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Even–Odd Year Differences in Walleye Year-Class Strength Related to Mayfly Production[1]

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Abstract.—Young-of-the-year walleyes *Stizostedion vitreum* are more abundant in even-numbered years than in odd-numbered years in Savanne Lake, Ontario. Differences among years were related to emergences of the burrowing mayfly *Hexagenia limbata*. Adult walleyes from even-numbered year classes are more abundant than those from odd-numbered year classes. We hypothesize that pulse production of *H. limbata* in even-numbered years positively affects walleye recruitment by enhancing egg production by adult walleyes and buffering young of the year against predation and cannibalism.

Factors that influence percid year-class strength include water temperature, wind velocity, water level of lakes or flow rate of rivers, water transparency, oxygen concentration, predation, cannibalism, prey availability, and size of spawning stock (Busch et al. 1975; Chevalier 1977; Koonce et al. 1977; Nelson and Walburg 1977; Colby et al. 1979). In northern boreal lakes, where climate, especially temperature, is thought to be the frequent cause of large fluctuations in survival of young-of-the-year (age-0) fish, year-class strength of walleye *Stizostedion vitreum* has rarely been related to a biotic factor such as prey availability (Koonce et al. 1977). However, in Savanne Lake, a northern Ontario boreal lake, production of the burrowing mayfly *Hexagenia limbata* is highest in even-numbered years, which may benefit walleyes during those years (Riklik and Momot 1982). Because of its seasonal importance in diets of walleyes, northern pike *Esox lucius*, and yellow perch *Perca flavescens*, *H. limbata* may have a positive effect on walleye recruitment by acting as a buffer forage reducing cannibalism by and predation on young walleyes.

We investigated the differences in year-class strength and abundance of age-0 walleyes in even-numbered and odd-numbered years. We obtained these data as part of a long-term study that began in 1972 and was designed to monitor community response to experimental exploitation of walleyes.

Study Area

Savanne Lake (48°49.5′N, 90°06.0′W) is a shallow, homothermous, mesotrophic, boreal lake located 128 km northwest of Thunder Bay, Ontario. It has a surface area of 364 hectares and a uniform bathymetry with mean depth of 2.6 m and maximum depth of 4.3 m. The stained brown water color indicates a relatively high dissolved organic content resulting in low transparency (Secchi disc measurements, 0.5–1.5 m). This lake supports a percid community composed of walleyes, northern pike, yellow perch, white suckers *Catostomus commersoni*, burbot *Lota lota*, ciscoes *Coregonus artedii*, and trout-perch *Percopsis omiscomaycus*. Savanne Lake is one of five lakes in the area that were designated as provincial fish sanctuaries in 1969 by the Ontario Ministry of Natural Resources. In 1980, experimental exploitation of the Savanne Lake walleye population was begun as part of a long-term walleye research study. Only those fish 25–54 cm in total length were removed annually. This harvest simulated the size range of walleyes that had been taken by sportfishing prior to closure of the fishery (Mosindy 1980).

Methods

Abundances of age-0 walleyes and yellow perch.—To determine abundances of age-0 walleyes and yellow perch, we seined on each sampling day at 11 stations (4 south, 6 west, and 1 east) from July to September 1972–1984. All seine stations had a sand substrate except station 4 which was rocky. On each sampling day, all stations were seined in the period from midday to late afternoon on calm, usually sunny days. These conditions appear to be

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ideal for inshore movements of age-0 yellow perch and walleyes. We found that 69% of the seine catches that produced at least one age-0 walleye occurred when the actual amount of sunshine was greater than 50% of the potential amount for that day of seining (Table 1).

The sampling sequence was determined with a random numbers table. An 18.3 × 1.8-m bag seine with a 3.2-mm-square-mesh bag and 6.5-mm-square-mesh wings was laid out parallel to shore at a distance of 30.5 m and hauled in from shore to sample standardized areas of 0.056 hectare. Each year's formal sampling period started on the first day an age-0 walleye was captured and extended until the end of August. Annual median abundance was computed from the number of fish seined per hectare. Because daily seine catches are not normally distributed, the median is the preferred statistic for the nonparametric applications used in this study (Sokal and Rohlf 1981).

Seasonal growth of age-0 fish.—Samples of walleye and yellow perch collected during seining were measured to the nearest millimeter on each sampling day. Seasonal growth rates (mm/d) were determined by regression of total length versus time (Table 2; Ritchie 1984).

Walleye year-class strength.—We sampled adult walleyes with trap nets from early May to the end of May or early June in 1972–1984, when adults were concentrated during spawning activity. Ages were determined by scale analysis. Scale impressions were read with an Eberbach scale projector at 40× magnification. Criteria used to define the annuli were described by Lagler (1956) and Calhoun (1966). Samples were stratified by 5-cm (total length) intervals and age composition was determined according to Ketchen (1950). Baccante and Sandhu (1983) found that ages of Savanne Lake walleyes less than 9 years old can be accurately assessed. To derive an index of relative year-class strength for walleyes, the contribution (%) of each year class to the spawning population at its age of effective recruitment (Ricker 1975) was expressed as a percentage of the contribution at effective recruitment by the strongest year class. The strongest walleye year class during the study hatched in 1966; its age at effective recruitment (when its annual percentage contribution to the spawning population was greatest) was age 7, and its contribution that year was 45.1% (Table 3). Maximum contributions of other year classes were expressed as percentages of 45.1.

TABLE 1.—Frequency of occurrence of seine-days (N = 100) relating duration of sunshine and age-0 walleye abundance in Savanne Lake, Ontario, July and August 1972–1977.

Sunshine duration[a]	Abundance[b] of age-0 walleyes				
	0	1–25	26–50	51–75	76–100
0–25	1	13	1	3	0
26–50	3	4	1	1	4
51–75	3	16	1	4	3
76–100	5	23	5	1	8
50–100	8	39	6	5	11

[a] Expressed as a percent of the potential amount of sunshine that could occur during each day of seining.

[b] Number of fish caught per seine-day (11 stations).

Results and Discussion

The abundance of age-0 walleyes was significantly greater in even-numbered than in odd-numbered years (Wilcoxon rank sum test; P = 0.016; N = 6, 6). This difference between even-numbered and odd-numbered year abundance has increased since experimental exploitation of adult walleyes began in 1980 (Table 2). In odd-numbered years, before and during exploitation of adults, 21 and 7% of all seine hauls, respectively, contained more than five age-0 walleyes, whereas in even-numbered years, 34 and 59% of all seine hauls, before and during exploitation, respectively, captured more than five age-0 walleyes.

High overwinter mortality rates of small age-0 walleyes suggest year classes that grow rapidly during their first year may experience lower mortality than slower-growing year classes (Forney 1966). However, seasonal age-0 walleye growth rates in Savanne Lake did not differ significantly between even- and odd-numbered years, despite the observed differences in year-class strength (Wilcoxon rank sum test; P = 0.749; N = 6, 6; Ritchie 1984).

Abundance of age-0 walleyes (number per hectare) was significantly correlated with relative year-class strength of adults that were captured in trap nets in 1972–1977 (Kendall's tau = 0.780; P < 0.05; N = 6; Table 3). Contributions of even-numbered year classes to spawning populations were greater than those for odd-numbered year classes; an exceptionally strong year class occurred in 1966 (Figure 1). Strong year classes in 1966 were also reported for nearby Dexter Lake (Moenig 1975), Lake of the Woods, Minnesota (Schupp and Macins 1977), and Lac des Milles Lacs, Ontario (Elsey and Thomson 1977), suggesting the importance of climatic effects in determining year-class strength. However, age-0 walleye abundance (1972–1984) was not significantly related to water temperature expressed as degree-days above 15°C (DD>15°C)

TABLE 2.—Median number per hectare of age-0 walleyes and yellow perch captured with seines in Savanne Lake, 1972–1984. Relative year-class strength is the ratio of median catch in a given year to maximum catch for the period, which occurred in 1984 for walleyes and in 1982 for yellow perch.

	Age-0 walleyes			Age-0 yellow perch		
Year class	Growth rate (mm/d)	Median number seined per hectare (range)	Relative year-class strength	Growth rate (mm/d)	Median number seined per hectare (range)	Relative year-class strength
1972	1.08	190 (37–1,105)	30.2	0.32	854 (168–2,796)	8.3
1973	0.87	14 (0–545)	2.2		358 (10–2,583)	3.5
1974	1.35	20 (0–172)	3.2	0.44	801 (333–3,580)	7.8
1975	1.24	10 (0–474)	1.6		544 (108–3,024)	5.3
1976	1.17	69 (24–598)	11.0	0.47	1,306 (425–11,675)	12.7
1977	1.23	8 (0–706)	1.3	0.47	696 (41–32,060)	6.8
1978[a]						
1979	1.12	76 (7–243)	12.1	0.69	9,213 (292–33,578)	89.9
1980	0.94	43 (8–662)	6.8	0.48	1,113 (231–22,616)	10.9
1981	1.19	8 (0–127)	1.3	0.66	2,081 (349–18,922)	20.3
1982	1.75	176 (0–772)	27.9	0.56	10,252 (2,727–22,224)	100.0
1983	1.61	6 (0–47)	0.1	0.71	8,957 (1,129–10,678)	87.4
1984	1.32	630 (349–1,571)	100.0	0.69	8,660 (2,120–8,706)	84.5

[a] No field data available.

from May 17 to June 30 (Kendall's tau = 0.200; $P = 0.392$; $N = 11$) or to the coefficient of variation of daily DD>15°C from May 17 to June 30 (Kendall's tau = −0.164; $P = 0.484$; $N = 11$). Fifteen degrees was chosen as the base temperature because it is the mean hatching temperature for walleye eggs and the minimum required for feeding and survival of percid larvae 30–45 d following hatching (Smith and Koenst 1975; Hokanson 1977).

Coincident with the even- and odd-numbered year trend in age-0 walleye abundance and subsequent year-class strength was the pulse production of the burrowing mayfly *Hexagenia limbata*. Riklik and Momot (1982) described two *H. limbata* populations with 2-year life cycles in Savanne Lake. During the even-numbered year of their study (1980), the production and density of *H. limbata* was greater than in 1981—7,660 mg/m^2 and 121 nymphs/m^2 compared to 1,930 mg/m^2 and 34/m^2. Based on field observations in 1972–1985, *H. limbata* emergences were substantially greater in even-numbered years. As a result, *H. limbata* may function as a buffer forage that effectively reduces cannibalism by and predation on young walleye. Chevalier (1973) and Forney (1976) found that

TABLE 3.—Year-class abundance of age-0 walleyes related to their subsequent strength of recruitment to the spawning population, as determined by spring trap-net sampling.

		Adults					
		Contribution (%) to the spring spawning population at age					
Year class	Age-0 fish: median number seined per hectare	5	6	7	8	9	Relative contribution to the spawning population[a]
1966			40.9	45.1	43.1		100
1967		7.0	6.9	9.5		6.6	21.1
1968		10.5	14.9		30.8	9.9	68.3
1969		18.1		19.1	26.8		59.4
1970			32.0	30.5		24.6	71.0
1971		3.1	16.3		19.9	9.0	44.1
1972	190	10.9		26.8	20.0	9.7	59.4
1973	14		10.2	25.8	16.0	11.4	57.2
1974	20	3.0	31.6	10.3	9.7	11.3	70.1
1975	10	4.0	13.9	7.6	9.5	6.5	30.8
1976	69	18.2	20.4	27.1	12.5		60.1
1977	8	9.6	13.2	15.1			33.5

[a] Percentage contribution at each year class's age of effective recruitment (when the contribution was greatest) relative to the contribution at effective recruitment by the large 1966 year class (45.1% at age 7).

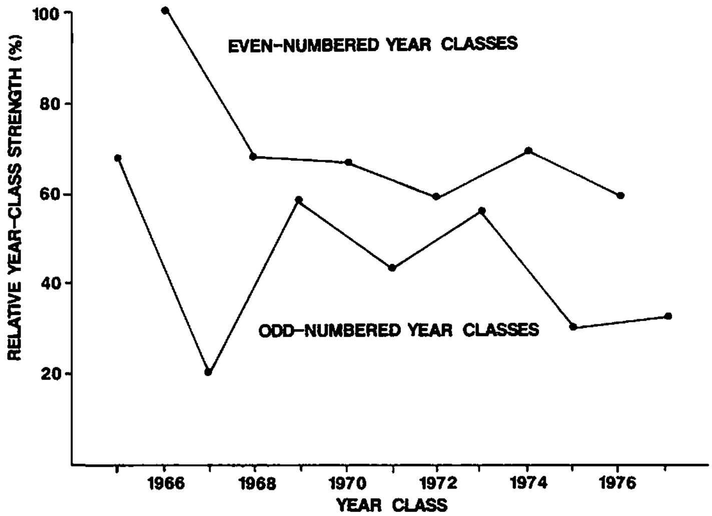

FIGURE 1.—Relative year-class strengths of walleyes from the year classes 1965–1977 in Savanne Lake. The estimated strength of each year class is shown as a percentage of the strongest year class (1966) during the entire period. Year-class strength was determined when each year class became effectively recruited to the spawning population (Table 3).

cannibalism by adult walleyes on young of the year was a decisive factor in the determination of walleye year-class strength in years when larval yellow perch, the major walleye prey, were scarce. Age-0 yellow perch are also an important forage for walleyes in Savanne Lake. However, diurnal activity by yellow perch reduces their availability to walleye predation in Savanne Lake (Ritchie 1984). Therefore, the effect of walleye predation on yellow perch abundance may be independent of *H. limbata* abundance. In Savanne Lake, age-0 yellow perch abundance was not significantly different between even-numbered and odd-numbered years (Wilcoxon rank sum test; $P = 0.522$; $N = 6, 6$) (Table 2).

Studies on walleye, northern pike, and yellow perch diets in Savanne Lake and nearby Henderson Lake reflect this differential availability of *H. limbata* in even-numbered and odd-numbered years. Walleyes, northern pike, and yellow perch in Savanne Lake consumed *H. limbata* nymphs from January to June, prior to emergence; a similar pattern of use was noted in nearby Henderson Lake (Mosindy 1980; Nunan 1982; Ritchie 1984). *Hexagenia limbata* occurred more frequently in walleye, northern pike, and yellow perch stomachs in even-numbered years. As a result of this increased availability of *H. limbata,* forage fish, including young walleyes, were less important food items (in terms of frequency of occurrence) for walleyes, northern pike, and yellow perch in spring and early summer when age-0 walleyes and yellow perch were pelagic and vulnerable to predation. Although diet analysis reflects the differential availability of *H. limbata,* vulnerability to predation of this forage item is probably due to a combination of movement and density. Riklik and Momot (1982) found that larger nymphs migrate in response to crowding. This movement was observed from September to November for the larger population in 1980, but not in 1981 for the smaller population.

In Lake Nipissing, Ontario, mayfly nymphs are used by a large proportion of the walleye population from May to July (M. J. Powell, Ontario Ministry of Natural Resources, unpublished report). This has been especially true in even-numbered years, when significantly larger hatches have occurred than in odd-numbered years. Mean winter angling catch per unit effort for yellow perch has been higher (0.61/rod-hour) in odd-numbered years (1979, 1981, 1983) than in even-numbered years (0.24; 1976, 1978, 1980, 1982). Yellow perch, which feed heavily on mayflies, may be less vulnerable to angling in even-numbered years when a larger number of mayflies are available. Therefore, the timing of peak availability of *H. limbata* in the spring of even-numbered years, when walleye fry are pelagic and vulnerable to predation, may be an important determinant of walleye year-class success, both directly and indirectly. The pulsed even-year production and availability of

H. limbata may contribute to the higher fecundity observed in larger walleye in "even" years in Savanne Lake (Baccante and Reid 1988, this issue). This, in combination with stronger even-numbered year classes and the increased number of older walleyes in the spawning population as a result of removal of predominantly intermediate-sized individuals since 1981, may increase the total number of eggs spawned in even-numbered years.

In small boreal lakes like Savanne Lake, where diversity of available forage is low and fish production depends on benthic rather than pelagic forage, recruitment and predator-prey interactions may be affected by a major forage event, such as mayfly emergence. We hypothesize that dominant alternate-year hatches of *Hexagenia limbata* positively influence walleye year-class strength by enhancing egg production, and providing a buffer against predation on age-0 walleye.

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