

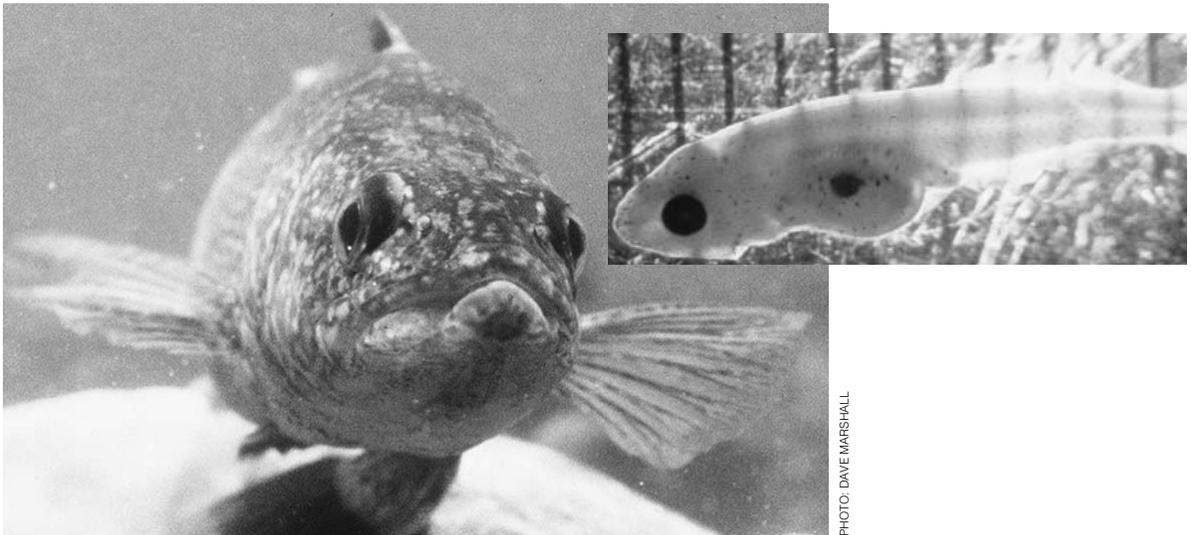
WISCONSIN DEPARTMENT OF NATURAL RESOURCES

RESEARCH REPORT 184

December 2000

Walleye Fry Hatching, Diet, Growth, and Abundance in Escanaba Lake, Wisconsin, 1985-1992

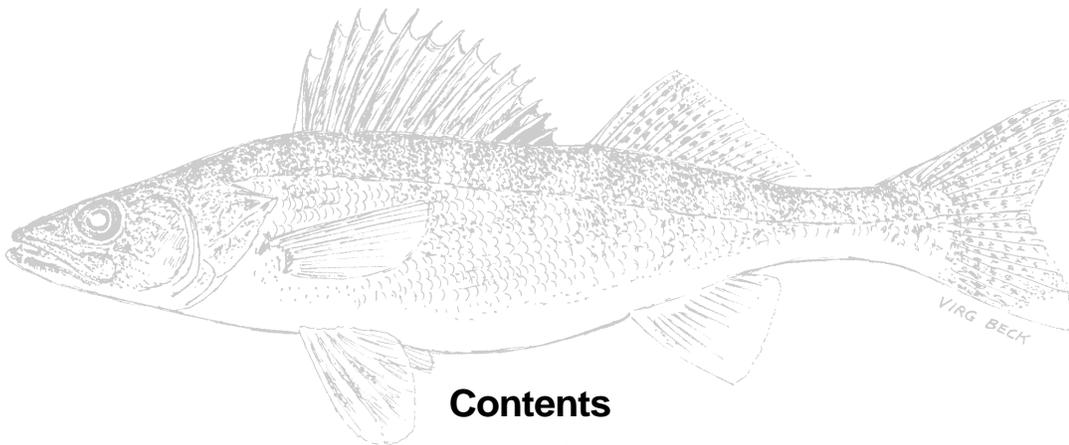
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Abstract

We examined the first six months of walleye (*Stizostedion vitreum*) life over an 8-year period (1985-1992) in north-central Wisconsin's Escanaba Lake to learn how water temperature and diet affect the hatching, growth, and abundance of age-0 walleyes. Walleye eggs incubated for 12-20 days and hatched significantly ($P = 0.04$) faster in years of rapid spring warm-up. Annual egg mortality varied from 38-81% in covered trays set on walleye spawning reefs and was not found to correlate with water temperature nor spring or summer fry abundance. Within 4-6 weeks of hatching, walleyes tow-netted offshore ate mostly planktonic Crustacea (especially *Daphnia*, *Leptodora*, and cyclopoid copepods), *Chaoborus* larvae, and some yellow perch (*Perca flavescens*). The walleye diet then shifted away from zooplankton to include chironomid larvae and pupae, larger insects, and more age-0 yellow perch. Fish increased in the walleye diet during years of high yellow perch abundance. Growth of age-0 walleyes occurred mainly from June through August, when mean total length increased 1.1-1.8 mm/day, depending on year. By September, these walleyes had reached 102-144 mm in mean total length, 36-310 fish/ha in estimated abundance, and 0.8-5.9 kg/ha in estimated biomass. Age-0 walleyes grew best in years of increased fish consumption and had their highest fall abundance in years of dense spring *Daphnia* blooms.

Cover photos: *Left: Adult walleye.*
Right: Age-0 walleye fry.



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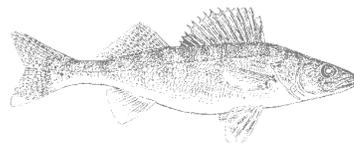




PHOTO: SANDY ENGEL

The steep and stony shore of a walleye spawning reef on Escanaba Lake.

Introduction

Annual differences in hatching, diet, and growth of age-0 walleyes (*Stizostedion vitreum*) affect abundance and harvest in later years (Colby et al. 1979). Although combined egg and fry mortality can reach 99% before walleyes reach 9-10 mm long (Forney 1976), more eggs hatch during warm weather when eggs develop fast and have a brief exposure to predators (Busch et al. 1975). Such abundant hatches can increase intraspecific food competition and thus reduce walleye growth in summer (Colby et al. 1987). Yet, few studies of age-0 walleyes have lasted long enough to assess annual variations in hatching, diet, or growth.

We followed walleyes from spring eggs to fall fingerlings for eight years in Escanaba Lake, north-central Wisconsin. Our objectives were to relate annual variations in walleye hatching success (percent of eggs that hatch), food habits, growth rate, and fall abundance to spring and summer differences in water temperature and prey availability. Two hypotheses were tested: (a) hatching success is dependent on ice-out date and spring warm-up, and (b) growth and abundance by fall is dependent on prey fish availability during spring and summer. We expected large hatches to heighten food competition and to improve fall survival only when prey fish were also abundant.

Walleye research at Escanaba Lake began in 1946 (Kempinger et al. 1975) when the Wisconsin

Conservation Department built a contact station for anglers and began a year-round compulsory creel census for all fish species. Research on age-0 walleye growth and abundance, with measurements of air and water temperature, began in 1958 (Serns 1982a, 1984). Research on walleye fecundity and first summer survival began in 1979 (Serns 1982b). Our study builds on this research base by focusing on the roles of diet and water temperature.

Study Area

Located in Wisconsin's Vilas County, Escanaba Lake (46°04' N latitude, 89°35' W longitude) is a 118.6 ha glacial ice-block basin with a maximum depth of 7.9 m and a mean depth (total volume/surface area) of 4.3 m. The shoreline of the lake with its four islands is 8.4 km long and forested except for a boat pier, a paved ramp, and the angler contact station near the south bay. Inshore deposits consist of silt and thin muck interrupted by stretches of sand and cobbles, ideal substrate for walleye spawning (Becker 1983). Sparse stands of arrowhead (*Sagittaria*), bulrush (*Schoenoplectus*), and spike-rush (*Eleocharis*) grow along shore. The lake has an inlet and a screened outlet — both intermittent — that discourage fish movement between lakes (Kempinger and Carline 1977).

Walleye ova streaming into a pail of lake water for fertilization.



PHOTO: MICHAEL H. HOFF

Gary R. Kubenik setting a screen-covered egg tray on a walleye spawning reef in Escanaba Lake.



PHOTO: SANDY ENGEL

The water column at the deepest area thermally stratifies from late May until early September, during which a dissolved oxygen deficit forms below a water depth of 5.4 m. Offshore water during spring overturn averages 46 $\mu\text{S}/\text{cm}$ in specific conductance (25°C) and 16 mg/L in total alkalinity (Kempinger and Carline 1977). Summer phytoplankton blooms reduce Secchi disk limit of visibility to 2-4 m by September, 40-70% of the water clarity in May. From 1985 to 1992, Escanaba Lake had open water between ice-out on 11-29 April and ice-up on 8 November-2 December.

Smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), and warmwater panfish (Centrarchidae) were common in Escanaba Lake before walleyes were introduced (Kempinger et al. 1975). Stocking 5.1 million age-0 walleyes in 1933-1942, at annual densities of 800-13,725 fish/ha, established walleye reproduction in the lake by at least 1946 when the compulsory creel census began (Patterson 1952). Repeated stockings also built reproducing populations of muskellunge (*Esox masquinongy*) and northern pike (*E. lucius*) that, with walleyes and yellow perch, made up 99% of the angling harvest during our study (1985-1992).

Methods

Walleye egg incubation and peak hatching were observed in screened trays set among cobbles on separate walleye spawning reefs. All trays started with 50 healthy-looking eggs, collected and fertilized on the same day. Eggs in 1985-1986 were collected with a kick net from the lake bed and distributed among eight uncovered trays, each 0.3 m². Eggs in 1987-1992 were artificially fertilized and distributed among two covered trays of 0.1 m². Eggs were fertilized each year by mixing ova from one female with sperm from 2-3 males in a wet pan for about 5 minutes and allowing all eggs to harden for an hour in a pail of lake water containing suspended clay (Piper et al. 1982). The process was repeated for two more females with different males.

Eggs were fertilized during peak spawning, judged from the proportion of ripe to spent females caught daily in fyke nets. All trays with eggs were set on walleye spawning reefs within hours of fertilization. Each year, the trays were examined first every few days and then daily to determine peak hatching date (when the greatest number of eggs hatched in 24



PHOTO: SANDY ENGEL

Michael T. Vogelsang, Jr. (left) and Matthew E. Stanley (right) about to lower a 50-cm tow net with flow meter to sample fish.



PHOTO: SANDY ENGEL

Michael T. Vogelsang, Jr. (left) and Matthew E. Stanley (right) dragging a bag seine on Escanaba Lake in late June.

hours) and incubation period (the number of days from peak spawning, when all eggs in the trays were fertilized, to peak hatching). After 1988, dead and hatched (shucked) eggs were also counted to calculate percent egg mortality and percent hatching.

Bottom water temperatures were recorded (nearest 0.3-0.5°C) with a wind-up or a battery-operated thermograph at a depth of 0.6-1.2 m on one of the walleye spawning reefs. Noon and midnight temperatures were averaged for the day of peak hatching to compute hatching temperature. Mean daily temperatures were pooled for the first 5 days of incubation (5-day incubation temperature), when egg mortality was greatest, and for the total incubation period (total incubation temperature).

Diet and growth were studied on age-0 walleyes sampled by tow netting every week in spring (mid-May to mid-June) and shore seining every two weeks in summer (late June through August). A cone net (50-cm mouth diameter, 752- μ m mesh) with a propeller flow meter was towed horizontally after dark to collect age-0 walleyes and age-0 yellow perch at depths of 0, 0.9, and 1.8 m from each of three sites (1985-1992) and at 2.7, 3.7, and 4.6 m from a central

site (1985-1988). Each depth tow lasted 3 minutes. Total counts of each fish species were combined from all sites to compute catch/effort (number of age-0 fish/1,000 revolutions clocked) for each sample depth. A bag seine (11.6 m \times 1.8 m, 3.2-mm² mesh) was dragged 61 m by about 8 m (0.2 ha) along four inshore sites to sample age-0 yellow perch during the day and age-0 walleyes during the day and night. Total counts of each species were combined from all sites to compute catch/effort (number of age-0 fish/ha seined). Up to 12 or 13 age-0 walleyes/sample, but no more than 25/month, were preserved in 10% formalin and later measured for total length (nearest 0.1 mm up to 10 mm long, nearest 1 mm over 10 mm long) before examining their diet.

Diet was examined by opening the whole digestive tracts of age-0 walleyes from tow nets and opening the stomachs of those from seines. All prey items were counted under a binocular dissecting microscope with a total magnification adjustable to 7-30 \times or 8-40 \times total magnifications. Carapace lengths, excluding the antennae and spines, of zooplankton prey were measured with an ocular micrometer (nearest 0.1 mm). Fish remains identifiable only to

family (Centrarchidae, Cyprinidae, or Percidae) were scored as “unidentified” fish. Frequency of occurrence (percent of stomachs or whole digestive tracts examined) and percent by prey number (percent of total prey in stomachs or whole digestive tracts) were calculated for each prey taxon. Although the digestive tracts of sac fry were examined for first prey, results were tabulated only for fish without any yolk-sac material.

Because many fish prey were too digested for species identification, we compared yellow perch abundance in the lake with that in the diet by estimating the frequency of occurrence for yellow perch from the proportion of stomachs or whole digestive tracts with known to unknown fish species. For example, if yellow perch prey occurred in 40% of stomachs with identified fish prey, we assumed yellow perch occurred in 40% of stomachs with unidentified fish prey.

Zooplankton were sampled within a few days of each fish sampling date. A cone net (15.2-cm mouth diameter, 110- μ m mesh) without a flow meter was used to collect two plankton samples around noon. Each sample consisted of five bottom-to-surface tows collected over the deepest site and preserved in 10% formalin (1985-1986) or 70% ethanol (1987-1992). The volume of water strained during each tow was estimated by substituting net diameter, number of hauls, and distance towed into the volume formula for a right-sided cylinder (Smith et al. 1968). Sample counts of each taxon were averaged for the two sites on each date and divided by the volume of sampled lake water to give population density (number/L). Rotifers, nauplii, and immature *Chaoborus* were excluded from the total counts to compute total density of edible Crustacea, the taxa ingested by the age-0 walleyes we examined.

Shannon-Wiener (SW) diversity index (H') was calculated from the proportion (R_i) of each taxon in the diet or in the lake water (Pielou 1975), by summing the product of R_i and its \log_2 : ($H' = -\sum R_i \log_2 R_i$). Evenness was then calculated from each SW diversity index as a proportion of the maximum diversity (H'_{max}) reached if all taxa had equal abundance: (H'/H'_{max}).

Growth from peak hatching through 30 September (growing season) was computed graphically

each year from weekly or biweekly length measurements plotted against calendar day. Annual growth rate was then computed as the daily total length increment (mm/day) averaged for each growing season.

The abundance and biomass of age-0 walleyes were estimated each September (1985-1992) by mark-recapture (Ricker 1975). A boom shocker delivering 230-V AC was motored after dark around all islands and the entire lakeshore. A random sample of 50 age-0 walleyes was measured individually for total length (nearest 1 mm) and, to save time, in lots of five for body weight (nearest 1 g); scale samples were aged to assess maximum length at age-0. The entire catch of unmarked age-0 walleyes was then fin clipped and released. After a few days, electrofishing resumed for 1-5 nights to sample marked and unmarked fish.

The association of water temperature with the hatching, diet, growth, and fall abundance of age-0 walleyes was examined with the nonparametric



Matthew E. Stanley holding a 15.2-cm cone net for sampling zooplankton in Escanaba Lake.

PHOTO: SANDY ENGEL



PHOTO: CHRISTOPHER N. HORNUNG

Sandy Engel (left) and Gary R. Kubenik (right) demonstrating a small boom shocker in the south bay of Escanaba Lake.

Table 1. Ice-out, walleye incubation period, and incubation temperatures averaged for the start (first 5 days), total (all days), and end (peak hatching day) of incubation in Escanaba Lake.

Year	Complete Ice-out	Incubation Period		Incubation Temperature (°C)		
		Start	Days	Start	Total	End
1985	23 Apr	22 Apr	18	8.2	11.4	15.7
1986	14 Apr	16 Apr	19	6.2	9.2	12.4
1987	11 Apr	17 Apr	15	11.2	11.5	12.1
1988	13 Apr	22 Apr	17	6.1	10.5	14.6
1989	27 Apr	3 May	15	7.2	10.4	17.1
1990	20 Apr	25 Apr	12	14.3	13.2	12.8
1991	19 Apr	23 Apr	20	7.5	9.1	15.1
1992	29 Apr	2 May	14	9.0	13.0	14.4

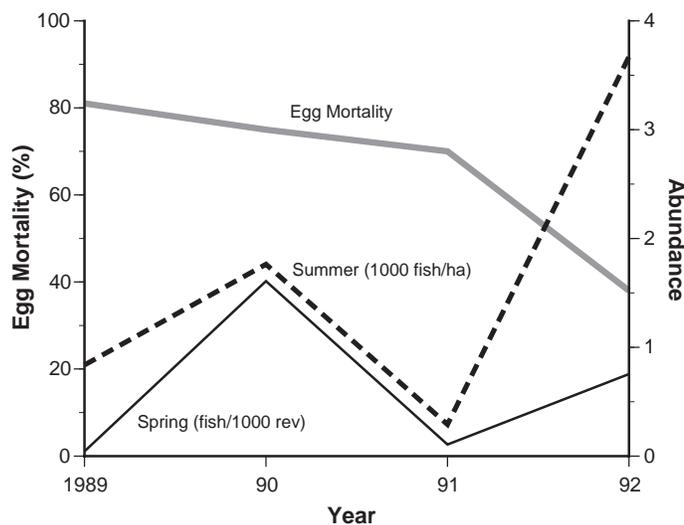


Figure 1. Walleye egg mortality in covered trays and abundance of age-0 walleyes in spring tow nets and summer seine hauls, 1989-1992.

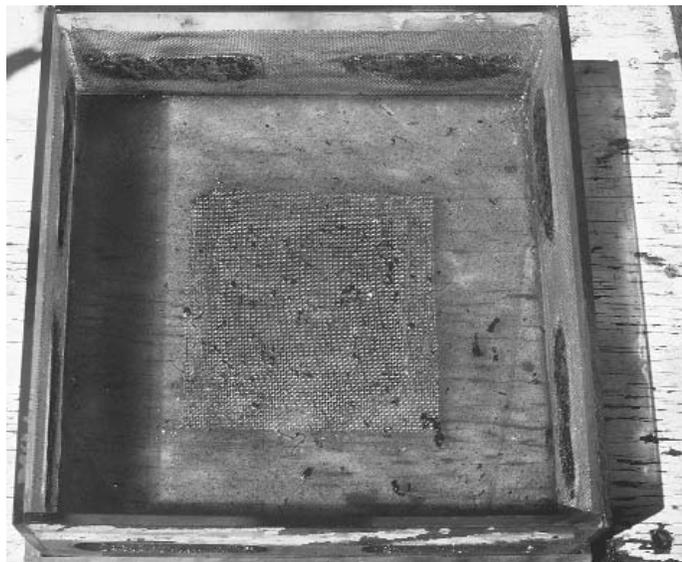


PHOTO: SANDY ENGEL

A 0.1-m² egg tray with cover removed to show sediment and unhatched walleye eggs after 28 days in Escanaba Lake.

two-sample Mann-Whitney rank sum U -test and Spearman's rank-order correlation r_s -test (Conover 1980, Siegel and Castellan 1988). We used Statistix[®] for Windows[®]-3.2 computer software (Anonymous 1996) to compare annual differences in diet, growth, and abundance for 1985-1992. Sample means and coefficients of variation for these eight sampling years were tested for spring (combined mid-May to mid-June samples), summer (combined late June through August samples), and fall (September sample). Probabilities computed for each test statistic were judged significant at the 0.05 α -level.

Results

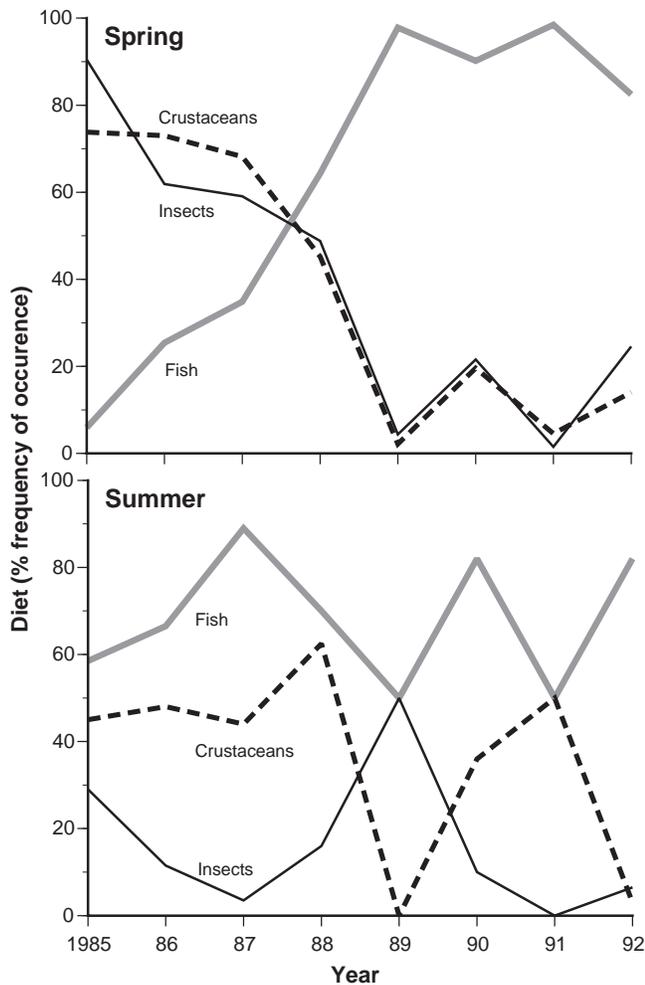
Hatching

Peak walleye spawning in Escanaba Lake, the start of incubation in our egg trays, occurred 1 day before complete ice-out in 1985, but 2-9 days after complete ice-out in 1986-1992 (Table 1). Walleye eggs in 1985-1992 hatched 17-26 days after complete ice-out and 12-20 days after peak spawning and fertilization.

Inshore water temperatures, averaged for all years, increased from 8.7°C for the first five days of incubation to 14.3°C at peak hatching. However, mean water temperatures varied among years by 6.1-14.3°C for the first five days of incubation and 12.1-17.1°C for the day of peak hatching.

Eggs developed faster during warm weather. Annual differences in length of incubation (days to peak hatching) had a negative correlation with means in total incubation temperature ($r_s = -0.87$, $P < 0.01$), but no correlation was found with coefficients of variation in total incubation temperature ($r_s = 0.50$, $P = 0.20$). Nor were lengths of incubation found to correlate with peak hatching temperatures ($r_s = 0.23$, $P = 0.59$). Longer incubations did not ensure that walleyes would hatch at warmer temperatures.

Annual egg mortality in 1989-1992, the only years when dead eggs were counted, averaged 66% and ranged from 38-81% (Figure 1). Dead eggs in these covered trays, looking milky or fungus-covered, clumped in silt on the tray bottoms.



Uncovered trays set in 1985-1986 were found with crayfish (*Orconectes propinquus*) and mottled sculpins (*Cottus bairdi*), egg predators that may have taken shelter from wave action. Placing eggs in covered trays seemed to increase egg mortality from spread of fungus, but decrease it from exclusion of predators.

Hatching success in 1989-1992 varied independently of water temperature in covered trays. Annual variations in percent egg mortality were not found to correlate with means ($r_s = 0.00$, $P = 1.00$) or coefficients of variation ($r_s = 0.40$, $P = 0.60$) in total incubation temperature. Although cool weather delayed hatching, neither cool nor variable water temperatures altered egg mortality.

Diet

Of the 849 age-0 walleye stomachs or whole digestive tracts examined in 1985-1992, 9% had no prey, 34% had invertebrates alone, and 57% had fish prey alone or with invertebrates. But invertebrate remains accounted for 98% by number of all prey and consisted mostly of cladocerans (chiefly *Daphnia* spp., *Holopedium gibberum*, *Latona*

Figure 2. The frequency of occurrence for fish, insects, and crustaceans in the spring and summer diets of age-0 walleyes, 1985-1992.

Table 2. The spring diet of 254 age-0 walleyes tow-netted offshore at night, expressed as percent by number (%N) and percent frequency of occurrence (%F) of prey items in whole digestive tracts with food.^a

Taxa	1985		1986		1987		1988		1989		1990		1991		1992		1985-1992	
	%N	%F	%N	%F														
Invertebrates	80	58	80	59	47	43	76	62	67	50	69	43	67	50	20	17	74	53
Crustaceans	49	45	64	48	45	43	68	62	0	0	64	36	67	50	13	8	57	44
Cladocera	33	29	34	37	19	24	42	23	0	0	55	31	0	0	13	8	35	30
<i>Daphnia</i>	32	29	34	37	19	24	39	23	0	0	45	26	0	0	13	8	33	29
<i>Bosmina</i>	0	0	0	0	0	0	3	8	0	0	7	7	0	0	0	0	1	2
<i>Chydorus</i>	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	<1	<1
Copepoda	16	18	30	38	26	27	26	38	0	0	8	10	67	50	0	0	21	25
Cyclopoida	15	18	21	27	18	19	13	31	0	0	8	10	33	50	0	0	16	20
Calanoida	0	0	5	9	8	14	11	23	0	0	0	0	0	0	0	0	3	7
Insects	31	29	16	11	2	3	8	15	67	50	5	10	0	0	7	8	17	15
Diptera	31	29	16	11	2	3	8	15	67	50	5	10	0	0	7	8	17	15
Chaoboridae	28	26	9	6	0	0	0	0	33	50	4	5	0	0	7	8	12	10
Chironomidae	3	6	7	9	2	3	8	15	33	50	2	5	0	0	0	0	5	7
Fish	20	58	20	66	53	89	24	69	33	50	31	81	33	50	80	100	26	73
Unidentified	16	46	12	38	19	32	8	23	0	0	11	29	0	0	53	67	14	39
Yellow Perch	5	14	8	27	34	57	16	46	33	50	20	52	33	50	27	33	12	34
Total (Number)	193	65	268	81	62	37	38	13	3	2	110	42	3	2	15	12	692	254
SW Diversity (H')	1.79		2.09		1.82		2.10		1.58		2.00		1.06		1.16		2.18	
Evenness (%)	37.7		44.2		38.4		44.4		33.4		42.1		22.3		24.4		45.9	

^a Of 285 walleyes examined, 34 had no prey and are not included in this table.

setifera, and *Leptodora kindtii*), C1-C6 post-larval instars (copepodids) of cyclopoid copepods (*Diacyclops thomasi*, *Mesocyclops edax*, and *Epischura lacustris*), and larval and pupal midges (chiefly *Chaoborus punctipennis* and Chironomidae). Fish remains accounted for 2% by number of all prey and consisted of unidentified fins, bones, flesh, or scales (51% by number of all fish items); yellow perch (38%); and other fish species (11%, including bluntnose minnows [*Pimephales notatus*], pumpkinseed sunfish [*Lepomis gibbosus*], and Iowa darters [*Etheostoma exile*]).

Newly hatched walleyes first ate crustaceans, some even before absorbing their yolk sacs. Of 52 sac fry examined in the eight years, all less than 9 mm long and barely a week old, 11 of them ingested cyclopoid or unidentified copepodids. The remaining sac fry had empty digestive tracts.

Some free-swimming walleyes ate fish within two weeks of hatching. Of 31 walleyes examined under

15 mm long, 71% of them ate fish. One 11-mm walleye had swallowed a 7-mm yellow perch. Fish prey items in other digestive tracts were too decomposed to measure length.

The spring diet of age-0 walleyes (Table 2), combined for all years, comprised crustaceans (57% by number of all prey in all years), insects (17%), and fish (26%). Walleye digestive tracts with food averaged nearly 3 prey items: 1.5 crustaceans, 0.5 insects, and 0.7 fish. The spring diet fluctuated among years (Figure 2), though Shannon-Wiener diversity ranged only from 1.06-2.10 and evenness held below 50%. The frequency of occurrence for fish in the spring diet, however, had a negative correlation with the frequency of occurrence for invertebrates alone ($r_s = -0.90$, $P = 0.002$). Walleyes either remained invertebrate feeders throughout spring or shifted early to a mixed diet of fish and invertebrates.

The summer diet of age-0 walleyes (Table 3), combined for all years, included 17 more taxa than

Table 3. The summer diet of 517 age-0 walleyes seined inshore at night, expressed as percent by number (%N) and percent frequency of occurrence (%F) of prey items in stomachs with food.^a

Taxa	1985		1986		1987		1988		1989		1990		1991		1992		1985-1992	
	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F
Invertebrates	100	95	100	84	100	71	99	60	6	7	95	27	30	6	96	28	99	52
Crustaceans	22	74	28	73	34	68	77	45	2	2	58	20	30	5	12	14	40	41
Cladocera	22	73	26	70	34	59	77	45	2	2	58	10	30	3	12	11	39	38
<i>Leptodora</i>	15	40	14	59	34	58	76	44	2	2	26	16	0	0	4	11	33	31
<i>Daphnia</i>	7	58	7	38	0	0	0	0	0	0	12	6	0	0	7	9	4	16
<i>Latona</i>	0	0	4	6	<1	3	1	5	0	0	1	2	0	0	0	0	1	2
<i>Holopedium</i>	<1	2	<1	14	0	0	0	0	0	0	11	2	2	2	1	4	<1	3
<i>Diaphanosoma</i>	0	0	<1	16	<1	8	<1	5	0	0	<1	2	14	2	0	0	<1	4
<i>Ceriodaphnia</i>	0	0	0	0	0	0	0	0	0	0	8	2	0	0	0	0	<1	<1
<i>Bosmina</i>	0	0	<1	2	0	0	0	0	0	0	<1	2	3	3	<1	4	<1	1
<i>Chydorus</i>	0	0	<1	6	0	0	0	0	0	0	<1	2	0	0	0	0	<1	<1
Copepoda	<1	7	2	25	<1	9	<1	8	0	0	<1	4	0	0	0	0	1	7
Cyclopoida	<1	4	1	13	<1	5	<1	8	0	0	<1	4	0	0	0	0	<1	4
Calanoida	<1	4	1	21	<1	6	<1	2	0	0	0	0	0	0	0	0	<1	4
Amphipoda	<1	5	<1	6	<1	2	0	0	0	0	<1	2	0	0	<1	2	<1	2
Insects	78	90	72	62	65	59	22	49	4	4	36	22	1	2	84	25	59	43
Diptera	78	89	71	59	65	56	22	41	2	2	35	16	1	2	84	19	58	39
Chaoboridae	68	75	70	48	62	45	16	27	0	0	33	10	0	0	78	14	54	31
Chironomidae	10	61	2	32	3	35	5	24	2	2	3	12	1	2	6	16	5	25
Ephemeroptera	0	0	<1	13	<1	8	<1	5	2	2	1	10	0	0	0	0	<1	5
Hemiptera	0	0	<1	2	0	0	<1	2	0	0	0	0	0	0	0	0	<1	<1
Odonata	0	0	0	0	0	0	0	0	0	0	<1	2	0	0	0	0	<1	<1
Coleoptera	0	0	<1	2	0	0	0	0	0	0	0	0	0	0	0	0	<1	<1
Fish	<1	6	<1	25	<1	35	1	65	94	98	5	90	70	98	4	82	1	58
Unidentified	<1	5	<1	25	<1	27	<1	1	62	63	3	61	39	52	2	42	<1	25
Yellow Perch	<1	4	0	0	<1	8	<1	25	32	35	2	33	20	39	2	47	<1	22
Bluntnose Minnows	0	0	0	0	0	0	0	0	0	0	0	0	2	3	0	0	<1	6
Pumpkinseed Sunfish	0	0	0	0	<1	2	<1	7	0	0	0	0	6	9	0	0	<1	3
Iowa Darters	0	0	0	0	0	0	<1	2	0	0	0	0	3	5	0	0	<1	1
Total (number)	5,471	84	7,169	63	5,548	66	6,562	84	53	46	930	51	105	66	1,428	57	27,266	517
SW diversity (H')	1.44		1.55		1.19		1.12		0.85		2.49		1.68		1.17		1.71	
Evenness (%)	30.3		32.7		25.1		23.5		17.9		52.6		35.3		24.7		36.1	

^a Of 564 walleyes examined, 46 had no prey and are not included in this table.

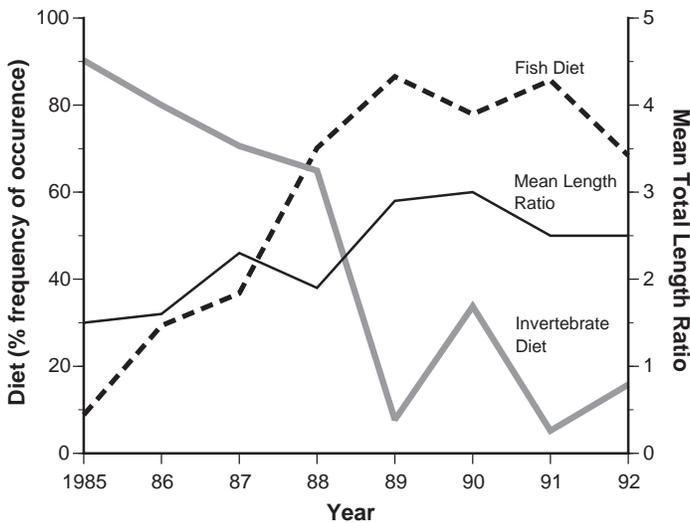


Figure 3. Mean total length ratio of age-0 walleye/age-0 yellow perch on 30 August and the frequency of occurrence for fish and invertebrates in the summer diet of age-0 walleyes, 1985-1992.

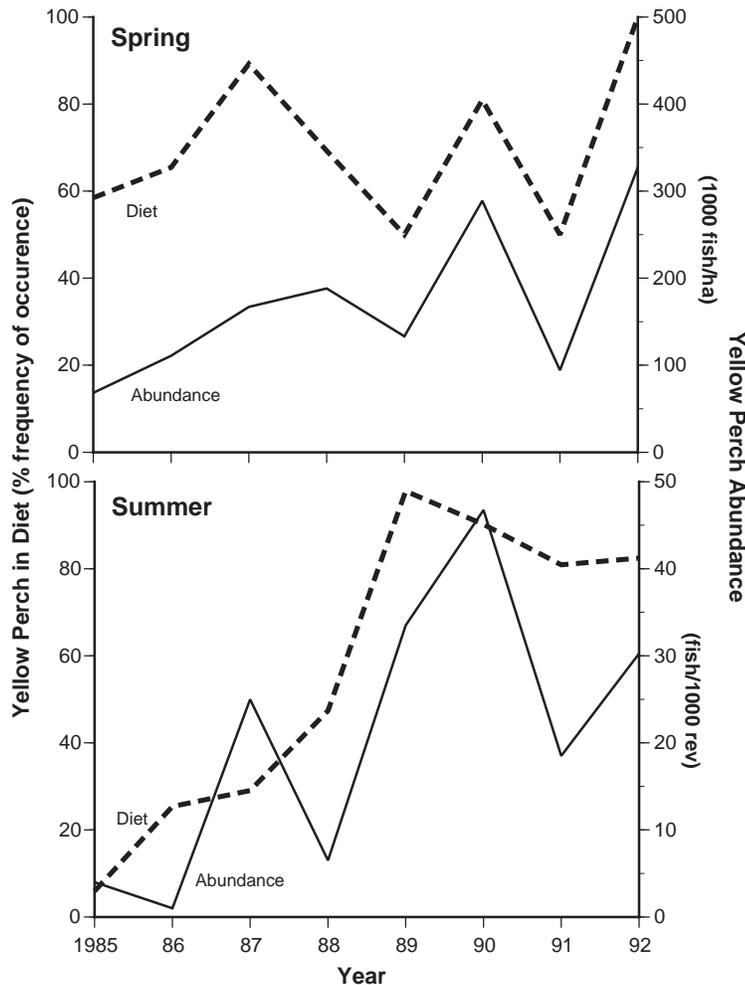


Figure 4. Age-0 yellow perch abundance and the frequency of occurrence for yellow perch in the diet of age-0 walleyes during spring and summer, 1985-1992. Tow-net catches were combined for water depths of 0, 0.9, and 1.8 m.

did the spring diet and comprised insects (59% by number of all prey), crustaceans (40%), and fish (1%). The stomachs examined in summer were much larger than the whole digestive tracts examined in spring and averaged 53 prey items apiece: 21 crustaceans, 31 insects, and 0.7 fish. Despite more prey taxa and larger digestive tracts, Shannon-Wiener diversity in summer remained below 2.5 with evenness typically below 50%. Still, the frequency of occurrence for fish during summer increased while that for insects and crustaceans decreased during the study.

The spring and summer diets were split between walleyes eating invertebrates alone and those eating fish with or without invertebrates. During summer, for example, 46% of age-0 walleyes examined ate fish: mostly yellow perch and some bluntnose minnows, pumpkinseed sunfish, and Iowa darters that were not identified in the spring diet. The frequency of occurrence for fish in the summer diet had a negative correlation with that for invertebrates alone ($r_s = -0.90$, $P < 0.01$).

More age-0 walleyes ate yellow perch, their principal fish prey, during summers of fast growth, when walleyes widened the length difference between predator and prey (Figure 3). Mean total length ratios of age-0 walleye/age-0 yellow perch on 30 August had a positive correlation with the frequency of occurrence for fish ($r_s = 0.79$, $P = 0.02$) and a negative correlation with that for invertebrates ($r_s = -0.76$, $P = 0.03$) in the summer diet. Fish prey in summer increased from 9% of stomachs in 1985, when age-0 walleyes averaged 1.5 times the mean length of age-0 yellow perch on 30 August, to 78% of stomachs in 1990, when the walleyes averaged 3.0 times the mean length of yellow perch. Age-0 yellow perch were most vulnerable to age-0 walleyes when their size difference was greatest.

More age-0 walleyes ate fish during years when age-0 yellow perch had high abundance (Figure 4). The frequency of occurrence for yellow perch in the walleye diet, estimated from the proportion of stomachs with known to unknown fish species,



PHOTO: MICHAEL H. HOFF

A 15-mm walleye from Escanaba Lake that swallowed an 8-mm yellow perch in May.

had a positive correlation with age-0 yellow perch catch/effort in spring tow nets ($r_s = 0.79$, $P = 0.02$) and summer seine hauls ($r_s = 0.88$, $P < 0.01$).

Age-0 walleyes of all sizes ate zooplankton, chiefly cladocerans and copepods, as well as larval and pupal *Chaoborus* that migrated off the bottom at night. These prey species together accounted for 93% by number of all food items, 48% of all age-0 walleyes with food.

But zooplankton were more diverse in the lake water than in all walleye stomachs or whole digestive tracts examined and consisted of 10% nauplii and 90% edible Crustacea. The total density of these edible Crustacea averaged 12.1 animals/L and comprised 40% cladocerans (chiefly *Daphnia* and *Bosmina*) and 60% cyclopoid and calanoid copepodids (chiefly *Diacyclops*, *Mesocyclops*, and *Diaptomus*).

Edible Crustacea in most years became more diverse in summer (Table 4). Although total density was only 20% higher for all years in spring than in summer, the spring samples averaged twice as many *Daphnia* (4.1 animals/L) and cyclopoid copepodids (8.0 animals/L) as did the summer samples. But the summer samples had more *Bosmina*, *Ceriodaphnia*, *Diaphanosoma*, *Eurycercus*, *Holopedium*, and *Leptodora* than did the spring samples. Shannon-Wiener diversity and evenness fluctuated among years for both spring and summer, but averaged higher than for prey items in the age-0 walleye diet.

Age-0 walleyes preferred eating cladocerans to copepods, large cladocerans to small ones, and calanoids to cyclopoids. Taxa averaging less than 0.6 mm long (*Bosmina*, *Ceriodaphnia*, *Chydorus*, and *Diaphanosoma*) made up 2% by number of crustaceans eaten, but 40% of edible ones netted. Taxa averaging more than 1.0 mm long (*Daphnia*, *Latona*, and *Leptodora*) made up 78% by number of crustaceans eaten, but only 23% of edible ones netted.

Table 4. Percent standing crop of planktonic Crustacea in Escanaba Lake during spring (Sp) and summer (Su), 1985-1992.

Taxa	1985		1986		1987		1988		1989		1990		1991		1992		1985-1992	
	% Sp	% Su	% Sp	% Su														
Cladocera	22.6	69.9	42.3	42.9	37.4	30.5	25.0	12.0	14.3	67.8	40.3	66.7	38.8	43.2	50.2	44.3	34.0	48.9
Leptodora	0.0	0.0	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.0	0.0	0.01
Daphnia	21.2	64.9	41.4	27.2	33.5	7.0	31.0	8.3	0.6	0.1	31.4	0.7	36.9	11.2	40.9	6.3	28.4	12.6
Holopedium	0.2	1.0	0.3	13.1	2.7	0.9	0.6	0.02	0.2	0.0	0.1	1.3	0.7	5.4	2.1	26.4	0.8	3.8
Diaphanosoma	0.0	2.3	0.1	7.7	0.1	14.1	0.1	3.9	0.1	0.2	0.0	0.1	0.0	5.3	0.0	0.0	0.04	4.5
Ceriodaphnia	0.0	0.6	0.0	0.5	0.03	1.9	0.03	0.3	0.1	0.7	0.0	0.0	0.0	3.0	0.0	0.0	0.02	1.2
Bosmina	1.4	2.0	0.1	3.6	1.0	6.0	2.1	10.1	13.6	67.0	8.5	64.8	1.1	26.7	6.4	11.5	4.5	26.2
Chydorus	0.0	0.1	0.8	3.8	0.1	5.6	0.1	0.7	0.4	0.2	0.3	0.7	0.04	0.2	0.0	0.1	0.2	0.6
Copepoda	77.4	30.1	57.7	57.1	62.6	69.5	75.0	88.0	85.7	32.2	59.7	33.3	61.2	56.6	49.8	55.7	67.1	56.7
Cyclopoida	58.4	23.2	46.5	31.7	46.3	59.3	43.0	67.2	58.2	21.5	51.4	25.2	27.9	18.7	32.0	28.7	49.5	36.0
Calanoida	19.0	6.9	11.3	25.3	16.3	10.3	32.0	20.8	27.5	10.7	8.3	8.0	33.3	36.9	17.8	27.1	17.6	20.7
Total (number/L)	27.9	12.6	12.4	11.3	13.8	11.5	10.7	13.6	8.2	9.8	20.9	7.9	7.6	16.7	5.6	4.5	14.0	11.2
SW diversity (H')	1.49	1.52	1.49	2.60	1.70	2.10	1.76	1.75	1.46	1.31	1.65	1.40	1.70	2.48	1.90	2.15	1.74	2.39
Evenness (%)	44.9	45.9	45.0	78.5	51.4	63.5	53.2	52.8	44.2	39.5	49.9	42.1	51.3	74.8	57.3	64.9	52.5	72.1

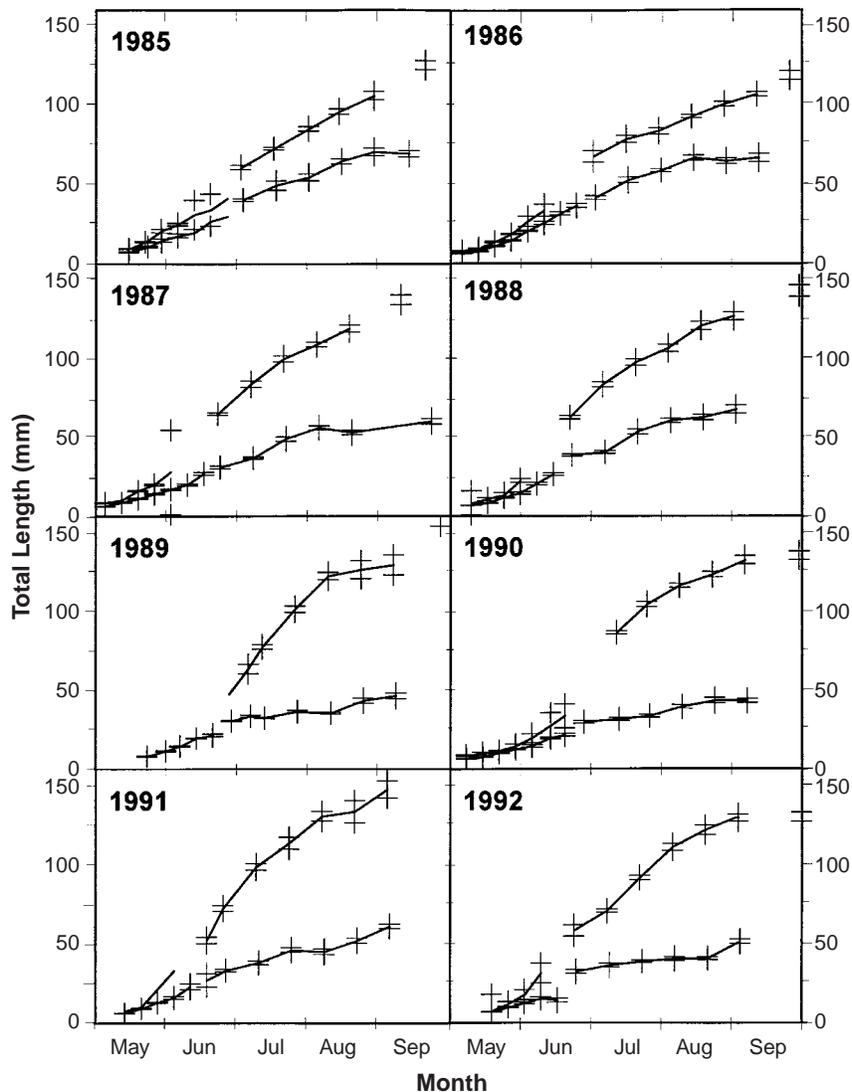


Figure 5. Growth of age-0 walleyes (upper curves) and yellow perch (lower curves) in Escanaba Lake for May-June (tow netting), June-August (seining), and September (electrofishing), 1985-1992. Thick slanted lines join mean total lengths; thin cross-lines bound 95% confidence intervals.

Growth

Nearly 7 mm long at hatching, age-0 walleyes during 1985-1992 reached a mean total length of 143 mm by October. Growth varied by month, season, and year. Age-0 walleyes grew an average of 1.5 mm/day in June, 1.2 mm/day in July, 0.7 mm/day in August, and 0.6 mm/day in September. Their mean total length for the eight years reached 20 mm by June, 66 mm by July, 103 mm by August, 125 mm by September, and 143 mm by October. Walleyes achieved more than half their first-year growth during 80-90 days of summer, when their mean total length increased by 103-134 mm, depending on year (Figure 5). The walleyes grew faster than did age-0 yellow perch by 2.3 times in June, 2.8 times in July, and 2.4 times in August. The combined spring, summer, and fall growth of age-0 walleyes (Figure 6) was slowest in 1986 (0.9 mm/day) and fastest in 1991 (1.3 mm/day).

The mean total length of age-0 walleyes on 30 September was not found to correlate with their fall abundance ($r_s = -0.67$, $P = 0.07$) or length of growing season ($r_s = -0.38$, $P = 0.35$). The growing season (peak hatching to 30 September) of age-0 walleyes varied from 150 days in 1989 to 167 days in 1986. Hatching earlier, therefore, did not ensure larger size by fall.

First-year growth seemed to improve on a fish diet. Age-0 walleyes with fish in their stomachs averaged 9 mm longer than did those with only invertebrates in their stomachs ($U = 4.0$, $P < 0.01$). But large size alone does not imply faster growth. Larger walleyes are more apt to capture fish and gain advantage in growth.

Despite hatching only 2-3 mm longer and 3-7 days earlier (Becker 1983), age-0 walleyes soon outgrew age-0 yellow perch. By 30 May, these walleyes

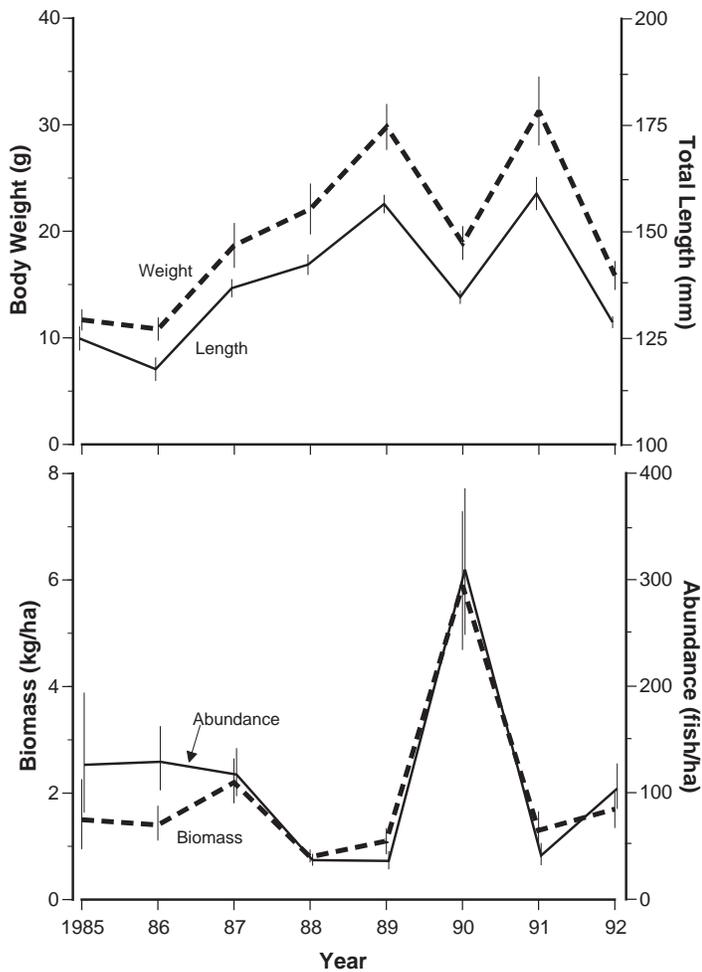


Figure 6. The mean weight and length and the estimated biomass and abundance of age-0 walleyes electrofished in September, 1985-1992. Thick slanted lines join means or population estimates; thin vertical lines join 95% confidence limits.

averaged 1.3-1.8 times (depending on year) the mean total length of age-0 yellow perch. The greater this mean length difference became by 30 May, the larger age-0 walleyes grew by 30 September ($r_s = 0.79$, $P = 0.04$). The two species differed least in mean length during 1985 and 1986, when fewer age-0 walleyes ate fish than in later years.

First-year growth of walleyes was related to earlier abundance (Figure 7). The mean total lengths of age-0 walleyes on 30 September had a negative correlation with their catch/effort in spring tow nets ($r_s = -0.81$, $P = 0.01$) and summer seines ($r_s = -0.83$, $P = 0.01$). Age-0 walleyes grew slowest during years of large catches, suggesting intraspecific food competition.

Abundance

Offshore tow netting at night in spring caught far more age-0 yellow perch than age-0 walleyes,

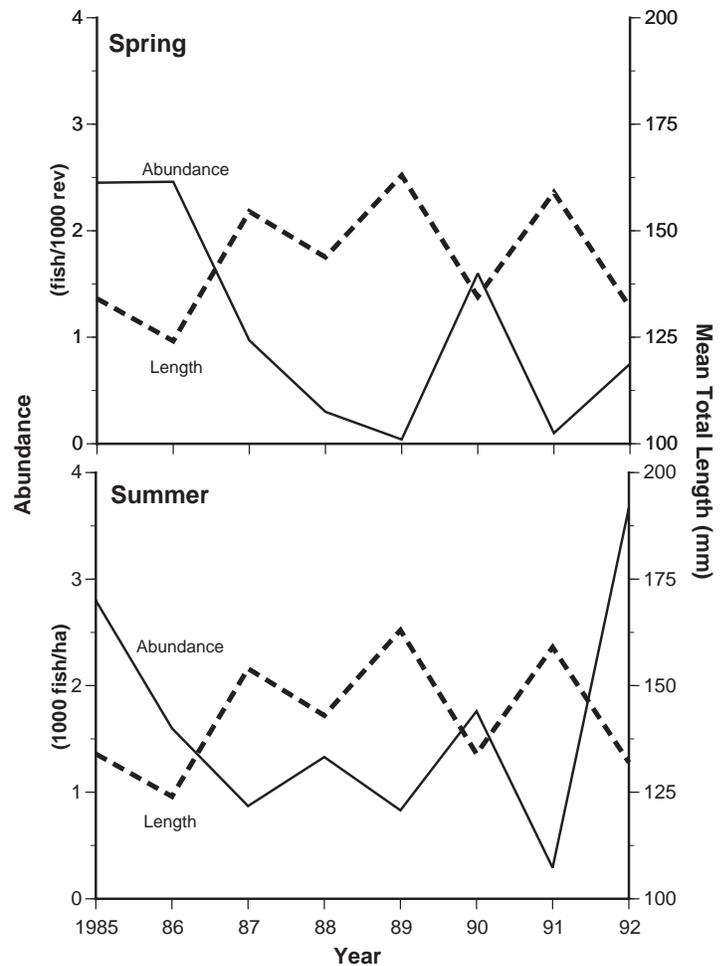


Figure 7. Mean total length of age-0 walleyes on 30 September and their spring and summer abundance, 1985-1992. Tow-net catches were combined for water depths of 0, 0.9, and 1.8 m.

though catch/effort fluctuated among years for both species (Table 5). Widespread in spring, age-0 walleyes were more common near the water surface. Age-0 walleye catch/effort in 1985-1988, when both shallow and deep tows were made, averaged 29% higher ($U = 2.5$, $P = 0.01$) for the three shallow tows (2.3 fish/1,000 revolutions) than for the three deep tows (0.7 fish/1,000 revolutions).

Spring and summer abundances of age-0 walleyes varied independently (for each test $r_s = -0.40$, $P = 0.60$) of walleye hatching success in 1989-1992, years when dead and hatched eggs were counted in covered trays (Figure 1).

Night tow netting became ineffective after mid-June, when over 90% of age-0 walleyes were seined inshore at night (Table 6). Few age-0 walleyes were seined inshore during daylight. Instead, the walleyes moved inshore after dark and became vulnerable to seining.

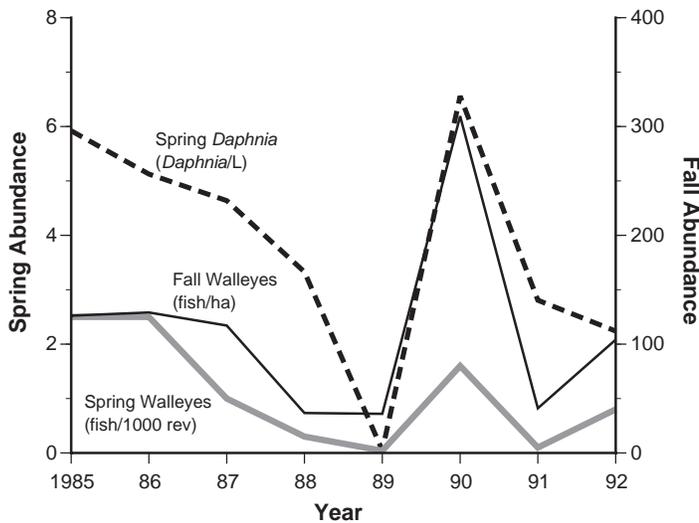


Figure 8. The spring and fall abundance of age-0 walleyes, estimated by tow netting and electrofishing, compared to the spring abundance of *Daphnia* in vertical net hauls, 1985-1992. Tow-net catches were combined for water depths of 0, 0.9, and 1.8 m.

Table 5. The spring catch/effort (fish/1,000 revolutions) of age-0 walleyes and yellow perch in night tow nets from Escanaba Lake, 1985-1992 (mean \pm 1 SE).

Year	Walleyes	Yellow Perch
1985	2.5 \pm 0.9	68 \pm 24
1986	2.5 \pm 1.1	111 \pm 45
1987	1.0 \pm 0.4	167 \pm 49
1988	0.3 \pm 0.1	188 \pm 70
1989	<0.1 \pm <0.1	133 \pm 58
1990	1.6 \pm 0.3	289 \pm 84
1991	0.1 \pm <0.1	94 \pm 39
1992	0.8 \pm 0.4	327 \pm 127

Table 6. The summer catch/effort (fish/ha) of age-0 walleyes and yellow perch in night or day seine hauls from Escanaba Lake, 1985-1992 (mean \pm 1 SE).

Year	Walleyes		Yellow Perch
	Night	Day	Day
1985	2,844 \pm 744	31 \pm 18	4,284 \pm 3,367
1986	1,611 \pm 542	12 \pm 4	1,174 \pm 160
1987	877 \pm 155	51 \pm 45	25,172 \pm 13,185
1988	1,339 \pm 533	11 \pm 7	6,489 \pm 1,622
1989	838 \pm 309	3 \pm 3	33,661 \pm 6,705
1990	1,762 \pm 831	12 \pm 3	46,786 \pm 9,420
1991	291 \pm 76	1 \pm 1	18,452 \pm 6,419
1992	3,670 \pm 790	59 \pm 24	30,249 \pm 14,515

The fall abundance and biomass of age-0 walleyes varied nearly 8-fold between 1985 and 1992 (Figure 5), averaging 112 ± 32 fish/ha and 2.0 ± 0.6 kg/ha (mean \pm 1 SE) for all years. Age-0 walleye abundance in Escanaba Lake averaged 91 ± 16 fish/ha for fall 1958-1980 (Serns 1982a), only 23% lower than our fall 1985-1992 average abundance ($U = 0.70$, $P = 0.48$).

Fall abundance of age-0 walleyes was related to the spring abundances of zooplankton and age-0 walleyes (Figure 8). Annual differences in fall abundance had a positive correlation with spring densities of *Daphnia* ($r_s = 0.88$, $P < 0.01$) and walleye catch/effort in spring tow nets at depths of 0, 0.9, and 1.8 m where most walleyes were caught ($r_s = 0.95$, $P < 0.01$). But no correlations were found between fall abundance and spring tow-net catches of either C1-C6 copepodids or cladocerans other than *Daphnia* ($P > 0.05$). Nor was fall abundance found to correlate with the abundance (catch/effort) of age-0 walleyes in summer seines ($r_s = 0.55$, $P = 0.16$), age-0 yellow perch in spring tow nets ($r_s = 0.00$, $P = 1.00$), or age-0 yellow perch in summer seines ($r_s = -0.12$, $P = 0.78$). The spring abundance of *Daphnia* and the spring tow-net catches of walleyes best gauged fall abundance.

Discussion

Was hatching success dependent on spring warm-up, as we hypothesized? Was walleye growth and abundance dependent on prey fish availability? Walleyes in Escanaba Lake did hatch faster at warmer inshore temperatures and grew larger on a fish diet. But their fall abundance had a negative correlation with variability in May water temperatures (Serns 1982a) and a positive correlation with May-June blooms of *Daphnia* (this study). Perhaps variable water temperatures reduce fall abundance by reducing spring *Daphnia* production.

Walleye eggs hatched more than a week earlier when total incubation temperatures averaged 4°C warmer than in other years. Even late ice-outs failed to delay hatching, if the inshore water warmed rapidly after ice-out. Eggs took only 17 days to hatch at 14.4°C in 1992, when ice-out on April 29 was the latest in our eight-year study.

By shortening incubation, a warm spring reduces the exposure of eggs to diseases and predators (Wolfert et al. 1975), especially crayfish and minnows. It reduces exposure to spring storms that dislodge eggs or reduce dissolved oxygen tension by increasing siltation (Allbaugh and Manz 1964, Oseid and Smith 1971). Warm weather also reduces the time when walleye incubation and yellow perch

spawning overlap; spent yellow perch lingering inshore can prey on walleye eggs (Wolfert et al. 1975). But egg predators and wave action were excluded from our covered egg trays, partly explaining why we found no correlation between incubation temperature and egg mortality.

Growth was faster in years when more age-0 walleyes ate fish instead of zooplankton. Both in 1964-1968 (Morsell 1970) and in 1985-1992 (this study), growth was best when mean total lengths of the age-0 walleyes averaged at least twice that of age-0 yellow perch. Yet we found, like Serns (1982a,b) and Smith and Pycha (1960), no correlation between fall abundance of age-0 walleyes and spring growth of newly hatched walleyes or yellow perch. Diet could have masked temperature effects on growth; age-0 walleyes lose the growth advantage of gorging zooplankton in spring if forage fish become scarce in summer. For example, age-0 walleye growth in Oneida Lake, New York was related to water temperature in spring but to prey-fish abundance in summer (Forney 1966).

When about 35 mm long in late June, age-0 walleyes switched from pelagic to littoral habitats and from eating zooplankton and some fish to eating midge larvae (Chaoboridae and Chironomidae) and many fish. The walleye diet then expanded to include larger and more diverse fish and insects, such as Iowa darters and aquatic stages of beetles (Coleoptera), dragonflies (Odonata), mayflies (Ephemeroptera), and true bugs (Hemiptera). A similar habitat and dietary shift, at 30-60 mm, was shown for age-0 walleyes in other northern lakes (Scott and Crossman 1973, Forney 1966, Colby et al. 1979, Wu and Culver 1992). Age-0 walleyes in a South Dakota lake consumed more fish and fewer zooplankton as summer advanced, but failed to eat many midge larvae in spring or summer (Beck et al. 1998).

Such segregation of habitat and expansion of niche breadth can reduce walleye cannibalism and its influence on year-class strength (Forney 1976). Although cannibalism was not found among Escanaba Lake walleyes in 1955-1972 (Kempinger and Carline 1977), we did find age-0 walleyes in the stomachs of adult walleyes during our study (S.P. Newman, Wisconsin DNR, unpublished data at the Escanaba Lake Checking Station). Stocked walleyes 20 mm and longer in Oneida Lake were cannibalized when they became demersal after mid-June, especially in years when yellow perch were scarce (Forney 1976).

Prey selection can be influenced by both prey abundance and age-0 walleye size (Johnston and Mathias 1994). Zooplankton in Escanaba Lake

became more varied but less abundant after June, while age-0 walleyes became larger and more demersal. Growth was greatest in years when more age-0 walleyes ate fish and fewer of them ate crustaceans. Stocked age-0 walleyes in Lake Oahe, South Dakota shifted to larger fish prey as the walleyes grew (Jackson et al. 1992). Although walleyes as short as 9 mm ate fish in Escanaba Lake and Oneida Lake (Houde 1967), larger walleyes are more efficient at capturing prey fish and less vulnerable to winter starvation (Jonas and Wahl 1998).

Fall abundance of age-0 walleyes, unlike spring and summer abundances, seemed unrelated to first-year growth. Simple correlations are unlikely to occur between growth and abundance because of annual variations and factor interactions with diet and length of growing season. Fall abundance in Escanaba Lake, for example, varied as much as 260-fold between years in 1958-1992 and ranged from 0.8 fish/ha in 1960 to 309 fish/ha in 1991 (Serns 1982a for 1958-1980; unpublished data for 1981-1984; this study for 1985-1992). These annual variations kept us from finding a significant difference in mean fall abundance between our study (1985-1992) and the preceding 23 years (Serns 1982a). Such fluctuations are common in walleye lakes (Faber 1967) and reflect mortality, especially during incubation and the transition from pelagic to demersal stages (Forney 1976).

Summary

1. Walleye eggs in Escanaba Lake took 12-20 days to incubate and hatched faster during warm springs. But two-thirds of all eggs never hatched in our covered trays, despite minimal egg predation. Egg mortality was not found to correlate with annual differences in mean or coefficient of variation in water temperatures.
2. The age-0 walleye diet, pooled for all years, comprised 98% by number of invertebrates (chiefly cladocerans, copepods, and immature midges) and 2% by number of fish (chiefly yellow perch). Of the 849 walleyes examined, 57% ate fish. Cladocerans, especially *Daphnia* and *Leptodora*, remained a staple food of these walleyes through spring and summer, though walleyes did eat fish within three weeks of hatching. Most walleyes ate fish during summer, especially yellow perch and some bluntnose minnows, pumpkinseed sunfish, and Iowa darters. Walleyes with fish in their stomachs averaged 9 mm longer during summer than did those with only invertebrates in their stomachs.

3. Age-0 walleyes for all years averaged 143 mm by October. But their first-year growth varied by month, season, and year. It was greatest in June and for 80-90 days of summer, but was slowest in 1986 (0.9 mm/day) and fastest in 1991 (1.3 mm/day). Annual differences in first-year growth had an inverse relation to spring and summer catches of age-0 walleyes and were not found to correlate with their fall abundance or length of growing season.
4. Walleyes moved offshore after hatching and became widespread, especially within 1.8 m of the water surface. After mid-June, the walleyes became progressively demersal and moved inshore at night. Their fall abundance had a positive correlation with the spring abundances of tow-netted walleyes and *Daphnia*.

Management Implications and Research Needs

Knowing how prey abundance and inshore water temperature affect walleye fry survival could help fish managers predict first-year growth and abundance of walleyes in lakes. Our 8-year study of age-0 walleyes in Escanaba Lake shows walleye hatching success and fall abundance are affected by spring warm-up and *Daphnia* blooms. How can these relations help walleye managers?

Managers could install a recording thermograph on spawning reefs in key walleye lakes to predict peak hatching. Data pooled for several lakes could establish a regional temperature-hatching relationship. Managers could also tow for *Daphnia* and walleye fry in spring to predict first-year growth and abundance.

Modelers should examine water temperature effects on walleye prey. Water temperature and spring *Daphnia* blooms can be just as important to the hatching success and post-hatching abundance of yellow perch, the principal prey of walleyes in Wisconsin lakes. For example, more age-0 walleyes

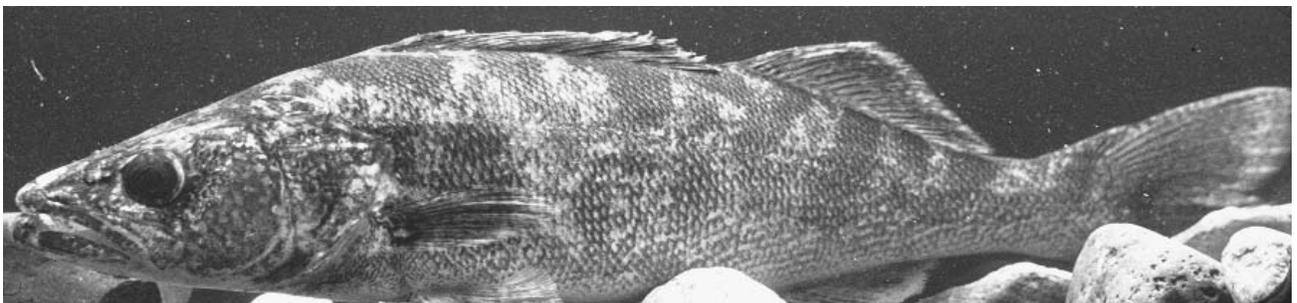
ate yellow perch in Escanaba Lake during years when the yellow perch were abundant. Strong *Daphnia* blooms, responding to favorable spring warm-up or algal blooms, could sustain a high abundance of newly hatched yellow perch as well as walleyes.

Collecting data on prey, diet, and temperature from a variety of walleye lakes, including stocked ones, could improve models to help managers predict walleye year-class strength, recruitment, and stocking quotas. For example, years of abundant walleye and yellow perch hatches could spell favorable walleye recruitment in later years. Predicting weak year-classes could help identify lakes that need walleye stocking, perhaps to augment natural reproduction, and determine the best years to stock the lakes.

Stocking decisions need to consider prey availability. Information on spring zooplankton blooms and the growth and abundance of prey fish can help hatchery managers decide how many walleyes to stock in a lake and whether to stock them as fry or fingerlings. Fry could starve if stocked when zooplankton are scarce or prey fish outgrow the fry. Models that predict prey availability could help managers fine-tune harvest regulations and stocking quotas on specific waters.

What are the implications of slow versus fast growth in age-0 walleyes? Slow growth after hatching could expose walleye fry to cannibalism from older walleyes. Cannibalism became a driving factor for walleye recruitment in Oneida Lake (Forney 1976), but not in Lake Erie (Madenjian et al. 1996). Slow growth could affect subsequent recruitment of walleyes through reduced first-winter survival, though first-year growth seemed unrelated to walleye recruitment in Lake Winnebago, Wisconsin (Priegel 1970).

Whether stocked or lake hatched, whether slow- or fast-growing, age-0 walleyes could alter feeding relations for the whole fish community. A large hatch of walleyes could leave fewer zooplankton or yellow perch fry for other fish species, such as the young of muskellunge and northern pike. More information is ultimately needed on how walleye fry survival affects the growth, recruitment, and harvest of other sportfish.



Adult walleye over rocks.

DNR PHOTO

Literature Cited

- Allbaugh, C.A. and J.V. Manz.
1964. Preliminary study of the effects of temperature fluctuations on developing walleye eggs and fry. *Progressive Fish-Culturist* 26:175-180.
- Anonymous.
1996. *Statistix® for Windows: User's manual*. Analytical Software, Tallahassee, FL. 333 pp.
- Beck, H.D., A.B. Starostka and D.W. Willis.
1998. Diet overlap of age-0 walleye and white bass in Lake Poinsett, South Dakota. *Journal of Freshwater Ecology* 13:425-431.
- Becker, G.C.
1983. *Fishes of Wisconsin*. Univ. Wisconsin Press, Madison. 1052 pp.
- Busch, W.-D.N., R.L. Scholl and W.L. Hartman.
1975. Environmental factors affecting the strength of walleye (*Stizostedion vitreum vitreum*) year-classes in western Lake Erie, 1960-70. *Journal of the Fisheries Research Board of Canada* 32:1733-1743.
- Colby, P.J., R.E. McNicol and R.A. Ryder.
1979. Synopsis of biological data on the walleye, *Stizostedion v. vitreum* (Mitchill 1818). U.N. Food and Agricultural Organization. *Fisheries Synopsis* (119):1-139.
- Colby, P.J., P.A. Ryan, D.H. Schupp and S.L. Serns.
1987. Interactions in north-temperate lake fish communities. *Canadian Journal of Fisheries and Aquatic Sciences* 44 (Supplement 2):104-128.
- Conover, W.J.
1980. *Practical Nonparametric Statistics*, 2nd ed. John Wiley & Sons, New York. 493 pp.
- Faber, D.J.
1967. Limnetic larval fish in northern Wisconsin lakes. *Journal of the Fisheries Research Board of Canada* 24:927-937.
- Forney, J.L.
1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York. *New York Game and Fish Journal* 13:148-166.
- Forney, J.L.
1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966-73. *Journal of the Fisheries Research Board of Canada* 33:783-792.
- Houde, E.D.
1967. Food of pelagic young of the walleye, *Stizostedion vitreum vitreum*, in Oneida Lake, New York. *Transactions of the American Fisheries Society* 96:17-24.
- Jackson, J.J., D.W. Willis and D.G. Fielder.
1992. Food habits of young-of-the-year walleyes in Okobojo Bay of Lake Oahe, South Dakota. *Journal of Freshwater Ecology* 7:329-341.
- Johnston, T.A. and J.A. Mathias.
1994. Feeding ecology of walleye, *Stizostedion vitreum*, larvae: Effects of body size, zooplankton abundance, and zooplankton community composition. *Canadian Journal of Fisheries and Aquatic Sciences* 51:2077-2089.
- Jonas, J.L. and D.H. Wahl.
1998. Relative importance of direct and indirect effects of starvation for young walleyes. *Transactions of the American Fisheries Society* 127:192-205.
- Kempinger, J.J. and R.F. Carline.
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.
- Kempinger, J.J., W.S. Churchill, G.R. Priegel and L.M. Christenson.
1975. Estimate of abundance, harvest, and exploitation of the fish population of Escanaba Lake, Wisconsin, 1946-69. Wis. Dept. Nat. Resourc. *Technical Bulletin* (84):1-30.
- Madenjian, C.P., J.T. Tyson, R.L. Knight, M.W. Kershner and M.J. Hansen.
1996. First-year growth, recruitment, and maturity of walleyes in Western Lake Erie. *Transactions of the American Fisheries Society* 125:821-830.
- Morsell, J.W.
1970. Food habits and growth of young-of-the-year walleyes from Escanaba Lake: Preliminary report. Wis. Dept. Nat. Resourc. *Research Report* (56):1-14.
- Oseid, D.M. and L.L. Smith, Jr.
1971. Survival and hatching of walleye eggs at various dissolved oxygen levels. *Progressive Fish-Culturist* 33:81-85.
- Patterson, D.L.
1952. The walleye population in Escanaba Lake, Vilas County, Wisconsin. *Transactions of the American Fisheries Society* 82:34-41.
- Pielou, E.C.
1975. *Ecological Diversity*. John Wiley & Sons, New York. 165 pp.
- Piper, R.G., I.B. McElwain, L.E. Orme, J.P. McCraren, L.G. Fowler and J.R. Leonard.
1982. *Fish Hatchery Management*. U.S. Fish and Wildl. Serv., Washington, DC. 517 pp.
- Priegel, G.R.
1970. Reproduction and early life history of the walleye in the Lake Winnebago region. Wis. Dept. Nat. Resourc. *Technical Bulletin* (45):1-105.

- Ricker, W.E.
1975. Computation and interpretation of biological statistics of fish populations. Canada Dept. Environment, Fisheries and Marine Serv. *Bulletin* (191):1-382.
- Scott, W.B. and E.J. Crossman.
1973. Freshwater fishes of Canada. *Bulletin of the Fisheries Research Board of Canada* (184):1-966.
- Serns, S.L.
1982a. Influence of various factors on density and growth of age-0 walleyes in Escanaba Lake, Wisconsin, 1958-1980. *Transactions of the American Fisheries Society* 111:299-306.
- Serns, S.L.
1982b. Walleye fecundity, potential egg deposition, and survival from egg to fall young-of-year in Escanaba Lake, Wisconsin, 1979-1981. *Transactions of the American Fisheries Society* 111:388-394.
- Serns, S.L.
1984. Walleye growth in relation to water temperature, food availability, and population density in Escanaba Lake, 1956-82. Wis. Dept. Nat. Resourc. *Research Report* (130):1-16.
- Siegel, S. and N.J. Castellan, Jr.
1988. *Nonparametric Statistics for the Behavioral Sciences*, 2nd ed. McGraw-Hill, New York. 399 pp.
- Smith L.L., Jr. and R.L. Pycha.
1960. First-year growth of the walleye, *Stizostedion vitreum vitreum* (Mitchill), and associated factors in the Red Lakes, Minnesota. *Limnology and Oceanography* 5:281-290.
- Smith, P.E., R.C. Counts and R.I. Clutter.
1968. Changes in filtering efficiency of plankton nets due to clogging under tow. *Journal du Conseil International pour l'Exploration de la Mer* 32:232-248.
- Wolfert, D.R., W.-D. N. Busch and C.T. Baker.
1975. Predation by fish on walleye eggs on a spawning reef in a western Lake Erie, 1969-71. *Ohio Journal of Science* 75:118-125.
- Wu, L. and D.A. Culver.
1992. Ontogenetic diet shift in Lake Erie age-0 yellow perch (*Perca flavescens*): A size-related response to zooplankton density. *Canadian Journal of Fisheries and Aquatic Sciences* 49:1932-1937.

Acknowledgments

We thank the following Wisconsin DNR employees for field or laboratory help: Connie J. Antonuk, David H. Bartz, Alan R. Braun, Gary A. Cholwek, Martin P. Engel, Stephen J. Gilbert, Joelle M. Grasso, Wesley O. Jahns, Paul D. Kanehl, Eric J. Kramer, Gary R. Kubenik, Rebecca A. Papke, David R. Picard, David E. Powell, Mary K. Rodman, Michael T. Vogelsang, Jr., and Jody P. Walters. Kent E. Bass and Jeffrey A. Bradisse helped with data computation. We also thank volunteer summer intern Robert S. Gaines of Augustana College, Illinois, and the following summer student interns of the University of Wisconsin-Stevens Point: Christopher A. Bill, Mitchell H. Bowers, Richard E. Bruesewitz, Paul N. Burns, Kevin J. Gauthier, Jason D. Smith, and Matthew E. Stanley.

Bryan A. Henderson, Nigel Lester, and Mark Ridgway of the Ontario Ministry of Natural Resources in Peterborough and Michael D. Staggs of the Wisconsin DNR reviewed a previous draft meant for journal submission. John M. Pitlo and Gary Siegwarth of the Iowa DNR and Ronald M. Bruch, Steven W. Hewett, Kendall K. Kamke, and Jeffrey M. Kampa of the Wisconsin DNR reviewed a later draft intended for this series. Edward E. Emmons provided statistical review and DuWayne F. Gebken provided administrative review and approval of our final peer reviewed draft.

This report completes Study 612 (renamed RSCU and SSCZ) that was funded in part by the Federal Aid in Sport Fish Restoration (SFR) Act under Dingell-Johnson Project F-83-R (renamed F-95-P).

We dedicate this work to the memory of Steven L. Serns, whose research on age-0 walleyes in Escanaba Lake laid the foundation for our study.

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