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Dynamics of an experimentally exploited walleye population: sustainable yield estimate

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Savanne Lake, Ontario is one of five lakes that have been closed to public fishing since 1969 to study the effects of exploitation on walleye. The study has four phases: pre-harvest (1972–79), harvest phase I (1980–85) simulating an angling fishery at an annual mean harvest level approximating 1.78 kg/ha, as recommended by the Ontario Provincial Guidelines, harvest phase II (1986–89) where the recommended mean harvest level was exceeded (1.95 kg/ha) in conjunction with a protected slot of 45 to 55 cm total length, and a recovery phase 1990 to the present. Prior to exploitation the adult walleye population density was averaging about 15/ha, then reduced to 10.5/ha in phase I, and 9.1/ha after phase II. Production and biomass also decreased. There was little change in the mean age of the population, declining slightly from 7 to 6.2 years. There were no significant changes in growth rates but condition factor and fecundity increased. Strong year classes were evident about every 4 to 6 years. About 78 percent of the strongest year-classes occurred in even-numbered years. We hypothesized that the pulse production of the mayfly (*Hexagenia limbata*), a major food item for walleye in Savanne, in even-numbered years enhances year-class strength of walleye. Year-class strength was positively correlated to young-of-the-year (YOY) abundance. The protected slot appeared to be ineffective in protecting the walleye biomass and production. Northern pike abundance was also reduced, although no cause-effect relationship has been established, considering that northern pike were not harvested. We suggest that an annual harvest of about 1.0 kg/ha, which is below the annual production of 1.39 kg/ha calculated for the unexploited population, can be sustained while providing a fishing experience approximating a remote unexploited lake. Harvest levels exceeding those recommended by our guidelines can quickly reduce population density, biomass and production, and have de-stabilizing effects on the community. This study shows that fish populations in small unproductive lakes can be impacted very quickly when harvest exceeds allowable levels. This study reaffirms the importance of long-term research to assess impacts of regulations on fish populations.

1. Introduction

In cooperation with the Department of Biology, Lakehead University controlled exploitation studies are being conducted on two walleye (*Stizostedion vitreum*) populations: a pulse-fishing perturbation in Henderson Lake (151 ha) and a pressing-type exploitation perturbation in Savanne Lake (364 ha). Results of the pulse experiment on Henderson Lake were reported by Reid and Momot (1985), and studies monitoring their rate of recovery are in progress. Here we describe the impact of the longer term press-type harvest on the walleye population in Savanne Lake.

Our purpose was to harvest walleye in Savanne Lake at a harvest level recommended by our Provincial guidelines, monitor fish populations and community changes, and test the utility of various population and angling quality indices. Thereafter, repeatedly increase the harvest in incremental steps and monitor the effects over time. This study involves four phases: a pre-harvest phase (1972–79), harvest phase I (1980–85) at a harvest level of 1.78 kg/ha, recommended by the Ontario Provincial Guidelines (OMNR 1982), followed by harvest phase II (1986–89) consisting of increased harvest (1.95 kg/ha), with a protected slot from 45 to 55 cm, and a recovery phase (1990 to present).

2. Study area

Savanne Lake is a shallow, unstratified, mesotrophic lake in Ontario's boreal forest, located 128 km northwest of Thunder Bay, Ontario. Savanne has a surface area of 364.29 ha, mean depth of 2.57 m and TDS of 50 mg/l. The water is typical of walleye lakes in the boreal forest, tea-coloured with a mean Secchi reading of only 1.5 m. In 1969, the Ministry of Natural Resources designated Savanne, and four other nearby lakes, as provincial fish sanctuaries to facilitate population dynamics studies of walleye and associated species. Savanne Lake supports a percid community typical of boreal forest lakes in northern Ontario. Walleye and northern pike (*Esox lucius*) are the top predators. Other species present include yellow perch (*Perca flavescens*), white sucker (*Catostomus commersoni*), burbot (*Lota lota*), cisco (*Coregonus artedii*) and trout-perch (*Percopsis omiscomaycus*). Incidental catches of blacknose shiners (*Notropis heterodon*), johnny (*Etheostoma nigrum*) and Iowa (*Etheostoma exile*) darters have also been made.

The low productivity of Savanne and other similar boreal lakes, makes the walleye population highly vulnerable even at low exploitation levels. Mosindy *et al*. (1987) found that 43 and 50% of the annual walleye and northern pike production was removed by angling at low effort (1.24 angler-hour/hectare). They concluded that potential angling yield from small boreal lakes is low. Thus, yield quotas and restrictions on angling effort are needed to conserve this stock of old, slow-growing fish.

Walleye production in Savanne Lake has been closely linked to mayfly (*Hexagenia limbata*) production. Mayfly nymphs are a major seasonal component among small prey items, constituting up to 76% of the total food volume of northern pike and up to 12% of the total food volume of walleye during the late and early spring (Mosindy 1980). In Savanne Lake (*Hexagenia limbata*) has a two-year life cycle with a larger cohort emerging in alternate years (Riklik & Momot 1982). These authors determined the mean biomass (*B*) varied from 0.36 to 2.98 g/m^2, wet weight, while mean numbers varied from 34 to 121/m^2. Annual production ranged from 4.78 to 5.59 g/m^2/yr, or about 48 to 56 kg/ha/yr.

Young-of-the-year walleye were found to be more abundant in even-numbered years than in odd-numbered years in Savanne Lake and were related to (*Hexagenia limbata*) emergences (Ritchie & Colby 1988). Adult walleye from even-numbered year classes are more abundant than those from odd-numbered year classes. It was hypothesized that pulse production of (*Hexagenia limbata*) in even-numbered years positively affects walleye recruitment by enhancing egg production by adult walleye and buffering young of the year walleye against predation and cannibalism. Baccante and Reid (1988) found the walleye populations in both Savanne and Henderson lakes had statistically significant annual increases in fecundity following the start of exploitation. Yearly fluctuations in fecundity, especially older fish, were noted in both lakes; high values occurring in even-numbered years and low values in odd-numbered years. They also hypothesized that the fecundity changes reflected food availability, particularly alternate-year fluctuations in the abundance of these large mayflies.

3. Methods

Annual fish population sizes were estimated using the Schumacher-Eschmeyer (1943) method, as described in Ricker (1975). The estimates were made during spawning season when adult walleye, white sucker and northern pike were most vulnerable to our trapnets. We used primarily 1.8 meter (6 feet) trapnets, but a few 2.4 meter (8 feet) trapnets were also used prior to 1980. Trapnets were set on known spawning shoals, with the intention of catching and marking as many fish as possible in a short period of time. Nets were also moved to new locations around the lake as the proportion of marked fish in each net approached 40 to 50 percent to avoid recapturing the more sedentary fish, and allow marked fish to mix among the population. Condition factors (*K*) were calculated using: $K = W/L^3$, where *W* and *L* are weight and length. Differences in condition factors were tested using the non-parametric Wilson Rank Sum test for two independent samples (Snedecor & Cochran 1980).

Total lengths and weights were measured in millimeters and grams. Materials for age determinations were collected using standard procedures. During the initial phases of the study, various aging materials were used for comparative purposes. Scales and opercles were used for walleye, scales and cleithra for northern pike. In later years, only scales were used. Age distributions were determined using age-length key (Ketchen 1949), by 10 millimeter intervals. Fish were marked by clipping fin rays or part of a fin using a different clip each year.

Index gillnetting was also used periodically to monitor changes in relative abundance of all fish species. Monofilament gillnets consisting of nine, 17-meter long panels, each panel with the following mesh sizes: 25, 38, 51, 64, 76, 89, 102, 114 and 128 millimeters. The nets were placed in all type of habitats within the lake, and the annual effort for the gillnets averaged 0.5 hours/hectare.

Estimates of mortality and survival rates were made for walleye using the method outlined by Robson and Chapman (1961). The theory of catch curve analysis is that the drop in frequency from one age group to the next, reflects the combined effect of mortality and the difference in initial year-class strength for the two groups. The age of walleye fully recruited to trapnets was estimated from the modal age of catch curves. Ricker's (1946) method was used to determine annual production (*P*) and biomass (*B*), from which *P*/*B* ratios were calculated.

From 1972–79 (pre-harvest phase) population estimates were made excluding 1975 and 1978 and population dynamics were described for walleye and northern pike. From 1980 to 1985 (harvest phase I) walleye were selectively removed from Savanne Lake using a predetermined size frequency distribution which approximates that found during the experimental angling creel census conducted during the pre-harvest phase. The harvest level averaged 1.74 kg/ha/yr, which approximates the annual production of 1.78 kg/ha. Note that the harvest of walleye smaller than 30 cm is much higher then anticipated because it includes incidental gill net catches during a yellow perch study (Ritchie 1984).

During harvest phase II (1986–89), a protected slot regulation (45 to 55 cm) was established and the harvest exceeded the recommended level. This pressure resulted in a drastic reduction of the stock vulnerable to our gear and the harvest was discontinued. Beginning in 1990, we began monitoring the recovery of the depressed population to its present abundance.

4. Results

Schumacher-Eschmeyer population estimates of walleye from spring trapnetting indicate that the number of adult fish vulnerable to the gear remained fairly constant during the pre-harvest phase (1972–79). The estimated numbers of adult walleye vulnerable to our trapnets varied between 4 415 and 6 508 during the pre-harvest phase (Fig. 1). These estimates are equivalent to adult densities of 12.1 and 17.9 walleye per hectare, with a mean value of 14.9 (Table 1).

In 1980 we began the first phase of exploitation.

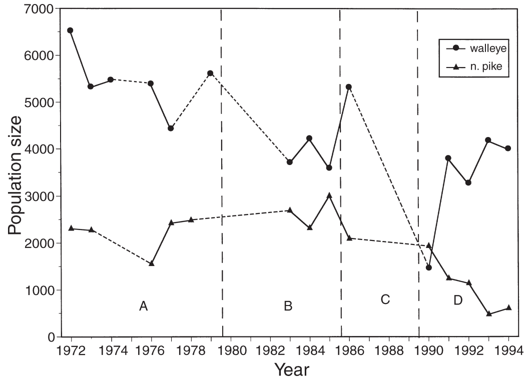

Fig. 1. Schumacher-Eschmeyer population estimates of walleye vulnerable to trapnets in Savanne Lake from 1972 to 1994. The pre-harvest, harvest phases I and II, and recovery phases are designated as A, B, C, D respectively. Dotted lines interpolate between years when no estimates were made.

The harvest during this initial phase (1980–1985) totalled 5 479 walleye (3 807 kg) and averaged 1.74 kg/ha/yr, ranging from 1.10 to 2.40 kg/ha/yr (Table 2). No population estimates were carried out until 1983. From 1983 to 1986 estimates indicated a gradual decline in adults and then an upturn in 1986 as the more abundant recruits entered the fishery. Prior to this upturn in abundance the population was reduced from 5 595 in 1979 to 3 576 in 1985 or from 15.4 to 9.8 fish/ha respectively, a drop of about 36 percent over a six year period. Exploitation rates determined from marked and recaptured fish varied between 11.9 and 16.2%, averaging 14.3%.

In the second harvest phase (1986 to 1989) the mean biomass harvested was increased to 1.95 kg/ha/yr, with a protected slot between 45 and 55 cm total length.

Table 1. Average trapnet *CUE* (fish/hour), and adult density (numbers/ha) as estimated by population estimates for walleye and northern pike in Savanne Lake, Ontario, during four study phases.

	CUE		Adult Density (indiv./ha)	
Years	Walleye	Pike	Walleye	Pike
1972–79	1.60	0.91	14.9	6.1
1980–85	0.77	0.73	10.5	7.3
1986–89	0.33	0.47	*	*
1990–94	0.51	0.37	9.1	3.0

* insufficient population estimate data

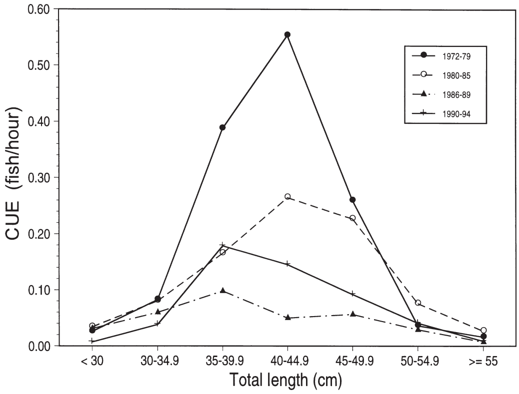

Fig. 2. Frequency distributions of trapnet *CUE* (fish/hour) by 5 cm length classes for Savanne Lake walleye during the study phases.

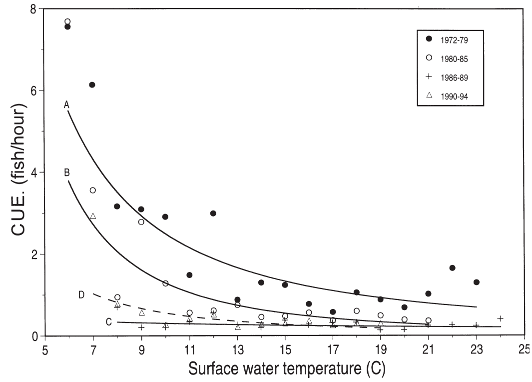

Fig. 3. *CUE* (fish/hour) from trapnets plotted against surface water temperatures (°C) for Savanne Lake walleye, for each of the four study phases. The average adult walleye densities during each phase were: 14.9/ha (line A), 10.5/ha (line B), ad 9.1/ha (line D). No density value is available for line C because of insufficient population estimates from 1986 to 1989.

The number of walleye removed was 4 655, for a total weight of 2 836 kg. (Table 2). During this phase no population estimates were made until 1990, when we discovered the population had been reduced to 1 455, a 73 percent reduction from 1986. However, we feel that the population size in 1990 was underestimated because of high variability in trapnet catches due to unfavourable weather conditions in the spring. We then discontinued the harvest and monitored the rate of recovery. The population slowly increased from 3 784 in 1991 to 3 990 in 1994. Exploitation rates during this phase were not calculated because of insufficient population estimates data, but we estimate they range between 17 and 20%. One-way ANOVA tests indicate that there are significant differences ($F_{2,12} = 9.16\ p < 0.01$) in population size among the three study periods.

Catch per unit of effort (*CUE*) values calculated as the number of walleye caught by trapnets per hour of fishing decreased for intermediate size groups and increased for smaller and larger fishes (Fig. 2) reflecting the size selective harvest. The *CUE* dropped from an average of 1.60 fish/hr during the pre- exploitation phase to 0.77 and 0.33 fish/hr during the two subsequent exploration phases. This decline was followed by an increase to 0.51 fish/hr during the 1990–94 recovery phase (Table 1). However, the pre-exploitation *CUE* is inflated by the high values in 1975 and 1979, years when the netting periods were much shorter than other years and effort was concentrated during the peak spawning, when temperatures were lower and catches were largest. We also observed that during spring trapnetting, water temperature influenced the catch rate. The *CUE*'s were highest (7–8 fish/hour) around 6°C, then declining sharply between 6 and 10°C, and then remained fairly stable. The *CUE* values for any given temperature are higher when adult density is also higher (Fig. 3).

Production and biomass estimates were made for the periods 1973–1976, 1983–1986, and 1990–1994

Table 2. Summary of walleye harvested from Savanne Lake, Ontario, during harvest phase I (1980–85) and harvest phase II (1986–89).

Year	Mean length (mm)	Mean weight (g)	Number removed	Biomass removed kg	kg/ha
1980	436	761	589	447	1.23
1981	373	560	1 459	872	2.40
1982	325	554	1 365	722	1.98
1983	412	805	497	400	1.10
1984	416	876	726	631	1.73
1985	411	872	843	735	2.02
		Totals	5 479	3 807	10.46
		Means	913	635	1.74
1986	401	703	1 230	865	2.38
1987	383	632	991	662	1.82
1988	357	499	1 065	568	1.56
1989	371	541	1 369	741	2.04
		Totals	4 655	2 836	7.80
		Means	1 164	709	1.95

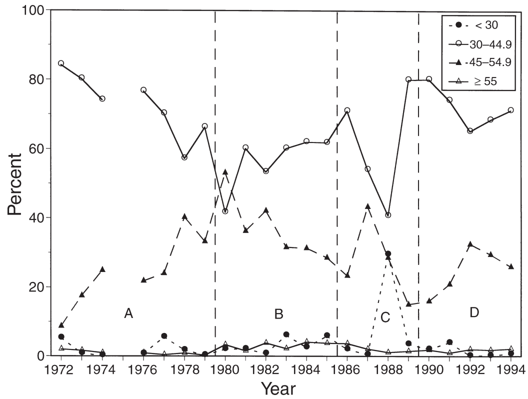

Fig. 4. Relative frequency (percent) of four different size categories of walleye caught by trapnets in Savanne Lake, Ontario, during the four study phases, as described in Fig. 1.

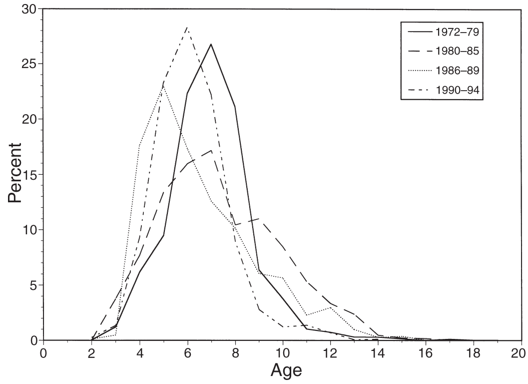

Fig. 5. Composite age distributions for walleye in Savanne Lake, Ontario, during four study phases.

using as similar a range of age groups as possible for comparative purposes. The average annual biomass of adult walleye (age 7 and older) vulnerable to our gear dropped from 7.34 kg/ha (1973–76) to 5.95 kg/ha (1983–1986), and during the 1990–94 period to 2.06 kg/ha (Table 3). The average annual production during the same three periods declined from 1.59 to 0.93 and then 0.48 kg/ha. Thus, during the study the biomass decreased about 72 percent and production 65 percent. The *P*/*B* ratio remained fairly constant because product and biomass decreased concurrently.

The size distribution of the catch changed from one which was more acutely modal having narrower width or size range prior to exploitation, to one having a wider size range with a lower and less acute mode during the initial harvest period. During the recovery period the mode began to rebound, reflecting increased adult densities (Fig. 2). Prior to exploitation, the relative abundance of walleye 45 to 54.9 cm in the trapnets increased steadily, while those 30 to 44.9 cm decreased in abundance. This was likely a result of the population getting older and more dense, in the absence of exploitation. During the first exploitation phase, the trend reversed and the relative abundance of 30 to 44.9 cm walleye increased, while 45 to 54.9 cm decreased (Fig. 4).

When the harvest level was increased, both size categories showed a decline in relative abundance, followed by a slow increase in the recovery phase. The peak in 1988 of walleye < 30 cm in length is due to a strong 1984 year class. The relative frequency of walleye ≥ 55 cm remained fairly stable throughout the duration of the study (Fig. 4).

The change in age distribution was similar to that observed for size. Pre-exploitation age distributions are characterized by a dominance of fewer age-classes, with a high mode as reflected by a plot of the mean numbers for each age group captured prior to and during exploitation (Fig. 5). During the initial exploitation phase the age distribution flattened out and the amplitude of the mode was reduced. The proportion of walleye 5 and younger and 9 and older increased, while the proportion of 6 to 8-year-old fish decreased (Fig. 5).

The composite age distribution for the pre-exploitation phase (1972–80) was dominated by ages 6, 7 and 8, which combined accounted for 70 percent of the age distribution in the catch. During six years

Table 3. Annual production, biomass, and *P*/*B* ratios estimates of adult walleye in Savanne Lake, Ontario, during the pre-harvest, harvest, and recovery phases.

Period of estimates	Age groups	Biomass (kg/ha)	Production (kg/ha)	*P*/*B* (kg/ha)
1973–1974	7–16	6.71	1.03	0.15
1974–1975	7–14	7.14	1.55	0.22
1975–1976	7–15	8.16	1.59	0.29
Means		7.33	1.39	0.22
1983–1984	7–14	6.34	0.61	0.10
1984–1985	7–14	6.00	0.56	0.09
1985–1986	7–15	5.52	1.63	0.29
Means		5.95	0.93	0.16
1990–1991	7–13	1.15	0.28	0.24
1991–1992	7–12	2.17	0.46	0.21
1992–1994	7–12	2.85	0.71	0.25
Means		2.06	0.48	0.23

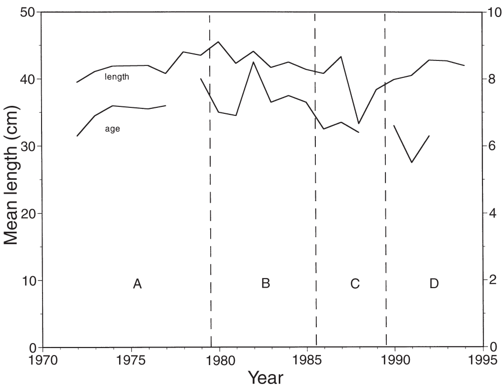

Fig. 6. Mean length and age for walleye in Savanne Lake, Ontario from 1972 to 1994. The four study phases are as described in Fig. 1.

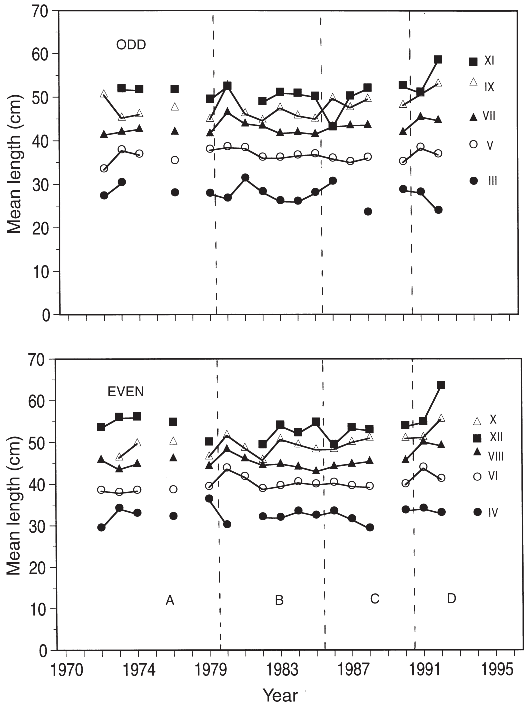

Fig. 7. Mean length at age for Savanne Lake walleye for each study phase as described in Fig. 1. Even and odd-numbered ages are separated in two plots for better clarity.

of exploitations (1980–85) those same age groups made up only 43 percent of the distributions within the catch. During the first years of exploitation phase there was a gradual decline in abundance of 7 to 9-year-old walleye in the catch, while walleye younger than age 6 and older than age 10 increased (Fig. 5).

The mean age of the catch varied similarly with the mean length of the catch (Fig. 6). The mean age increased gradually as the population became older prior to exploitation. The mean age and size declined as walleye were harvested (1980–85), further declining as the level of harvest increased above the recommended level. A gradual increase is evident since we stopped harvesting in 1990.

Estimates of survival fully recruited to trapnets ranged from 31 to 58 percent (mean = 47) during the pre-exploitation phase (1972–79), 56 to 76 percent (mean = 69) during the first exploitation phase (1980–85), and 64 to 72 (mean = 69) for the period 1986–89. Conversely, the mean total annual mortality decreased from 53 to 32, and then 31 percent for the same time periods. These results are artifacts due to flattening of the catch curve, and do not reflect the de-stabilizing effect of the rapid removal of walleye.

Growth rates for all age groups remained virtually unchanged throughout the study. Mean length at age for age groups 3 to 14 showed no significant changes during the study period (Fig. 7). Conversely, the condition factor (K), increased significantly ($p < 0.05$) in all age groups since exploitation began. The relative fecundity of walleye increased from 39 700 eggs/kg in 1980 to 43 200 eggs/kg in 1985 (Baccante & Reid 1988). Although no data on egg production is available for the pre-exploitation period (1972–80), the 1980 data was collected before harvest impact began, and likely represents pre-harvest fecundity.

The mean age to maturity for both male and female walleye did not change appreciably during the first harvest phase. The mean age to maturity for males ranged from 4.2 to 5.8 years of age and for females from 6.0 to 8.4 years. No statistical significance was associated with these age to maturity values because of insufficient samples. However, data from trap net catches during spawning indicate the size of ripe fish has not changed. Since there was no change in growth rates, we assume that the age to maturity has not changed appreciably.

The number of walleye of each groups recruiting to our sampling gear generally reflected relative year-class strength. The largest year class to-date was the 1966 year-class which dominated the 1972, 73 and 74 catches as six, seven and eight-year-old fish, respectively. As a measure of relative year-class strength, we expressed all year classes as a fraction of the 1966 year class following the approach of Ritchie and Colby (1988), and varied from 1.00 to

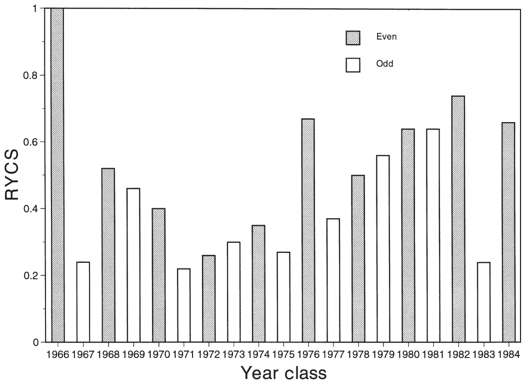

Fig. 8. Relative year-class strength (*RYCS*) of Savanne Lake walleye arranged from the strongest to the weakest.

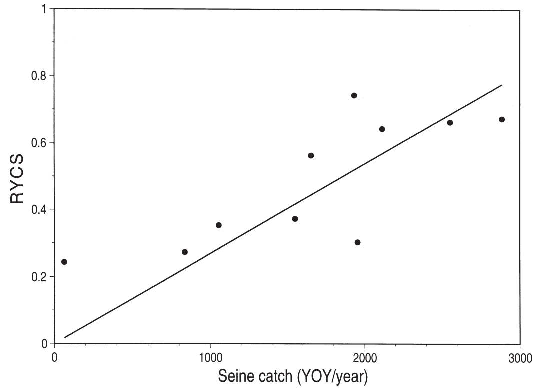

Fig. 9. Plot of relative year-class strength (*RYCS*) as determined from trapnets catches of adults, against seine catches of young-of-the-year (YOY) of walleye in Savanne Lake, Ontario.

0.22 for the 1966 and 1971 year-class respectively (Fig. 8). Strong year classes occur more frequently in even rather than odd years, as reported by Ritchie and Colby (1988). This difference between even and odd-numbered years was also observed by Baccante and Reid (1988) in their study of walleye fecundity. We hypothesize that the pulse production of the mayfly (*Hexagenia limbata*), a major food item for walleye in Savanne Lake in even-numbered years, enhances year-class strength of walleye. The high frequency of strong year classes also reflects low recruitment variability in the population.

The stronger even year classes reflected by adult fish recruiting to the gear is in agreement with YOY walleye abundance indices (Ritchie & Colby 1988) indicating that in Savanne Lake year-class strength is determined during their first summer of life. Further evidence of the importance of young-of-the-year (YOY) abundance in determining year-class strength is the strong positive correlation ($r = 0.77, p < 0.01$) between *RYCS* from trapnet catches of adult fish, and seine net catches of YOY walleye (Fig. 9).

The fish community in Savanne Lake was monitored by conducting population estimates, and by periodic experimental gillnets. Gillnet sampling in each of the four study phases show that before exploitation, walleye was relatively more abundant as measured by percent occurrence in the gillnets, making up about 49 percent of the catch by numbers (Fig. 10). Following the initial harvest of walleye, the percent composition of walleye in gillnets was reduced to 23.8% in 1985, and 21.6% in 1987 following increased harvest levels (Fig. 10). After harvesting was suspended in 1990, the relative abundance of walleye increased back to 48.2% in 1992.

Interestingly, over the same time period the relative abundance of cisco and yellow perch caught in experimental nets increased. Both are major food items for walleye in Savanne Lake, yellow perch being targeted by YOY and juvenile walleye, and cisco by adults. Relative abundance of cisco increased from 14 to 28 to 45% in 1976, 1985 and 1987, respectively. Cisco abundance then declined to 23 percent in 1992 following the increase in walleye abundance. Over the same time period, relative abundance of yellow perch went from 10 to 24 to 22, and finally 17% (Fig. 10). White sucker abundance in gillnet catches changed little during that time period. Population estimates of adult white suckers from our spring trapnetting are highly variable because of their relatively low vulnerability to the gear during spring sampling. Estimates from 1972 to 1994 indicate that the size of the adult sucker population vulnerable to our gear has ranged from 1 253 to 4 384, averaging about 2 100 fish.

The adult northern pike population as estimated from spring time trapnetting, had remained fairly stable throughout the study period, averaging about 2300 from 1972 to 1986 (range 1 553 to 3 002). From 1990 to 1994 the population then declined from 1936 to 475 in 1993, then up slightly to 604 in 1994 (Fig. 1). The relative abundance of northern pike in the gillnets also declined, reflecting the results of our population estimates. In 1976 and 1985 northern pike accounted for 14 and 19 percent of the gillnet catch, respectively, then declined to 5.8 percent in 1987 and 1992. The decline of the northern pike population is interesting and worthy of further study,

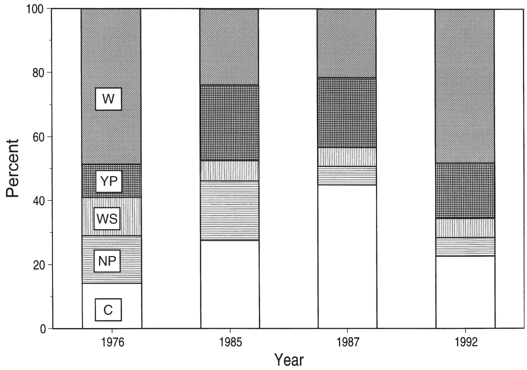

Fig. 10. Percent composition of fish species by numbers, from experimental gillnets in Savanne Lake, Ontario during sampling in 1976, 1985, 1987 and 1992. Species abbreviations are: W = walleye, YP = yellow perch, WS = white sucker, NP = northern pike, and C = cisco.

considering the pike have not been harvested, except for minimal numbers for food studies and incidental mortality from sampling gear.

5. Management implications

We believe a sustainable annual harvest for Savanne Lake is approximately 1.0 kg/ha and agrees with Adams and Olver (1977) sustainable yield recommendation of 1.00 to 1.25 kg/ha for Northern Ontario lakes with relatively low productivity. Our agency's guidelines yield of 1.78 kg/ha exceeded pre-harvest biomass production estimate of 1.39 kg/ha by 28 percent and harvests at this level resulted in alteration of the population's age structure, reductions in biomass, production, and standing crop of the walleye population. When additional fishing pressure was applied in exploitation phase II and walleye yields exceeded the recommended level, the walleye population was greatly reduced from 5 300 in 1986 to 1 455 in 1990 when we discontinued the annual harvest. The population has been recovering since 1990 but to date has not reached pre-harvest abundance (Fig. 1).

A review of our present and proposed harvest guidelines and biological characteristics of the Savanne walleye population (Table 4) suggest that an annual harvest of 1.0 kg/ha is sustainable. Although we have not proven that 1.78 kg/ha/yr is not sustainable after six years, we feel exceeding the estimated annual biomass production would cause the fishery to deteriorate over time. If a safety factor of 25% of pre-harvest biomass production was evoked, then a yield 1.04 kg/ha/yr (1.39 less 25%) should suffice and would be in agreement with the lower harvest recommendations in Table 4. In government jurisdictions where resources are not adequate for extensive monitoring of all fish stocks a conservative sustainable yield estimate is recommended. Using a financial analogy, for Savanne Lake a sustainable harvest of 1.0 kg/ha/yr should allow harvesting the interest without reducing the principle, and provide a fishing experience approximating a remote unexploited lake. Harvest exceeding 1.0 kg/ha/yr risks reducing the quality of the angling experience and if commercially harvested, would require the expense of additional monitoring.

Walleye recruitment in Savanne Lake is relatively constant, with the weakest year class recorded, the 1971 year-class being 22 percent of the largest (1966) year-class over a period of about 30 years. Age class distributions for Savanne walleye suggest that a strong year class occurs about every 4 to 6 years. This low recruitment variability ensures adequate compensation following harvest, if the population is allowed to rebuild. In lakes with higher recruitment variability, harvest levels need to be monitored more carefully.

Growth and maturity rates did not change noticeably during the first exploitation phase and would have been of little value as exploitation indices for this study. Although there is much supporting evidence in the literature showing compensatory growth as a result of increased exploitation (Kennedy 1948, Nikolsky 1963, Spangler *et al.* 1977, Healey 1978, Colby & Nepszy 1981, Muth & Wolfert 1986), this response does not always occur. Kempinger and Carline (1977) found that growth rates of walleye in Escanaba Lake, Wisconsin, did not change over a period of 15 years, despite four fold variations of adult densities over the same time period. These authors suggest that walleye were able to exploit alternate food sources.

Our results in Savanne Lake agree with Reid and Momot's (1985) finding in Henderson Lake that changes in growth as measured by length-at-age did not occur among older walleye but younger fish were responsive although in different ways. In Henderson Lake, the younger fish grew more rapidly whereas in Savanne Lake, the growth of age two walleye declined slightly. These differences in growth between Henderson and Savanne may be explained by differences in recruitment between the two lakes. In Henderson Lake, recruitment was poor and competition for food reduced where as in Savanne Lake recruitment and survival was good and competition for food among younger fish was more likely.

In contrast to growth which did not vary, except for age two walleye, we did observe a significant increase is the condition factor (*K*), for all age groups, following exploitation. Increases in values of *K* have been associated with improved feeding condition (Rose 1951, Arnold 1960). The increase in *K* in Savanne Lake, walleye may be due to a combination of increases in somatic and reproductive growth. Baccante and Reid (1988) found significant increases in fecundity of walleye following exploitation. Thus, increased fecundity likely contributed to increased *K*-values, at least for mature walleye.

6. Conclusion

Our interpretations of results to date suggest the sustainability of the OMNR guideline yield of 1.78 kg/ha/yr is questionable since the biomass and production of the fishable stock was declining at that harvest level and a protected slot between 45 to 55 cm while increasing harvest didn't seem to help. If the SPOF 12 (OMNR 1982) guidelines of 1.78 kg/ ha/yr are not sustainable in Savanne Lake then new guidelines, possibly those being proposed such as, 1.36 kg/ha/yr (OMNR walleye synthesis in progress) or 1.04 (Rempel & Colby 1991) are more appropriate (Table 4).

The quality of the fishing experience did not change appreciably during the first exploitation phase, when major dynamic changes within the population were occurring. Thus, angling indices in a lake of this size (364 ha) may not be sufficiently sensitive by themselves to provide an early warning of overharvest or stock status until after the fact. Possibly in larger bodies of water where the fish are less vulnerable to angling the indices may better reflect the dynamics of the population over longer periods of time.

Table 4. Evolution of walleye guidelines and their application to Savanne Lake, Ontario, including estimates of Savanne Lake walleye production (P) for comparative purposes.

Authority: comments	Annual walleye yield (kg/ha)
1. Conclusions from Adams and Olver 1977:	
1.1. Few northern Ontario lakes capable of sustaining percid (99.7% walleye) yields.	>1.50
1.2. Problems occur in most lakes where long-term percid yields exceed:	1.25
1.3. Sustainable yield of percids (99.7% walleye) is probably reasonable for moderately to intensively fished lakes in northern Ontario.	1.00 to 1.25
2. Adams and Olver 1977; Kerr 1977; Proposed 30% rule: MEI yield (Ryder, 1965) × 0.30 =	1.67
3. Ryder (1965) and OMNR (1982): 3.1.Angling fishery; MEI yield × 0.32 =	1.78
3.2. Commercial fishery; MEI yield × 0.20 =	1.11
4. Rempel and Colby (1991) and OMNR 1982:	
4.1. Angling fishery; MEM × 0.32 =	1.04
4.2. Commercial fishery; MEM × 0.20 =	0.65
5. Ricker (1975): yield per recruits model; pre-exploitation phase (1972–1979).	1.33
6. Baccante and Colby (1996): Walleye yield = 1.81(Lake area)$^{0.9314}$ =	1.21
7. OMNR (in prep): new guideline proposal; $\log_{10}$(yield) = – 2.44 + 0.09(mean annual air temp) + 2.43(S.I.)[a] =	1.36
8. Production estimates (fully recruited ages)	Biomass Production (kg/ha/yr)
8.1. 1973–76 (ages ≥ 7) =	1.39
8.2. 1983–86 (ages ≥ 5) =	0.93
8.3. 1990–92 (ages ≥ 5) =	0.60

[a] S.I. = walleye spatial Index which represents the proportion of the lake surface area where depths are less than the thermocline depth, where S.I. = 1 for Savanne Lake.

As observed in Henderson Lake (Reid & Momot 1985) biomass and production estimates were good indicators of stock status but their determination required much effort. Abrosov's mean age to mean age at maturity would be of limited value since protecting a portion of the larger fish would likely confuse this index. However, the mean age of the catch did respond somewhat to the harvest and stock recovery. Growth rates remained unchanged except for the youngest fish. Trapnet catch-per-unit-effort data in both Savanne and Henderson Lakes (Reid & Momot, 1985) reflected density changes of walleye vulnerable to the gear. Fecundity and condition factors also reflected the value of these indices but were more descriptive than predictive because of the delayed response.

Obviously more studies are desirable to refine sustainable yield estimates though they are time consuming. In the interim, regardless of which guidelines are used when walleye yields approach chosen guideline values, managers should monitor the stocks for possible signs of over harvest. This is especially true for the more northern walleye stocks where energy and nutrients needed to compensate for harvest are limited. We propose to harvest walleye at 1.0 kg/ha/yr which we believe is sustainable for several years and monitor population and fish community indices.

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