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Harvest, density and reproductive characteristics of North American walleye populations

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A synopsis of walleye population characteristics from North American lakes is presented. Harvest, density and reproductive data from the primary literature, agency reports and personal communications were summarized, and include: sport fishing harvests, exploitation rates, population densities, relative fecundity, and age to 50% maturity. Empirical relationships between yield, population size, lake area, relative fecundity, age to maturity and growing degree-days are described. Factors affecting these empirical relationships are also discussed. Quartiles were used to describe the frequency distributions of harvest, yield and density parameters. Managers can use these empirical relationships and descriptive statistics as comparative diagnostic tools for interpreting the status of their walleye fishery. We feel this is a useful approach because managers are often having to make decisions regarding their fishery with minimal information. The interpretive value of minimal data can be enhanced when comparative information is available.

1. Introduction

For many fisheries, especially those with limited access, such as in Northern Ontario (above 50° latitude), there is limited information with which to make management decisions. Reduced funding for fishery management programs, prevents further reduction of uncertainty in the decision making process. However, a limited amount of harvest information along with some data describing the physico-chemical features of a water body is frequently available to assess a fishery.

The interpretive value of limited data can be greatly enhanced when comparative information is available. The purposes of our paper are: (1) to synthesize available harvest, density, exploitation and reproduction data from numerous walleye populations over a large geographical area; (2) describe empirical relationships between these parameters; and (3) discuss factors which determine stock status. Although uncertainty is implicit in this approach, due to unexplained variances inherent within and

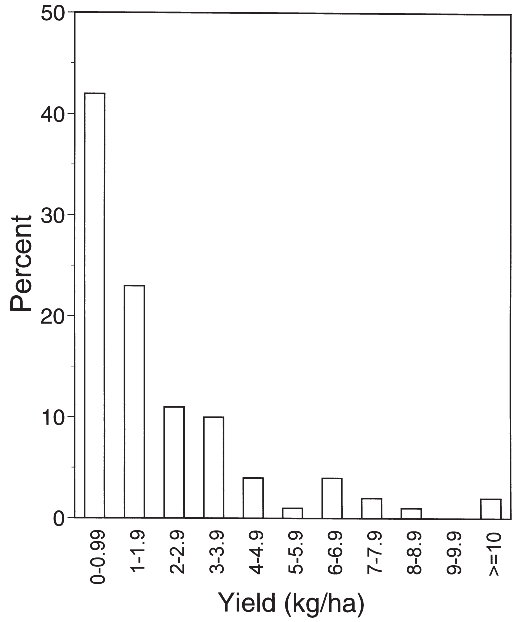

Fig. 1. Frequency distribution of walleye angling yields (kg/ha) from 168 North American waters.

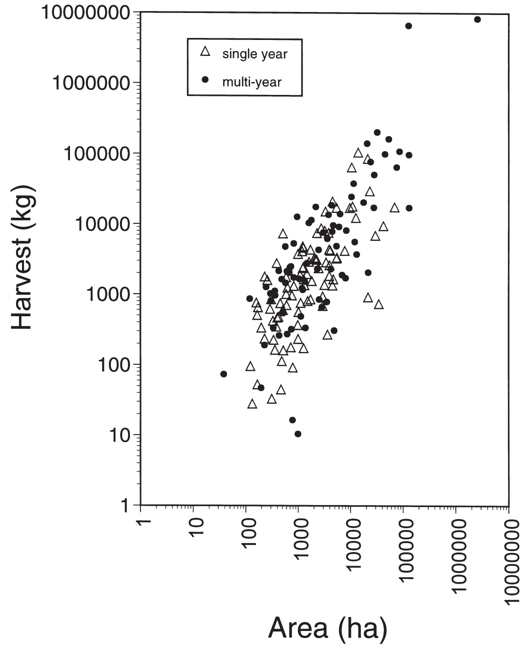

Fig. 2. Plot of annual walleye angling harvest (kg) against lake area (ha) for 92 single-year, and 75 multi-year (two or more years) observations.

between aquatic communities, this review provides an improved understanding of the limits that can be expected for various population characteristics, and how they relate to each other.

2. Methods

Walleye harvest and density data was compiled from the primary literature, internal agency reports and extensive personal communication with fisheries workers from the Ontario Ministry of Natural Resources and other resource agencies. We analysed data from a range of walleye populations to observe their variation, common properties and dynamics in various habitats. Quartiles were used as descriptive statistics because values of yield, population density and exploitation rates have skewed distributions that do not conform to standard probability models. Thus, the frequency distribution is divided into equal quartiles, 25, 50 and 75%. The 50% quartile is the median.

The number of observations varied among populations, and estimates of total harvest included both commercial and angling yields when available. About 95% of the walleye populations were harvested by angling only. Estimates of population and yield characteristics varies between water bodies. We assumed that both single-year and multi-year observations reflected long-term averages and approximates sustainable yields at least as they are presently impacted by our cultural practices. The degree of error associated with this assumption will only become apparent with time, hopefully it will be minimal and manageable.

Table 1. Harvest characteristics of North American walleye populations showing the 25, 50, and 75 percent quartiles for angling exploitation rates (percent), adult density (number/ha), harvest weight (kg) and yield (kg/ha). Also shown are sample sizes (n) and range of values.

	Quartiles				
	25	50	75	*n*	Range
Exploitation Rates	14	21	25	46	3–55.6
Adult Density	7.8	14.8	23.9	85	0.1–168
Harvest Weight	0.48	0.58	0.67	113	0.26–1.18
Yield	0.50	1.24	2.95	168	0.01–49.6

3. Results

3.1. Yield

The distributions of walleye yields is highly skewed to the right (Fig. 1). The mode of the distribution is for yields less than 1 kg/ha (42% of the sample). The 25% quartile corresponds to a yield of 0.50 kg/ha, the 50% quartile (median) is 1.24 kg/ha, and the 75% quartile is 2.95 kg/ha (Table 1).

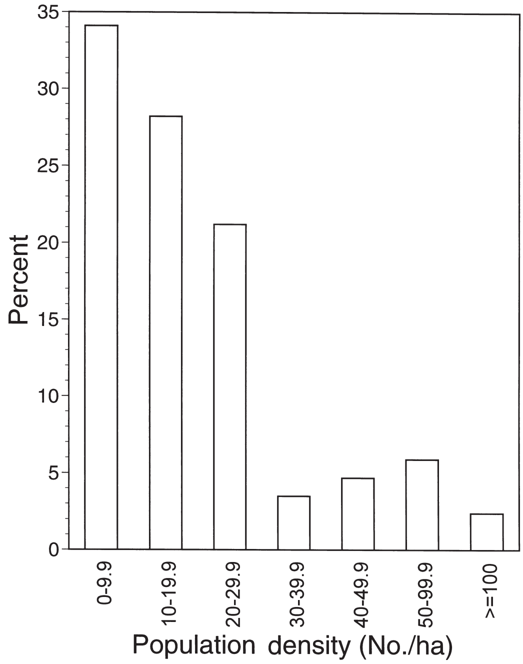

Fig. 3. Frequency distribution of adult walleye population densities (numbers/ha) from 85 North American waters.

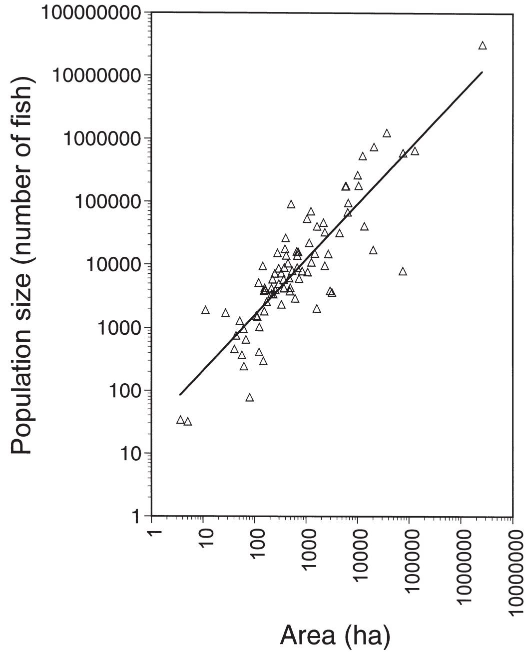

Fig. 4. Plot of adult walleye population size against lake area (ha) for 81 North American waters.

There is a significant ($p < 0.01$) relationship between total walleye yield (kg) and lake area (ha). We regressed 168 observations of log yield against log area (Fig. 2) and obtained the following significant ($p < 0.01, R^2 = 0.59$) relationship:

$$YIELD = 1.81AREA^{0.931} \tag{1}$$

Out of 167 observations, 92 (55%) consisted of single-year yield estimates, and 75 (45%) had two or more years of data. We fitted separate regression lines to single- and multi-year data, and found that the slopes were not significantly different (ANOVA F-test, $p < 0.01$). Therefore, we combined the data to generate equation 1.

3.2. Population size

The frequency distribution of population density expressed as number of walleye per hectare, is also skewed to the right (Fig. 3). The mode of the distribution occurs at a density of less than 10 walleye/ha (34% of the sample). The 25, 50 and 75% quartiles for walleye density are 8.1, 14.8 and 23.9 walleye/ha respectively (Table 1).

The size of a walleye population increases with lake area (Fig. 4). A log-log regression of lake area (ha) with population size of adult walleye (*POP*) for a sample of 81 lakes resulted in the following significant ($p < 0.01, R^2 = 0.75$) relationship:

$$POP = 27.31AREA^{0.79} \tag{2}$$

3.3. Reproduction

Fecundity is defined as the number of eggs present in a fish prior to spawning. It can be expressed as the total number of eggs per female (absolute fecundity), or number of eggs per kilogram of body weight (relative fecundity). Table 2 shows relative fecundities of walleye populations, and the number of Growing Degree-Days (*GDD*) for those locations. *GDD* are defined as the number of degree-days above 5 Celsius and is a standard measurement reported by Environment Canada's Weather Service. *GDD* have been used to quantify energy available for walleye growth and reproduction (Colby & Nepszy 1981).

The mean relative fecundity (*RF*), expressed in eggs per kilogram, was plotted against *GDD* (Fig. 5). The resulting relationship is a statistically-significant ($p < 0.01, R^2 = 0.67$) straight line:

Table 2. Fecundity of walleyes, expressed as number of eggs per kilogram, and growing degree-days (GDD), from North American waters.

Waterbody	Location	Year of study	*GDD*	Range	Mean	Ref.
George Lake	ON	1983	1 200		39 267	1
Lower Tweed Lake	ON	1983	1 200		39 029	1
Upper Kesagami Lake	ON	1983	1 200		38 540	1
Wakwaycwkastic Lake	ON	1983	1 200		46 130	1
Kowashkagama River	ON	1982	1 250	33 102–59 064	43 922	2
Onaman Lake	ON	1982	1 250	35 914–65 035	51 792	3
Henderson Lake	ON	1980	1 287		41 300	4
Henderson Lake	ON	1981	1 287		52 500	4
Henderson Lake	ON	1982	1 287		49 800	4
Henderson Lake	ON	1983	1 287	29 822–83 286	48 900	4
Henderson Lake	ON	1984	1 287	44 750–56 216	50 900	4
Henderson Lake	ON	1985	1 287	45 068–63 783	51 500	4
Lac Des Mille Lacs	ON	1982	1 287	34 700–46 860	58 360	5
Savanne Lake	ON	1980	1 287	28 966–48 666	39 690	4
Savanne Lake	ON	1981	1 287	32 850–50 579	39 800	4
Savanne Lake	ON	1982	1 287	22 681–54 016	42 400	4
Savanne Lake	ON	1983	1 287	36 145–56 411	43 200	4
Savanne Lake	ON	1984	1 287	28 138–69 698	49 300	4
Savanne Lake	ON	1985	1 287	33 510–60 948	43 580	4
Home Lake	MB	1977	1 400	34 260–51 590	40 513	6
Wapun Lake	MB	1977	1 400	24 674–61 095	52 508	6
Lake Winnipeg (north end)	MB	1975	1 419	27 354–106 379	59 233	7
Lake Winnipegosis	MB	1987	1 440		50 487	7
Lake of the Woods	MN	1941	1 657		50 000	8
Little Cutfoot Sioux Lake	MN	1954	1 662	48 840–73 700	65 239	9
Lake Winnipeg (south end)	MB	1981	1 688	26 394–69 814	50 665	7
Lake Nipissing	ON	1984	1 780	25 275–83 414	47 387	10
Balsam Lake	ON	1987	1 800	43 600–63 690	53 094	11
Pigeon Lake	ON	1987	1 800	55 926–87 604	68 051	11
Lake Gogebic	MI	1947	1 864	57 922–67 797		12
Muskegon River	MI	1947	1 864	65 778–95 955		12
Big Sand Lake	MN	1900		61 370		13
Moon River	ON	1900		43 925–100 313	65 083	14
Escanaba Lake	WI	1979–81	1 901	48 441–74 161	67 914	15
Otter Tail Lake	MN	1910		45 298		16
Bay of Quinte (L. Ontario)	ON	1962	2 000	57 096–100 031	73 486	17
Fox River	WI	1986	2 144	31 000–92 600	51 600	18
Lake Winnebago	WI	1964–67	2 187	63 441–96 116		19
Lake Erie (W. basin)	OH	966	2 600	41 191–96 914	61149	20
Lake Erie (W. basin)	OH	990–91	2 600	52 980–147 160	84 710	21
Lake St. Clair	ON	1977	2 500		87 397	22
Lake Erie (E. basin)	OH	1966	2 300	56 314–123 249	82 700	20
Columbia River (John Day Pool)	OR	1981	2 730	69 000–101 000	82 900	23
Lake Meredith	TX	1968–71	3 691	36 500–72 200	52 000	24
Center Hill Reservoir	TN	1965–66	4 078	37 954–143 827	64 715	25
Norris Reservoir	TN	1939–40	4 078	28 415–32 727	29 700	26
Mississippi River				50 600–110 100		27
Utah Lake	UT			27 900–52 562	47 410	28
Wisconsin waters	WI			28 600–99 000		29

1. Armstrong and Jolkowski (unpub. data), 2. Sobchuk (unpub. data), 3. Walroth (unpub. data), 4. Baccante and Reid (1988), 5. Fruetel (unpub. data), 6. Babuluck (pers. comm.), 7. Lysak (pers. comm.), 8. Carlander (1945), 9. Johnson (1971), 10. Jorgensen (unpub. data), 11. Deacon (unpub. data), 12. Eschmeyer (1950), 13. P. Jacobson (pers. comm.), 14. Winterton (1975), 15. Serns (1982), 16. D. Schreiner (pers. comm.), 17. Payne (1963), 18. Balcer *et al.* (1986), 19. Priegel (1970), 20. Wolfert (1969), 21. Muth and Ickes (1993), 22. MacLennan (pers. comm.), 23. Maule and Horton (unpub. data), 24. Kraai and Prentice (1974), 25. Muench (1966), 26. Smith (1941), 27. Nord (1967), 28. Arnold (1960), 29. Niemuth *et al.* (1966).

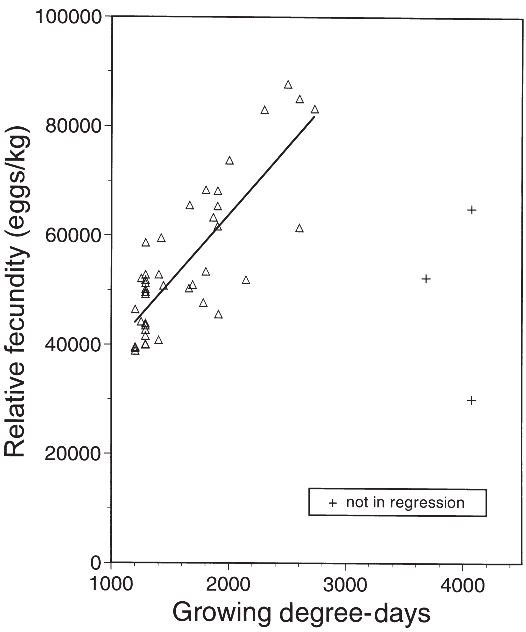

Fig. 5. Plot of relative fecundity (eggs/kg) against growing degree days (above 5°C) for 45 North American walleye populations.

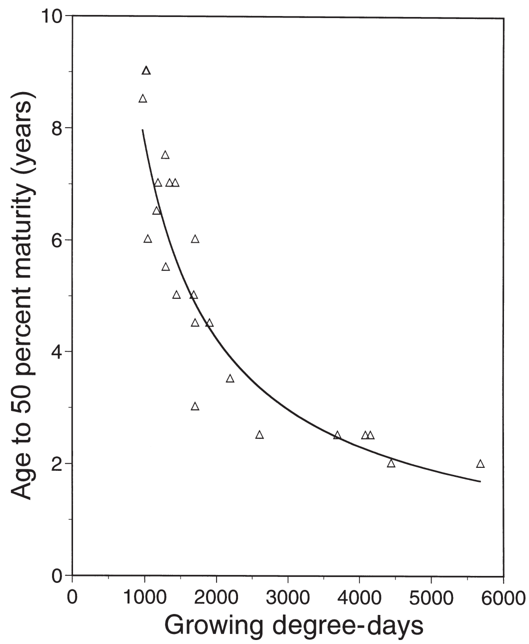

Fig. 6. Plot of age to 50 percent maturity against growing degree days for 23 North American walleye populations.

$$RF = 24.668GDD + 14\,514 \qquad (3)$$

The three outliers in Fig. 5 are excluded from the regression. These populations are from the extreme southern range (Tennessee and Texas) of the species and are subject to physiological constraints on reproduction, mentioned in the discussion section of this paper.

Beverton (1987) tabulated data from Colby and Nepszy (1981) and plotted age to 50% maturity (T_m) against *GDD*. We added additional data and fitted a line to quantify the relationship (Fig. 6). The resulting best-fit is a power curve of the form:

$$T_m = 3184.72GDD^{-0.871} \qquad (4)$$

The regression is statistically significant ($p < 0.01, R^2 = 0.87$).

3.4. Exploitation rates

Angling exploitation rates for walleye from various sources were compiled and tabulated (Table 3). The median exploitation rate in a sample of 46 observations is 21%, and range from 3 to 55.6% (Table 1). The frequency distribution of the exploitation rates show a skewed distribution with a mode at the 20–30% category (Fig. 7).

We plotted exploitation rates against Growing Degree-Days (*GDD*), for 16 lakes (Fig. 8). On the graph we have used different symbols to indicate which fisheries have "collapsed" or severely depleted, and which have been able to support their respective level of exploitation (sustainable). The data suggest that there may be a curvolinear relationship between exploitation and energy, with an upper threshold beyond which the population will not sustain itself. The line on the graph is not fitted statistically, rather, it represents our best guess, based on long-term data from a few lakes, of maximum, long-term sustainable exploitation rates.

4. Discussion

4.1. Yield

Our results indicate that lake area provides adequate first-order estimation of walleye yield. Yield in kilograms and lake area in hectares both increase proportionally over a logarithmic scale. Thus, larger lakes produce larger walleye yields. However, we must caution that, yield estimates may not reflect

Table 3. Walleye exploitation rates (percent) as reported in various angling fisheries.

Waterbody	Location	GDD	Area (ha)	Mean	Range	Period	Duration (seasons) (*months)	Ref.
Abamasagi Lake	ON		1 526	32		1981	1	1
Big Sand Lake	MN	1 900	664	21.9[a)]		1990–92		2
Big Sand Lake	MN	1 900	664	22.3[b)]		1990–92		2
Branched Oak Lake	NE		728	22.1	19.9–24.2	1979–80	2	3
Cass, Andrusia, Big Wolf Lakes	MN		7 369	15.8[a)]		1971–75		4
Cass, Andrusia, Big Wolf Lakes	MN		7 369	26.0[b)]		1971–75		4
Cutfoot Sioux Lake	MN	1 662	953	17	11–22	1957–58	2	5
DuBay Lake	WI		2 692	18.8		1983–84	1	6
Escanaba Lake	WI	1 901	119	25		1953–82	30	7
Fife Lake	MI		251	5.1		1964–65	2	8
Flambeau Flowage	WI		5 792	21	2–43	1975–76	2	9
Gogebic Lake	MI	1 864	5 986		2–6	1947, 1976		10
Goulais River	ON			29		1962, 1964	15*	11
Green Bay (L. Michigan)	MI			4.1	1.6–6.3	1957–63		12
Henderson Lake	ON	1 250	151	55.6	49–66.2	1980–82	3	13
Home Lake	MB	1 400	169.8	22.5	16–29	1979–80	2	14
Hoover Reservoir	OH		1143	29		1967	1	15
Inland Waterway (Burt Lake)	MI		6 758		7–18	1950's–75		10
Jewett Lake	MI		5.2	8.9		1979–82	4	12
Kabetogama Lake	MN	1 241	10 428	23		1984–85	2	16
Kenogamissi Lake	ON		2499	10.5		1974	1	17
Lake Erie	ON	2 600	2 569 000	18.8	14.9–23.9	1977–86		18
Lake of the Woods	MN	1 657	128 294	13.7		1982		19
Many Point Lake	MN		694	27	21–33	1955–57	3	20
Meredith Lake	TX	1 905	4 452	5	1.6–9.6	1986–93	8	21
Michigan Average	MI	1 900		21				22
Mille Lacs	MN	1 900	53 419	25				23
Mississauga River	ON			14		1965	1	24
Moon River	ON	1 900		15.6[c)]	11–22	1969–72	4	25
Muskegon River	MI	1 864		16.1	9.7–25.5	1947–50	3	12
Nipigon Bay, (L. Superior)	ON	1 200		18	7–34	1955–57	3	26
Okoboji Lake (East and West)	IA	2 250	2 301	19.4		1991	1	27
Oneida Lake	NY	2 500	20 640	23	10–47	1957–59	3	28
Otter Tail Lake	MN	1 900	55 54	34		1983		29
Pike Lake	WI		211	21.6	20.7–22.4	1959–62	3	30
Sallie Lake	MN		504	9.3		1954		31
Savanne Lake	ON	1 250	364	16.6	11.9–23.6	1983–86	4	12
Spirit Lake	IA	2 250	2 288	22	15–29	1947, 1954, 1991	3	32
St. Louis River Estuary	MN			8.1		1980–82		33
Touchwood Lake	AB	1 100	2 900	3	2–4	1991	1	34
Upper Chukuni River (Red Lake)	ON	1 348		25.9	22.5–29.2	1984–85	2	35
Vermillion Lake	MN		16 413	5		1940		36
Wapun Lake	MB	1 400	212.6	52.5	52–53	1979–80	2	14
Whitefish Lake	ON	1 200	3015	12	10–30	1989–90	2	37
Winnibigoshish Lake	MN		23 693	10.2		1937–39		38
Winnibigoshish Lake	MN		23 693	26.1[a)]		1975–77		39
Winnibigoshish Lake	MN		23 693	23.1[b)]		1975–77		39
Wolf Lake	WI		159	8.6	5.7–12.3	1972–76	4	40
Wolf Lake	AB	1 100	3 150	22.0[b)]	21–23	1991	1	35

[a)] Mature females, [b)] Mature males, [c)] An additional 12 percent due to commercial fishing, [d)] An additional 3 percent due to commercial fishing.

1. Sobchuk (1981), 2. Jacobson (pers. commun.), 3. Schainost, S. (1983), 4. Strand (1980), 5. Johnson and Johnson (1971), 6. Hauber, A. (1989), 7. Serns (1985), 8. Schneider (1969), 9. Lealos and Bever (1982), 10. In: J. C. Schneider (1978), 11. Rose (1984), 12. Schneider (1977), 13. Reid and Momot (1985), 14. Babaluck, J. (F&O pers. comm.), 15. Erickson and Stevenson (1967), 16. Kallemeyn, L. W. (1986), 17. Deyne (1983), 18. OMNR unpub. report, 19. Payer et. al. (1987), 20. Olson (1958), 21. Munger, C. (TX P.F. & W., pers. comm.), 22. Schneider (1978), 23. Schupp (MNDNR pers. comm.), 24. Payne (1965), 25. Winterton (1975), 26. Ryder (1968), 27. Larscheid, J. (1992), 28. Forney (1967), 29. Schreiner (1987), 30. Mraz (1968), 31. Olson (1955), 32. Rose (1955); Larscheid, J. (1992), 33. Osborn et. al. (1991), 34. Sullivan, M. (AB Nat. Res., per. comm.), 35. Weilandt (1984), 36. Carlander (1941), 37. Fruetel (1994), 38. Stoudt and Eddy (1939), 39. Osborn et. al. (1985), 40. Serns (1981).

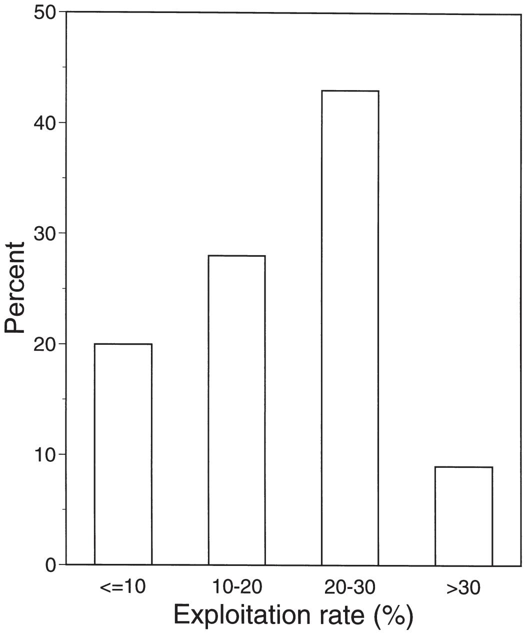

Fig. 7. Frequency distribution of angling exploitation rates (percent) for 46 North American walleye populations.

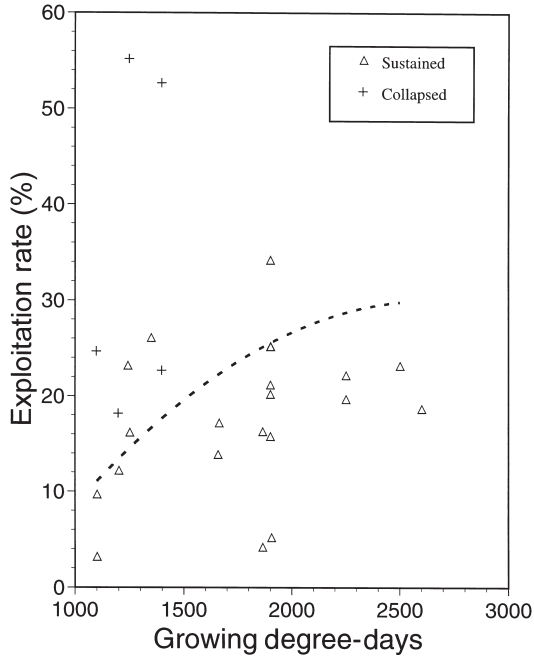

Fig. 8. Plot of angling exploitation rates that have been sustained or have resulted in the collapse of walleye from a sample of 27 North American waters. The line was not fitted statistically, it represents our estimate of maximum sustainable rates over the energy cline.

populations in equilibrium. In reality, some of these lakes may not be in equilibrium and present yields may exceed long-term stable or sustainable yields. This reiterates the importance of long-term monitoring studies in fisheries science.

The strong relationship between walleye yield and lake area is consistent with other studies which correlate fish productivity with lake morphometry (Leach *et al.* 1987). However, in the literature review provided by Leach *et al.* (1987), it is evident that, although walleye yield has been correlated to macrobenthos production (Matuszek 1978), climate and effort (Schlesinger & McCombie 1983), none of the studies deal specifically with walleye yield and lake area relationships.

Lake area has been correlated with the number of fish species on a global (Barbour & Brown 1974), and regional scale (Harvey 1978). Rounsefell (1946) found an inverse relationship between fish yield and lake area, that is, large lakes produce less fish per unit area than small lakes. However, because large lakes are generally deeper than small lakes (Hayes 1957), yield is really a function of depth as well as area. Also, smaller, shallower lakes have a larger proportion of the substrate in the euphotic zone, which is important for fish production. Conversely, most of the substrate in the larger, deeper lakes may be in the profundal zone, which is aphotic, and acts as a sink for nutrients, making them unavailable to production. Rawson (1952) hypothesized that increasing lake depth constrains fish production beyond the limit where increase in area has any effect.

Rousenfell's (1946) observation of the inverse relationship between fish yield per unit area and lake area, has been confirmed by other researchers (Jenkins & Morais 1971, Carlander 1977). Although it has been recognized for years that small lakes produce more yield per unit area than large lakes, this cornerstone of fisheries management has spurred a healthy dose of controversy. Youngs and Heimbuch (1982) suggested that there is a spurious correlation between lake area and yield expressed in kilograms per hectare, since the variable area occurs in both the dependent and independent variable. More recently, Jackson *et al.* (1990), criticized the use of ratios, such as the *MEI*, in aquatic research applications because the distribution of the ratio variables is not known which, they feel, leads to errors in prediction.

Rempel and Colby (1991) developed the morphoedaphic model (*MEM*) in response to criticism of the *MEI* (Jackson *et al*. 1990), and use the *MEM* to predict fish yield in lakes. The *MEM* consists of two morphometric (area and volume) and one edaphic variable (*TDS*). Basin morphometry alone accounts for about 97% of the variation in fish harvest. Although lake volume and *TDS* only account for an additional 2.5 and 0.64% of the variability in harvest, the authors included them to explain variations in lakes with atypical basin morphometry and *TDS* levels.

Despite criticism, the *MEI* has proved to be a useful tool for predicting fish yields in lakes. It generally accounts for about 60 to 78% of the variation in fish yields. Youngs and Heimbuch (1982) showed that, the *MEI* is a valid predictor for two reasons. First, large lakes produce greater fish yields than small ones. Second, large lakes are generally deeper, thus mean depth in the *MEI* acts as a surrogate for surface area. These authors show that area alone can be a more powerful predictor of yield. They found that area accounted for about 94% of the variation in fish yield in three sets of data reported in the literature. They also found that the variation accounted for by the regression increased to only 95% when *TDS* was added. Surface area accounts for 61% of the variation in walleye yield in the set of data we reported here. The variation about the yield-area regression line can be attributed to a number of factors, such as, community structure, habitat type, nutrient loading, methods of harvest, and fishing effort characteristics.

The first three factors were dealt with by Rempel and Colby (1991). They provide good examples of how each affects yield. Elsey and Thompson (1977) provide evidence of how different methods of harvest can influence walleye yields. Schlesinger and McCombie (1983) recognized that failure to partition effort by species in a multi-species fishery can add variance to yield predictions. Future research should be directed towards further understanding of how each of the above-mentioned factors affect walleye yield.

4.2. Population size

The relationship between lake area and walleye population size is analogous to the yield-area relationship, that is, larger lakes have more walleye but a less dense population when divided by area or volume. Hansen (1989) reported a relationship between walleye abundance (numbers) and lake area (acres), and found that the latter explained 65% of the variation in walleye abundance in a set of 104 Wisconsin lakes. We did not have abundance data on all of Hansen's (1989) lakes , but used 19 from lakes in Hansen *et al*. (1991) in our set of 81 lakes and found that area explained 76% of the variation in walleye abundance. The abundance figures we used were all obtained from mark-recapture estimates, mostly reported in unpublished literature, obtained through personal communications with other researchers.

An empirical relationship between walleye abundance and lake area has proven to be helpful in estimating walleye abundance in northern Wisconsin lakes when other information was lacking (Hansen 1989). This approach provides inexpensive estimates of walleye abundance based on lake area. Safety factors can then be derived to allow setting of harvest quotas based on these estimates of walleye abundance (Hansen *et al*. 1991).

Between-lake differences in adult walleye density can be attributed to various parameters, such as, energy input, community type, habitat suitability, etc. These factors directly or indirectly affect walleye survival from the egg to the adult stages. Table 4 shows an example of how walleye density differs in two lakes, Savanne (Ontario) and Escanaba (Wisconsin). Savanne, a relatively unexploited lake, has an area of 364 ha, and is typical of many small- to medium-size mestrophic walleye lakes in Northern Ontario. Escanaba has an area of 119 ha, and has supported heavy angling pressure since the 1940s (Kempinger & Carline 1977). Table 4 shows that Escanaba Lake has about three times more egg production per hectare than Savanne Lake. The higher fecundity is likely a result of greater energy input, 1 367 *GDD* in Savanne and 1 901 *GDD* in Escanaba (Table 5). The survival from egg to each age group is similar in both lakes, but since Escanaba walleye have much higher relative fecundity (67 914 eggs/kg) than those in Savanne (39 690 eggs/kg) (Table 2), the resulting adult density is higher.

Availability of ideal habitat is also a very crucial factor which determines population density. The importance of habitat as an indicator of successful establishment and reproduction of walleye populations has been well documented in the literature. A recent summary of these observations is provided by Colby *et al.* (1991). Equally important is the accuracy of the estimate of adult abundance. Hansen *et al.* (1991) provide a detailed summary of factors which can affect this accuracy, such as changes in the vulnerability of the fish during the sampling period (see also Colby & Baccante 1996). Hansen *et al.* (1991) also caution that if the estimate is used for management purposes, for example to set harvest quotas, the accuracy of population estimates declines over time from the year the estimate was obtained to the year it was used. They used data from Escanaba Lake, which has abundance estimates from 1953 to the present, to test the accuracy of population estimates over time. Hansen *et al.* (1991) stress the importance of long-term series of abundance estimates as a calibration tool. This has allowed them to corroborate their results from other lakes where abundance estimates were based on irregular sampling.

4.3. Reproduction

The shape of the curve in Fig. 6 suggests that relative fecundity (*RF*), expressed as the mean number of eggs per kilogram is higher in systems with greater insolation. However, *RF* decreases when *GDD* values reach values greater than 3 500. This limiting effect is indicative of physiological constraints to reproduction which have been well-documented by Colby and Nepszy (1981). They have shown that, ovary maturation may not occur in environments receiving too much energy. They cite data by Hokanson (1977) which indicate that a minimum winter temperature of 10°C is near the upper limit for maturation of gonads in yellow perch and walleye. The southern-most walleye population in Ontario is in western Lake Erie, with 2 300 *GDD*, thus reproduction is not limited by lack of cool temperatures during the maturation cycle.

Describing how *RF* changes over an energy cline (abiotic effects) is important for determining variations in reproductive potential among lakes. Knowledge of these variations can be particularly useful in simulation modelling. Of great importance is also describing how *RF* changes within a population. These variations are due to density-dependent factors (biotic effects) which affect growth, survival, abundance and fecundity. Within-lake studies describing temporal changes in walleye fecundity are scarce. Baccante and Reid (1988) describe changes in fecundity in Savanne and Henderson lakes walleye over a six-year period. They hypothesized that variations in food abundance within each lake, were responsi-

Table 4. Estimated abundance (number of fish), density (number of fish per hectare), and survival rates (percent) from egg stage to each age groups for walleye in Savanne Lake (Ontario), and Escabana Lake[1] (Wisconsin).

	Savanne Lake			Escabana Lake		
	Abundance	Density	Survival	Abundance	Density	Survival
eggs	83 786 000	230 055		85 892 607	723 611	
Age						
0	10 254	28	0.0122	23 220	195.6	0.0270
1	7 618	21	0.0091	9 000	75.8	0.0105
2	5 660	16	0.0068	3 500	29.5	0.0041
3	4 205	12	0.0050	1 846	15.6	0.0021
4	3 124	9	0.0037	1 165	9.8	0.0014
5	2 321	6	0.0028	840	7.1	0.0010
6	1 724	5	0.0021	442	3.7	0.0005
7	1 281	4	0.0015	192	1.6	0.0002
8	1 261	3	0.0015	11	1.0	0.0001
9	271	1	0.0003	92	0.8	0.0001
≥10	337	1	0.0004	197	1.7	0.0002
	weighted mean = 0.0073			weighted mean = 0.0183		
	median = 0.0028			median = 0.0010		

[1] Steve Serns, WI. Dept. Nat. Res., pers. comm.

ble for changes in fecundity during the study period.

More recently, Muth and Ickes (1993) compared 1966 walleye fecundity (Wolfert 1969) to 1990–91 data. They found that, mean egg production of the dominant age group of spawners (ages 4 to 8) was approximately 25% lower in 1990–91 than 1966. However, *RF* was much higher in 1990–91, 84 710 eggs per kilogram (K. Muth, Sandusky, OH pers.

Table 5. Morphometric, yield and egg production data for walleye populations in eleven lakes. Units as indicated. Yields in kg/ha, densities in number/ha and egg data in thousands.

	Wapun	Home	Savanne	Mille Lacs	Escanaba	Otter Tail
Location	MB	MB	ON	MN	WI	MN
Degree days	1 200	1 200	1 367	1 905	1 901	1 910
Area (ha)	213	170	364	53 419	119	5 968
Shoreline (km)	18	11	15	126	8	14
Maximum depth (m)	7	4	4	11	8	38
Mean depth (m)	3	2	2	6	4	13
TDS (mg/l)	45	50	42	133	34	228
MEI	14	28	16	22	8	19
Total potential yield	4.6	6.3	4.9	5.6	3.6	5.2
Walleye yield	3.4	1.6	1.8	3.0	7.0	2.8
Exploitation rate (%)	52	23	16	25	28	25
Adult density	15[a]	14[a]	15[b]	30	41[c]	28
Fingerling density			28[d]		59[d]	
Standing crop	10	10	7	14	19	12
Inst. mortality	0.8	0.4	0.7	0.5	0.5	0.7
Annual mortality	0.5	0.3	0.5	0.4	0.5	0.5
Mean eggs/kg	52.5	40.5	39.7		67.9	45.3
Range eggs/kg	24–61	34–51	29–67		48–74	
Pot. egg prod. ($\times 10^6$)	55.2	34.7	83.8	23 247[e]	85.9	1 596
Eggs/ha	260	210	229	435	724	268
Eggs/kg of yield	76	131	128	145	103	96
Eggs: standing crop	0.006	0.007	0.007	0.007	0.006	0.010
Data source	1	1	2	3	4	5
	Big Sand	**Lake of the Woods**	**Leech**	**Dauphin**	**St. Clair**	
Location	MN	MN	MN	MB	ON	
Degree days	1 900	1 657	1 900	1 500	2 500	
Area (ha)	671	125 858	45 123	52 200	75 600	
Shoreline (km)	13		314	119	270	
Maximum depth (m)	41	12	46	4	6	
Mean depth (m)	14	7	6	3	3	
TDS (mg/l)	190	138	172	353	123	
MEI	14	19	31	141	41	
Total potential yield	4.6	5.3	6.5	13	7.4	
Walleye yield	2.3	1.6	2.1	0.3	0.9	
Exploitation rate (%)	20	15	25		8	
Adult density	19	8	14		8	
Fingerling density			83			
Standing crop	24					
Inst. mortality					0.4	
Annual mortality					0.3	
Mean eggs/kg	61.4	60.3			87.4	
Range eggs/kg					59–233	
Pot. egg production	409	16 400	11 000[e]	2 817	5 650	
Eggs/ha	609	130	244	54	75	
Eggs/kg of yield	264	80	116	217	84	
Eggs:standing crop	0.003	0.006	0.006		0.01	
Data source	6	3	3	1	7	

[a] ≥ age 4, [b] ≥ age 7, [c] ≥ age 3, [d] from mark-recapture studies, [e] model-based estimates.
1. J. Babaluk (Fisheries & Oceans, MB, pers. comm.), 2. Our study, 3. D. Schupp (MN DNR, pers. comm.), 4. S. Serns (WI DNR, pers. comm.) and Serns (1982), 5. D. Schreiner (MN DNR, pers. comm.), 6. P. Jacobson (MN DNR, pers. comm.), 7. D. MacLennan (OMNR, pers. comm.).

comm.) versus 61 149 eggs per kilogram in 1966 (Wolfert 1969). The increase in *RF* is due to a decrease in mean weight-at-age from 1966 to 1990–91.

Colby and Nepszy (1981), and more recently Henderson and Nepszy (1994), have shown how environmental factors influence maturity. Northern stocks mature later and over a greater number of years than southern stocks. Rate of maturity is affected by growth, thus faster-growing stocks will reach maturity earlier. As a result, more southern walleye populations have a greater capacity to compensate to exploitation than northern ones. However, in the extreme southern range of their distribution, the lack of sufficient cool temperatures may inhibit egg development (Colby & Nepszy 1981).

4.4. Exploitation rates

As our results indicate, the frequency distribution of exploitation rates is skewed to the right. This reflects the fact that most of the fisheries for which we have exploitation rates data, are from medium to heavily-exploited populations in the upper U.S. Midwest. Very little information is available for lakes with low fishing intensity, representative of the large number of lakes in northern Ontario. The reason for this lack of data is that, in northern Ontario creel surveys to estimate harvest rates are usually initiated after a decline in fishing success and yield was perceived (Baccante & Colby 1991).

Spangler *et al*. (1977) provide a synthesis of response indicators of percids to exploitation. They conclude that changes in recruitment variability, growth rates and age to maturity are the most conspicuous responses to exploitation. Thus, the maximum sustainable exploitation rate depends on how rapidly the population can compensate to reductions in density within the bounds of habitat and energy availability. Although exploitation rates reported in the literature may not reflect maximum sustainable rates for the respective fisheries, they likely reflect rates characteristic of fairly heavily exploited fisheries because of the demand for walleye.

We plotted walleye exploitation rates over an energy cline, as measured by *GDD* (Fig. 8). Although we cannot quantify the sustainability of these rates, using few, long-term data sources (Savanne Lake, Ont.; Wisconsin lakes and Lake Erie), we drew a line which we feel approximates levels beyond which over exploitation is likely to occur. It is difficult to generalize about allowable exploitation rates because they are influenced by factors such as lake productivity, habitat and management objectives, however, we feel that very few walleye populations will sustain exploitation rates beyond 30%, without significant loss in fishing quality. A lake with lower productivity will not support as high exploitation rates as a more productive lake within the same *GDD* zone. For example, Whitefish and Savanne lakes, Ontario, both receive about 1 900 *GDD*, however Whitefish is much more productive than Savanne, *MEI* of 33 and 16, respectively. Higher productivity translates into higher adult population density, about 25/ha in Whitefish and 15/ha in Savanne. Habitat can also influence survival, density and ultimately allowable harvest. Deep, clear lakes favour lake trout/bass/pike communities with marginal walleye populations which cannot support harvest rates similar to populations in shallower, dark water lakes with more favourable walleye habitat (Johnson *et al*. 1977). Management objectives also dictate the rate of exploitation. If the management objective is to preserve fishing quality, then harvest should be kept at a much lower level than the maximum allowable rate. However, if the objective is to maximize angling harvest opportunities, then higher fishing quality may be traded off for higher harvest, set within the biological constraints of the system (Baccante & Colby 1991).

Exploitation rates that have resulted in collapses of walleye populations in four lakes are also shown on the graph (Fig. 8). The waterbodies are: Henderson Lake (Ontario), Nipigon Bay (Lake Superior, Ontario), Wapun Lake (Manitoba) and Wolf Lake (Alberta). Henderson and Wapun Lakes fisheries were exploited as part of research studies by the Ontario Ministry of Natural Resources and Fisheries and Oceans Canada, respectively. The exploitation rates in both lakes were very high, around the 50% range (Table 3). The walleye in Nipigon Bay was mostly harvested by commercial fishery, however, Ryder (1968) postulated that pollution from a kraft paper mill was also responsible for the demise of the population. Although fishing mortality increased from 7 to 34% from 1955 and 1957, Ryder felt that this was of secondary importance compared to habitat degradation. The walleye population in Wolf Lake, Alberta, has been subjected to tremendous increases in angling pressure. From 1979, when creel surveys were first started, to 1992, angling pressure has increased 600% (Mike Sullivan, Dept. of Environ. Protection, Edmonton, Alberta, pers. comm.). Sullivan also reports significant increases in angler skill levels, and better fishing equipment (sounders, Lindy Rigs, leeches, etc.). As the walleye density declined in Wolf Lake, the fish concentrated in two small areas, which made them extremely vulnerable to anglers.

Although exploitation rates as high as 35% are considered sustainable in some lakes, for example in Wisconsin (Staggs *et al*. 1990), we feel that exploitation rates exceeding 25% is probably optimum in high energy systems with good walleye production. One lake which has produced unusually high walleye yields (9 kg/ha) over a long time period (over 30 years) with exploitation rates averaging around 28%, is Escanaba Lake, Wisconsin. Escanaba has relatively low fertility (*MEI* of 7.9) but good survival of young walleye which grow fast, mature early and have high fecundity. We suspect that Escanaba's combination of dark water, which provides competitive advantage for walleye, and sufficient weed beds to protect young fish from cannibalism and predation, provides ideal conditions for high turnover rates. Also, yellow perch do not grow to large sizes, possibly due to predator density, thus reducing the impact on young walleye. Overall, energy in Escanaba is efficiently channelled through the walleye component of the community.

In less productive systems, typical of a large number of boreal lakes in northern Ontario and other parts of Canada, it is unlikely that many populations can support exploitation rates in excess of around 15%, without significant loss of fishing quality. However, as we have already pointed out, the scarcity of exploitation rates data for these types of lakes makes it difficult to predict safe rates over a broad geographic area. However, at the northern limits of their distribution, even exploitation rates of 10% may be too high for adult walleye. Confidence in setting safe rates is enhanced if managers have available adequate population, community and habitat information.

5. Management implications

Comparing population variables for walleye throughout their distributional range provides insights regarding the magnitude of variation among these parameters. For instance, by tabulating the data into quartiles (Table 1), we describe quantitatively where a given body of water might lie along a gradient of population density, exploitation rates or yield. This comparative approach helps to categorize a lake based on its population characteristics, and helps to derive appropriate management actions.

A comparative approach is useful because long term data sets are scarce. More common are single year observations or sporadic ones, often a few years apart. This is true particularly for estimates of population abundance. Hansen *et al*. (1991) used long-term data from Escanaba Lake, Wisconsin, to evaluate the accuracy of population estimates from other lakes where reliable data were lacking. The estimates were then used to set harvest quotas. They concluded that the accuracy of estimates of adult walleye abundance declined over time from the year the estimates was obtained to the year it was used to set a harvest quota. This underscores the need and importance of long-term studies as reference points when comparing single year or a limited number of observations. Consider a given walleye population having an average density, and a higher than average exploitation rate. We would than expect the average size of fish harvested to be smaller, and the sustainable harvest to be average or better. In more northern latitudes especially on the Canadian shield we expect to find lower sustainable exploitation rates and yields associated with declining insolation and nutrient availability, a sustainable harvest of larger size fishes (due to slower growth and delayed maturity), more variable densities due to slower recovery rates.

If, observations on a remote fishery appear aberrant or unexpected, in respect to quartiles (Table 1) an investigator might consider the data suspect , and request further research or information initiating regulations. For example, population estimates may be suspect if other parameters such as harvest, exploitation rates, harvest size, and potential yields appear incompatible with other population parameters. The same would apply when comparing estimates of the other variables with each other. Finally, we suggest that a person trained in monitoring the status of walleye populations will find the comparative information presented here useful for interpreting harvest and environmental impacts on lightly monitored stocks.

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References

Arnold, B. B. 1960: Life history notes on the walleye, (Stiozostedion vitreum vitreum) Mitchill, in a turbid water, Utah Lake, Utah. — M.Sc.-thesis, Utah State Univ., Logan, Utah. 114 pp.

Baccante, D. A. & Colby, P. J. 1991: Quantifying walleye angling success. — American Fisheries Society Symposium 12: 397–405.

Baccante, D. A. & Reid, D. M. 1988: Fecundity changes in two exploited walleye populations. — North American Journal of Fisheries Management 8: 199–209.

Balcer, M. D., McCauley, D. J., Niemi, G. J. & Brooke, L. T. 1986: Ecological assessment of factors affecting walleye ova survival in the lower Fox River. — A Final Report Submitted to U.S. E.P.A., Environmental Research Laboratory, Duluth, MN, in Partial Fulfilment of Cooperative Agreement #CR-811723-02-0. 110 pp.

Barbour, C. D. & Brown, J. H. 1974: Fish species diversity in lakes. — American Naturalist 103: 473–489.

Beverton, R. J. H. 1987: Longevity in fish: some ecological and evolutionary considerations. — In: Woodhead, A. D. & Thompson, K. H. (eds.), Evolution of longevity in animals: A Comppeartive Approach. Plenum Press, New York. 354 pp.

Carlander, K. D. 1941: Tagging returns on Lake Vermilion walleye, 1940. — Minnesota Department of Conservation, Investigative Report No. 23: 8 pp.

— 1945: Age, growth, sexual maturity and population fluctuations of the yellow pike-perch (Stiz ostedion vitreum vitreum), with reference to the commercial fisheries, Lake of the Woods, Minnesota. — Transactions of the American Fisheries Society 73(1943): 90–103.

— 1977: Biomass, production, and yields of walleye (Stizostedion vitreum vitreum) and yellow perch (Perca flavescens) in North American lakes. — Journal of the Fisheries Research Board of Canada 34: 1602–1612.

Colby, P. J. & Baccante, D. A. 1996: Dynamics of an experimentally exploited walleye population: sustainable yield estimate. Ann. Zool. Fennici 33: 589–599.

Colby, P. J. & Nepszy, S. J. 1981: Variation among stocks of walleye (Stizostedion vitreum vitreum): management implications. — Canadian Journal of Fisheries and Aquatic Sciences 38: 1814–1831.

Colby, P. J., Lewis, C. A. & Eshenroder, R. L. 1991: Status of walleye in the Great Lakes: Case studies prepared for the 1989 workshop. — Special Publication No. 91–1. Great Lakes Fishery Commission, Ann Arbor, MI. 222 p.

Colby, P. J., Lewis ,C. A., Eshenroder, R. L., Haas, R. C. & Hushak, L. J. 1994: Walleye rehabilitation guidelines for the Great Lakes area. — Great Lakes Fishery Commission. 112 p.

Deyne, G. 1983: Analysis and interpretation of Kenogamissi fish data, 1971–75. — Ontario Ministry of Natural Resources, Manuscript Report. 48 pp.

Elsey, C. A. & Thompson, R. T. 1977: Exploitation of walleye (Stizostedion vitreum vitreum) in Lac Des Mille Lacs, northern Ontario, by commercial and sport fisheries, 1958–75. — Journal of the Fisheries Research Board of Canada 34: 1769–1773.

Erickson, J. & Stevenson, F. 1967: Management consultation and experimental design. — Ohio Department of Natural Resources, Fed. Aid Fish Wildlife Restoration Project. F-29-R-6, Job No. 12. 7 pp.

Eschmeyer, P. H. 1950: The life history of the walleye (Stizostedion vitreum) in Michigan. — Michigan Department of Conservation, Institute of Fisheries Research, Bulletin No. 3. 99 pp.

Forney, J. L. 1967: Estimates of biomass and mortality rates in a walleye population. — New York Fish and Game Journal 14: 176–192.

Fruetel, M. 1994: Whitefish Lake: A summary of Creel Surveys and Assessment Programs from 1963 to 1990 with an evaluation of Walleye, yellow Perch and Northern Pike Population Status. — Northwest Region Science and Technology Technical Report #78. 67 pp.

Hansen, M. J. 1989: A walleye population model for setting harvest quotas. — Wisconsin Department of Natural Resources, Bureau of Fisheries Management. Fish Management Report 143.

Hansen, M. J., Staggs, M. D. & Hoff, M. H. 1991: Derivation of safety factors for setting harvest quotas on adult walleyes from past estimates of abundance. — Transactions of the American Fisheries Society 120: 629–628.

Hauber, A. 1989: Impact of continuous fishing on the walleye population of Lake Dubay, Marathon County, Wisconsin, 1983–84. — Wisconsin Department of Natural Resources, Bureau of Fisheries Management. Fish Management Report 142.

Hayes, F. R. 1957: On the variation in bottom fauna and fish yield in relation to trophic level and lake dimensions. — Journal of the Fisheries Research Board of Canada 14: 1–32.

Henderson, B. A. & Nepszy, S. J. 1994: Reproductive tactics of walleye (Stizostedion vitreum) in Lake Erie. — Canadian Journal of Fisheries and Aquatic Sciences 51: 986–997.

Hokanson, K. E. F. 1977: Temperature requirements of some percids and adaptations to the seasonal temperature cycle. — Journal of the Fisheries Research Board of Canada 34: 1524–1550.

Jackson, D. A., Harvey, H. H. & Somers, K. M. 1990: Ratios in aquatic sciences: statistical shortcomings with mean depth and the morphoedaphic index. — Canadian Journal of Fisheries and Aquatic Sciences 47: 1788–1795.

Jenkins, R. M. & Morais, D. I. 1971: Reservoir sport fishing effort and harvest in relation to environmental variables. — American Fisheries Society Special Publication 8: 371–384.

Johnson, F. H. 1971: Survival of stocked walleye fingerlings in northern Minnesota Lakes as estimated from age-composition of experimental gill net catches. — Minnesota Department of Natural Resources, Investigative Report No. 314. 12 pp.

Johnson, F. H. & Johnson, M. W. 1971: Characteristics of the 1957–1958 and 1939 sport fishery of Lake Winnibigoshish and connecting waters with special empha-

sis on the walleye population catch. — Minnesota Department of Natural Resources, Division of Game and Fish section of fisheries, Investigative Report No. 312. 31 pp.
Johnson, M. G., Leach, J. H., Minns, C. K. & Olver, C. H. 1977: Limnological characteristics of Ontario lakes in relation to associations of walleye (Stizostedion vitreum vitreum), northern pike (Esox lucius), lake trout (Salvelynus namaycush), and smallmouth bass (Micropterus dolomieui). — Journal of the Fisheries Research Board of Canada 34: 1592–1601.
Kallemeyn, L. W. 1986: Impact of sportfishing on walleye in Kabetogama Lake, Voyageurs National Park. — In: Larson, G. & Soukup, M. (eds.), Proceedings of the 4th Conference On Research in the National Parks and Equivalent Reser. ves, July 13–18, 1986: 23–39.
Kempinger, J. J. & Carline, R. F. 1977: Dynamics of the walleye (Stizostedion vitreum vitreum) population in Escanaba Lake, Wisconsin, 1955–72. — Journal of the Fisheries Research Board of Canada 34: 1800–1811.
Kraai, J. E. & Prentice, J. A. 1974: Walleye life history study. — Texas Parks Wildlife Department, Federal Aid Fish Wildlife Restoration Project. F-7-R-23, Job No. 17a. 28 pp.
Larscheid, J. G. 1992: Contribution of stocked walleyes and population dynamics of adult walleye in Spirit and East and West Okoboji Lakes. Assessment of actors impacting YOY fish abundance in Spirit and East and West Okoboji Lakes. — Project No. F-135-R-3. Note: Iowa Department of Natural Resources, Federal Aid to Fish Restoration Annual Performance Report, Natural Lakes Investigations Project No. F-135-3. 125 pp.
Leach, J. H., Dickie, L. M., Shuter, B. J., Borgmann, U., Hyman, J. & Lysack, W. 1987: A review of methods for prediction of potential fish production with application to the Great Lakes and Lake Winnipeg. — Canadian Journal of Fisheries and Aquatic Sciences 44(Suppl. 2): 471–485.
Lealos, J. M. & Bever, G. G. 1982: The Flambeau Flowage Fishery. Wisconsin Department of Natural Resources Bureau Of Fisheries Management. —Fish Management Report No. 110. 17 pp.
Matuszek, J. E. 1978: Empirical predictions of fish yields of large North American lakes. — Transactions of the American Fisheries Society 107: 385–394.
Mraz, D. 1968: Recruitment, growth, exploitation and management of walleyes in a Southeastern Wisconsin Lake. — Wisconsin Department of Natural Resources. Technical Bulletin No. 40. 39 pp.
Muench, K. A. 1966: Certain aspects of the life history of the walleye, (Stizostedion vitreum vitreum), in Center Hill Reservoir, Tennessee. — M.Sc.-thesis, Tennessee Technical University, Cookeville, Tenn. 66 pp.
Muth, K. M. & Ickes, B. S. 1993: Fecundity of walleyes in Western Lake Erie, 1966 and 1990–91. — Journal of Great Lakes Research 19: 715–719.
Niemuth, W., Churchill, W. & Wirth, T. 1959: The walleye: Its life history, ecology, and management. — Wisconsin Conservation Department Publication 227: 3–14.
Nord, R. C. 1967: A compendium of fishery information on the Upper Mississippi River. — Upper Mississippi River Conservation Committee. 238 pp.
Olson, D. E. 1955: Notes on the size, structure and mortality rates of the walleye (Stizostedion vitreum) population of Lake Sallie. — Minnesota Department of Conservation, Investigative Report No. 158. 7 pp.
— 1958: Statistics of a walleye (Stizostedion vitreum) sport fishery in a Minnesota lake. — Transactions of the American Fisheries Society 87: 52–72.
Osborn, T. C. & Schupp, D. H. 1985: Long-term changes in the Lake Winnibigohish walleye sport fishery. — Minnesota Department of Natural Resources, Investigative Report No. 381. 41 pp.
Osborn, T. C., Close, T. L., Colvin, S. E. & Pereira, D. L. 1991: The walleye sport fishery of the St. Louis River Estuary, 1980–1982. — Minnesota Department of Natural Resources, Division of Fish and Wildlife, Section of Fisheries. Investigative Report No. 412. 13 p.
Payer, R. D., Pereira, D. L., Larson, M. L., Younk, J. A., Frie, R. F., Schupp, D. H. & Osborn, T. C. 1987: Status and simulation model of Lake of the Woods, Minnesota, walleye fishery. — Minnesota Department of Natural Resources. Investigative Report No. 389. 160 pp.
Payne, N. R. 1963: The life history of the yellow walleye, (Stizostedion vitreum vitreum) (Mitchill) in the Bay of Quinte. — M.Sc.-thesis, University of Toronto, Toronto, Ontario. 40 pp.
— 1965: A progress report on the Mississagi River walleye (Stizostedion vitreum) study, Sault Ste. — Marie District, Ontario Department of Lands and Forest., Manuscript Report. 29 pp.
Priegel, G. R. 1970: Reproduction and early life history of the walleye in the Lake Winnebago region. — Wisconsin Department of Natural Resources. Technical Bulletin No. 45. 105 pp.
Rawson, D. S. 1952: Mean depth and fish production of large lakes. — Ecology 33: 513–521.
Reid, D. M. & Momot, W. T. 1985: Evaluation of pulse fishing for the walleye, (Stizostedion vitreum vitreum), in Henderson Lake, Ontario. — Journal of Fish Biology, 27: (Suppl. A): 235–251.
Rempel, R. S. & Colby, P. J. 1991: A statistically valid model of the morphoedaphic index. — Canadian Journal of Fisheries and Aquatic Sciences 48: 1937–1943.
Rose, G. A. 1955: The fluctuation in abundance of walleye in Spirit Lake, Iowa. — Proceedings of the Iowa Academic Sciences 62: 67–575.
— 1984: The Goulais River walleye population – an account of the demise of a fishery. — Ontario Ministry of Natural Resources. Report 56. 23 pp.
Rousenfell, G. A. 1946: Fish production in lakes as a guide for estimating production in proposed reservoirs. — Copeia 1946: 29–40.
Ryder, R. A. 1968: Dynamics and exploitation of mature walleye (Stizostedion vitreum vitreum) in the Nipigon Bay region of Lake Superior. — Journal of Fisheries Research

Board Canada 25: 1347–1376.
Schainost, S. 1983: Harvest and population dynamics of the walleye in Branched Oak Lake, Nebraska. — Nebraska Game Parks Committee. Technical Services 12. 35 pp.
Schlesinger, D. A. & McCombie, A. M. 1983: An evaluation of climate, morphoedaphic and effort data as predictors of yield from — Ontario sport fisheries. Ontario Fisheries Technical Report Series 10: 14 p.
Schneider, D. R. 1969: Results of experimental stocking of walleye fingerlings, 1951–1963. Michigan Department of Natural Resources. — Fisheries Research Report 1753. 31 pp.
— 1978: Selection of minimum size limits for walleye fishing in Michigan. — In: Kendall, R. L. (ed.), Selected Coolwater Fishes of North America: 398–407. American Fisheries Society Special Publication No 11.
— 1987: Analysis of historical walleye information on Otter Tail Lake. — Minnesota F-29-R (P)-6, Study 5, Job 49, Completion Report. 62 pp.
— 1987: Analysis of historical walleye information on Otter Tail Lake. — Minnesota Department of Natural Resources, Completion Report F-29-R(p)-6: 63.
Schneider, J. C. 1977: A synopsis of walleye tagging experiments in Michigan, 1929–1965. — Michigan Department of Natural Resources, Fisheries Research Report No. 1844: 29.
Serns, S. L. 1981: Effects of a minimum length limit on the walleye population of Wolf Lake, Vilas County, Vilas County, Wisconsin. — Wisconsin Department of Natural Resources. Fish Management Report No.106. 11 pp.
— 1982: Walleye fecundity, potential egg deposition, and survival from egg to fall young-of-the-year in Escabana Lake, Wisconsin, 1979–1981. — North American Journal of Fisheries Management 4: 388–394.
— 1985: Proportional stock density index – is it a useful tool for assessing fish populations in northern latitudes? — Wisconsin Department of Natural Resources. Research Report No. 132. 11 pp.
Smith, C. G. 1941: Egg production of walleyed pike and sauger. Norris Reservoir fish differ from some species in other localities. — Prog. Fish-Cult. 54: 32–34.
Sobchuck, M. 1981: Estimated abundance, harvest and exploitation of a river spawning walleye population. — Ontario Ministry of Natural Resources Report. 54 pp.
Spangler, G. R., Payne, N. R., Thorpe, J. E., Byrne, J. M., Regier, H. A. & Christie, W. J. 1977: Responses of percids to exploitation. — Journal of the Fisheries Research Board of Canada 34: 1983–1988.
Staggs, M. D., Moody, R. C., Hansen, M. J. & Hoff, M. H. 1990: Spearing and sport angling for walleye in Wisconsin's ceded territory. — Department of Natural Resources, Bureau of Fisheries Management. Administrative Report No. 31.
Stoudt, J. H. & Eddy, S. 1939: Walleye pike tagging study, 1937–1938, Chippewa National Forest. — Transactions of 4th North American Wildlife Conference. 4: 305–310.
Strand, R. F. 1980: The walleye (Stizostedion vitreum) sport fishery in three upper Mississippi reservoir Lakes: Cass, Audrusia, and Big Wolf, 1971–75. — Minnesota Department of Natural Resources. Investigative Report No. 368. 38 pp.
Weilandt, P. 1984: Walleye tagging project on the Upper Chunkuni River. — Ontario Ministry of Natural Resources Report. 41 pp.
Winterton, G. K. 1975: Structure and movement of a spawning stock of walleye, (Stizostedion vitreum vitreum) (Mitchell) in Georgian Bay. — M.Sc.-thesis. University of Guelph, Guelph, Ontario. 95 pp. + Append.
Wolfert, D. R. 1969: Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. — Journal of the Fisheries Research Board of Canada 26: 1877–1888.
Youngs, W. D. & Heimbuch, D. G. 1982: Another consideration of the morphoedaphic index. — Transactions of the American Fisheries Society 111: 151–153.