faster in Mendota than in Oneida. Consequently, most Lake Mendota YOY yellow perch are too large to be preyed on by young walleyes, which are relegated to feeding on alternate prey, mainly YOY bluegills. Bluegills also grow quickly in Lake Mendota, with the average YOY bluegill outgrowing vulnerability to YOY walleye predation by late summer. Even when small prey individuals are abundant, growth and survival of YOY walleye is poorer when centrarchids dominate the prey base than when more fusiform prey are available (Beyerle 1978, Santucci & Wahl 1993).

It can be difficult to interpret predator-prey dynamics from aggregate measures such as predator and prey mean length, and prey catch per unit effort. Individual-based models offer the means to improve resolution in field predation studies. An individualbased model of YOY walleye-prey interactions (Madenjian et al. 1991) suggested that at Mendota temperatures YOY walleyes could grow to a considerably larger size by their first fall if a higher proportion of the prey population were of ingestible size. Simulations predicted that stocking strategies that initially increased walleye size relative to their prey (stocking larger or earlier) allowed walleyes to grow faster during the first summer of life, which then presumably improves their chances for surviving to age-1. These predictions remain to be scientifically tested. While predation appears to have been an important factor influencing stocking success, there is still considerable uncertainty regarding the dominant mechanisms controlling walleye fingerling survival in Lake Mendota and elsewhere.

Many billions of walleye have been stocked by U.S. management agencies (Conover 1986) since Laarman (1978) reviewed the history of walleye stocking and concluded that while some gross patterns exist, variability from unknown sources was high. Despite considerable research into the problem, predicting the success of a given walleye stocking remains nearly impossible (Ellison & Franzin 1992, Larscheid 1995). We are not aware of a comprehensive assessment of pikeperch stocking programs, and thus are reluctant to generalize beyond *Stizostedion vitreum*. But for walleye, there appears to be no concensus on the life stage or density to stock-success of fry, small and large fingerling stockings vary wildly across systems and through time.

This is not to say that we know little about the factors important to walleye recruitment via stocking. On the contrary, various studies have demonstrated the importance of abiotic factors such as water temperature (Paragamian & Kingery 1992, Santucci & Wahl 1993) and chemical or physical characteristics (Bennett & McArthur 1990, Fielder 1992); walleve condition (McWilliams & Larscheid 1992, Mitzner 1992); handling and transport stress (LaJeone et al. 1992, Mitzner 1992, Paragamian & Kingery 1992); prey community size structure, abundance, and species composition (Beyerle 1978, Madenjian et al. 1991, Santucci and Wahl 1993); and predation (Santucci & Wahl 1993). Clearly, many of these factors interact strongly. For example, temperature of the recipient system affects stocking stress and then presumably susceptibility to predation, predator consumption rates, and growth rates of young walleye and their prey. High prey recruitment may improve prey encounter rates for young walleye allowing them to grow out of a vulnerable size more quickly and buffering them from predation by larger piscivores.

We believe the unpredictability of walleye stocking arises because 1) synergistic effects are complex and difficult to study, and hence, poorly understood, 2) the scale of our measurements may not match the scale of important interactions in the environment, and 3) many apparently influential factors are beyond the biologist's control and are themselves inherently unpredictable (e.g. seasonal climate, prey recruitment). As was concluded by Ellison and Franzin (1992), we recommend continued research into processes controlling walleye recruitment by stocking. This mechanistic approach ought to be more productive than trial and error evaluations because it contributes to a theoretical framework (e.g. Wahl et al. 1995) rather than relying on the accumulation of experience to form an heretofore elusive underlying pattern. Studies should take care to control for the potentially confounding effects of variable fish condition and thermal and handling stress and focus on ecological processes such as competition and predation. Stocking evaluations should also be of sufficient duration to encompass important survival stanzas including immediate post-stocking, survival to the first fall, and overwinter survival. Experimental management, in which stocking events are designed and implemented explicitly to learn about the recruitment process should be more informative than the traditional approach where evaluation is subordinate to fishery objectives and production system considerations.

In the face of high uncertainty regarding stocking outcomes, stocking policy should be adaptive (Walters 1986). Biologists should have contingency plans to respond to unpredictable stocking results. These might include flexibility in annual stocking quotas and harvest regulations. High variance and low mean survival rates suggest that inflexible policies such as every other year stocking will be slow to enhance walleye populations. Pulsed management, whereby stocking is repeated until a target year class strength is achieved, followed by no stocking for a period of years may be an effective strategy when cannibalism diminishes the success of consecutive stockings.

6. Conclusions

Although our study is unreplicated, as are most large-scale enhancement programs, there are some conclusions to be drawn. We stocked a total of 6.7 $\times 10^7$ walleye fry which we believe was completely ineffective. Fingerling survival to age-1 was variable but always $\leq 10\%$. Survival to fall did not predict subsequent survival to age-1. Thus, we conclude that stocking success should be evaluated no sooner than the cohort's second spring (age-1) in systems where overwinter mortality could be high and unrelated to first summer survival rate. No single factor could be isolated as controlling fingerling stocking success, rather, synergistic effects of abiotic factors, prey availability and predation appeared to be important. The intensity of predatory mortality may have been regulated by unpredictable factors such as length of the growing season and prey year class strength. Difficulty in predicting stocking success suggests that stocking policies should be adaptive.

We stocked more walleye fingerlings into a single lake each year than the total annual hatchery production of at least 40 U.S. states (Conover 1986). Despite our best efforts to dramatically enhance the walleye population, we achieved slightly more than a doubling of the 1987 catchable walleye abundance, and a 3.8 fold increase in biomass in seven years. However, the success of the stocking program might also be judged from a sport fishery standpoint. In response to the highly publicized stocking program and increasing catch rates fishing effort directed at walleyes increased about 5-fold during the study (Johnson & Carpenter 1994). As a result, exploitation of walleyes was high (> 40%) in some years. Thus, in addition to the apparently high predatory mortality of fingerlings, sportfishing constrained our ability to increase adult walleye biomass with stocking.

As most fishery professionals well-know, stocking is not a panacea. This study reinforces the notion that anglers and fishery managers alike should be prepared for modest gains in population size from even the most ambitious of stocking programs. While we believe the improvements in the walleye fishery justified the cost of this stocking effort, more realistic expectations of what can be accomplished by stocking will help the public and agencies better evaluate management strategies and allocate increasingly scarce resource management funds appropriately.

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