



Effects of Prey and Predator Abundances on Prey Consumption and Growth of Walleyes in Western Lake Erie

Kyle J. Hartman & F. Joseph Margraf

To cite this article: Kyle J. Hartman & F. Joseph Margraf (1992) Effects of Prey and Predator Abundances on Prey Consumption and Growth of Walleyes in Western Lake Erie, Transactions of the American Fisheries Society, 121:2, 245-260, DOI: [10.1577/1548-8659\(1992\)121<0245:EOPAPA>2.3.CO;2](https://doi.org/10.1577/1548-8659(1992)121<0245:EOPAPA>2.3.CO;2)

To link to this article: [http://dx.doi.org/10.1577/1548-8659\(1992\)121<0245:EOPAPA>2.3.CO;2](http://dx.doi.org/10.1577/1548-8659(1992)121<0245:EOPAPA>2.3.CO;2)



Published online: 09 Jan 2011.



Submit your article to this journal [↗](#)



Article views: 144



View related articles [↗](#)



Citing articles: 64 View citing articles [↗](#)

Effects of Prey and Predator Abundances on Prey Consumption and Growth of Walleyes in Western Lake Erie

KYLE J. HARTMAN¹

Environmental Biology Program, The Ohio State University
1735 Neil Avenue, Columbus, Ohio 43210, USA

F. JOSEPH MARGRAF²

U.S. Fish and Wildlife Service, Ohio Cooperative Fish and Wildlife Research Unit³
1735 Neil Avenue, Columbus, Ohio 43210, USA

Abstract.—Declining growth and delayed age at maturity of walleye *Stizostedion vitreum* from 1965 to 1984 indicated that the species' large Lake Erie population was taxing the capacity of the prey fish community to support it. We examined the effects of prey and predator abundances on walleye diets and estimated the total predatory demand of age-0 through age-6 walleyes in western Lake Erie during 1986–1988. Walleye diets reflected prey fish abundances. Gizzard shad *Dorosoma cepedianum* and shiners (emerald shiner *Notropis atherinoides* and spottail shiner *N. hudsonius*) were the major prey in years when they were abundant. In years when these prey species—especially gizzard shad—were not abundant, walleyes consumed more white perch *Morone americana* and (to a lesser degree) yellow perch *Perca flavescens*. Total consumption by the walleye population was relatively constant, ranging from 83,700 tonnes in 1987 to 94,300 tonnes in 1986. Bioenergetics modeling showed that greater fishing mortality imposed on strong walleye year-classes could reduce competition among older cohorts; however, because diets of age-0 and age-1 walleyes differ from diets of older fish, few prey made available by greater harvests would be used by small walleyes to increase their growth. Walleye density and gizzard shad availability interact to influence prey consumption and walleye growth in western Lake Erie. High predatory demand and reduced growth of walleyes occur when large walleye year-classes predominate.

The historically important sport and commercial fishery for walleye *Stizostedion vitreum* in Lake Erie has undergone a well-documented decline and subsequent recovery (Parsons 1970; Hartman 1973; Leach and Nepszy 1976; Hatch et al. 1987). However, management agencies were concerned during the mid-1980s that the large population of walleyes might be taxing the prey fish community; declining growth rates and increased age at maturity of walleyes from 1977 to 1984 (Hatch et al. 1987) indicated that prey levels were inadequate to sustain walleye biomass. However, neither the abundance of prey nor the predatory demand had been quantified.

Walleyes primarily eat age-0 fishes (Chevalier 1973; Forney 1974; Knight et al. 1984), particularly in western Lake Erie (Parsons 1971; Knight et al. 1984; Hartman 1989), and they select for soft-rayed prey (Forney 1974; Knight et al. 1984). In Lake Erie, the abundance of age-0 prey fish, primarily soft-rayed gizzard shad *Dorosoma cepedianum* and spiny-rayed white perch *Morone americana*, varies considerably (ODW 1989; U.S. Fish and Wildlife Service, Sandusky Biological Laboratory, unpublished data). Annual variability in age-0 prey fish abundance may be naturally induced, or it could be structured by the predatory demand and selectivities of piscivorous species.

We hypothesized that walleye diets, growth, and prey consumption are influenced by changes in the density of walleyes that influence the relative abundance and composition of the prey fish community in a given year or season. To test this hypothesis we used bioenergetics modeling to estimate the predatory demand by walleyes in 1986–1988, to evaluate the potential merit of flexible harvest regulations upon walleye production, and to evaluate the role of walleye and prey fish abundance on prey consumption by and diet composition of walleyes.

¹ Present address: Chesapeake Biological Laboratory, University of Maryland System, Post Office Box 38, Solomons, Maryland 20688, USA.

² Present address: West Virginia Cooperative Fish and Wildlife Research Unit, Post Office Box 6125, Morgantown, West Virginia 26506, USA.

³ The Unit is jointly sponsored by the U.S. Fish and Wildlife Service, the Ohio Department of Natural Resources, The Ohio State University, and the Wildlife Management Institute.

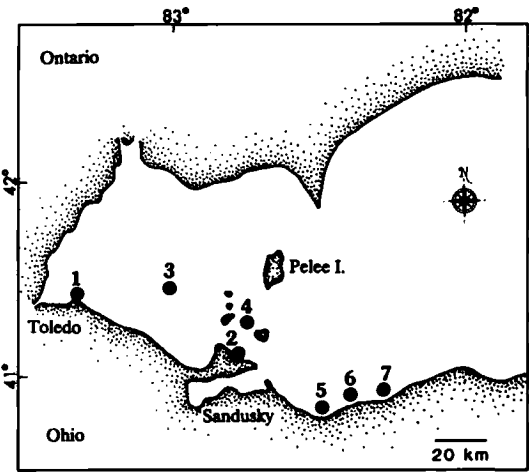


FIGURE 1.—Primary collection sites for walleye and prey fish in western Lake Erie: 1 = Bono, 2 = East Harbor, 3 = Middle Sister, 4 = Kelley-Ballast, 5 = Berlin Heights, 6 = Vermillion, 7 = Lorain. Bottom trawling was done at all sites; coincident gill-net sampling was done at sites 3–6.

Methods

Diet and Growth

We collected walleyes cooperatively with the Ohio Division of Wildlife twice monthly from June through October 1986–1988. Prey fish and small walleyes (<300 mm total length) were sampled from Lake Erie’s western basin with 10–15-min bottom tows of an otter trawl (11-m head-rope) at seven primary sites (Figure 1); larger walleyes were caught in gill nets during trawl sampling at four sites. We fished experimental monofilament gill nets, with mesh sizes ranging from 51- to 127-mm stretched mesh in 12.7-mm increments, overnight (about 8 h).

Regular collections were supplemented by fish taken from an interagency trawling program and

from gillnetting in autumn by the Ohio Division of Wildlife. Sites for these supplemental collections were selected in a stratified-random fashion. Supplemental collections were pooled with primary collections because diet data obtained from the two sets of collections did not differ significantly (z-test, $P < 0.05$).

Fish collected in the field were frozen on dry ice until returned to the laboratory; freezing stopped digestion of prey in walleye stomachs and kept all fishes in good condition until their lengths and weights could be measured. We measured total and fork lengths of walleyes (± 1.0 mm), recorded wet weights (± 1.0 g), collected scales and sagittal otoliths for age determination, and removed and refroze stomachs for later analysis. We used standard methods (Jearld 1983) to age walleyes and made three independent readings of each scale or otolith. Impressions of scales were made in acetate slides that were read with a microfiche reader. Otoliths were cracked latitudinally and their broken surfaces were polished with 600 grain silicone carbide paper. Otoliths were read under a dissection microscope with perpendicular fiber-optical lighting. Walleye ages derived from scales and otoliths showed 96% agreement up to age 5. Beyond age 5 scales tended to underestimate walleye age (61% agreement), so otoliths were used to age all fish in this study.

We processed stomach contents within several months of collection, thawing the material and wet-weighing prey items individually (± 0.1 g). All prey were identified to the lowest practical taxon, usually species for fish and family for invertebrates. All food items were measured to the nearest mm (total, standard, or backbone length, as practical).

Diet biomass was based on the wet weight of prey before digestive losses. We used equations from Knight et al. (1984) to convert standard and

TABLE 1.—Relationships of log₁₀-transformed total length (TL) to wet weight (WW) for common Lake Erie prey fish. Equations are of the form: log₁₀(WW) = $a \cdot \log_{10}(\text{TL}) - b$.

Species	Constants		N	R ²	TL range (mm)
	a	b			
Alewife <i>Alosa pseudoharengus</i>	3.868	-6.515	22	0.995	25–141
Emerald shiner <i>Notropis atherinoides</i>	2.976	-5.170	121	0.950	31–83
Freshwater drum <i>Aplodinatus grunniens</i>	2.030	-2.983	45	0.976	38–123
Gizzard shad <i>Dorosoma cepedianum</i>	3.090	-5.191	66	0.987	28–105
Rainbow smelt <i>Osmerus mordax</i>	3.462	-6.236	28	0.972	30–135
Spottail shiner <i>Notropis hudsonius</i>	3.010	-5.052	54	0.976	67–134
Trout-perch <i>Percopsis omiscomaycus</i>	2.876	-4.840	131	0.980	61–127
White perch <i>Morone americana</i>	3.153	-5.214	74	0.981	25–63
Yellow perch <i>Perca flavescens</i>	3.421	-5.734	21	0.998	29–83

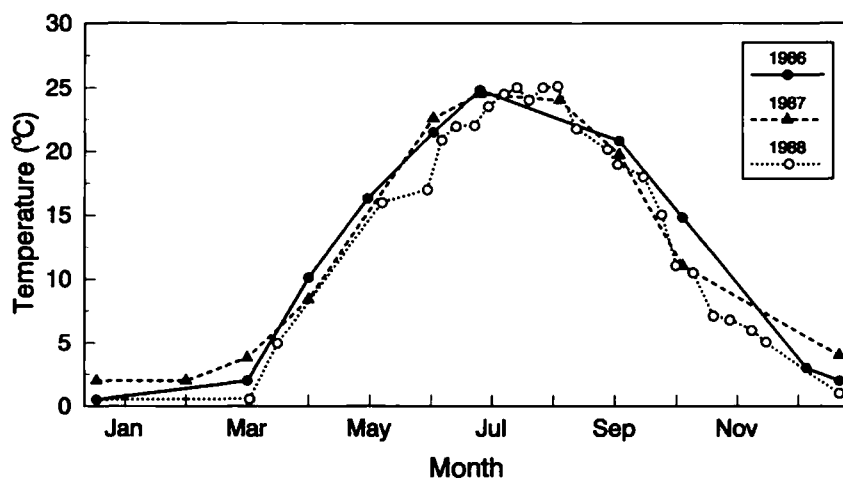


FIGURE 2.—Annual temperature cycles for subsurface (2 m) waters of western Lake Erie, 1986–1988.

backbone lengths to total length, and estimated wet weight before ingestion from regressions of total length versus wet weight determined from prey fishes collected in the study (Table 1).

Relative Abundance of Prey Fish

We evaluated prey abundance by examining the catch of age-0 fishes from the U.S. Fish and Wildlife Service (USFWS) summer (mid-August) and autumn (mid-October) trawling series at East Harbor, Ohio (USFWS, Sandusky Biological Laboratory, unpublished data). We chose the mean catch over the 9-year period 1980–1988 to standardize the prey fish abundance for two reasons: before 1977 walleye numbers were considerably lower than after 1980 (Hatch et al. 1987), and before 1980 white perch were still in the early stages of colonizing western Lake Erie (Schaeffer and Margraf 1986; ODW 1989). We divided the index value for a particular season within a year by the 9-year average for that season. The standardization of the trawling data allowed us to distinguish below-average (< 1.0) and above-average (> 1.0) indices for age-0 prey fish species.

Walleye have low or negative electivities for spiny-rayed fishes and trout-perch and positive electivities for soft-rayed species (Forney 1974; Knight et al. 1984). Based upon these preferences we grouped age-0 prey by two types: “preferred” being soft-rayed species (gizzard shad, emerald shiner, spottail shiner, and rainbow smelt), and “nonpreferred” being spiny-rayed or low-electivity species (white perch, freshwater drum, trout-perch, and yellow perch).

In addition to trawling indices, P-values derived from bioenergetics model simulations can be another indicator of prey fish abundance or success of predation by predators. These P-values represent the proportions of maximum consumption achieved by a cohort given the constraints of temperature, walleye size, and energy content of the walleye and its food. In the modeling work we conducted, these factors could be controlled because seasonal water temperatures in Lake Erie varied little from year to year (Figure 2) and we maintained the same energy content of predators and prey within a modeled cohort. Further, observations within the same age-class tend to limit biases associated with body size. Therefore, differences we observed between years in seasonal P-values within an age-class may be considered to reflect between-year differences in the relative predation success by walleye, which could be due to changes in relative abundance of prey or in behavior of predators or prey.

Consumption and Bioenergetics Modeling

Cumulative individual consumption (grams of food per individual walleye within a cohort per year) measures annual diet as a function of growth and consumption rate, and provides an annual index to the importance of diet items. Low catch rates of walleye in daylight gill-net sets and potential problems associated with the use of gill-netted fish for consumption estimates (Hayward et al. 1989) prevented direct estimates of prey consumption rates by walleyes. However, we were able to estimate consumption indirectly with

TABLE 2.—Temperatures used in our bioenergetics model for optimum temperatures for consumption and respiration and thermal maxima of age-0 through adult walleyes.

Walleye cohort	Consumption		Respiration	
	Optimum (°C)	Maximum (°C)	Optimum (°C)	Maximum (°C)
Age-0	26	32	29	34
Age-1	24	30	28	33
Age ≥ 2	22	28	27	32

Hewett and Johnson's (1987) bioenergetics model. The Hewett-Johnson model is based upon the balanced energy equation (Winberg 1956):

$G = C - R - (F + U) - SDA;$

G = growth, *C* = consumption, *R* = respiration, *F* = egestion, *U* = excretion, and *SDA* = specific dynamic action. In the walleye model, *F* and *U* are functions of meal size and temperature, *SDA* is a constant percentage of consumption (*C*), and consumption and respiration are functions of both fish size and temperature. Detailed descriptions of all components of this model have been published extensively (Kitchell et al. 1977; Hurley 1986; Hewett and Johnson 1987) and are not discussed here.

The physiological variables we used to model walleye consumption were those used in Hewett and Johnson's (1987) model (which were taken from Kitchell et al. 1977), with the exception of the optimum temperatures for consumption and respiration, which we varied by cohort. Recent information suggests that juvenile walleyes continue to grow at temperatures near 30°C and that the thermal optima of juvenile walleye may be close to 26°C (Hokanson and Koenst 1986). The temperature relationship for walleye developed by Smith and Koenst (1975) is reasonably consistent with the thermal optimum of 22°C used by Kitchell et al. (1977). Therefore, we assumed an ontogenetic physiological gradient between age-0 and adult (age ≥ 2) walleyes and used thermal optima for consumption and respiration of age-0, age-1, and age-2 or older walleye ranging between 22 and 29°C and thermal maxima ranging from 28 to 34°C (Table 2).

To estimate consumption rate with the Hewett and Johnson (1987) model, several variables are necessary: diet, energy content of prey and predator, temperature experienced by the predator, and predator growth. Temperature was measured con-

TABLE 3.—Energy density (joules per gram wet weight) of predators and prey used in the bioenergetics models for walleye.

Species	Energy density (J/g)	Source
Age-0 walleyes	4,186.8 ^a , 4,605.5 ^b	Kelso (1972), modified to account for increasing energy content with ontogeny.
Age-1 and older walleyes	4,605.5	Kelso (1972)
Clupeids	4,123.6	Pierce et al. (1980)
Shiners	5,008.7	Kelso (1972)
<i>Morone</i> spp.	5,029.2	Wissing (1974)
Rainbow smelt	5,700	Hurley (1986)
Yellow perch	5,700	Hurley (1986)
Trout-perch	4,101.8	Modified from Pierce et al. (1980), based upon wet weight : dry weight ratios from Hartman (1989).
Freshwater drum	4,101.8	Modified from Pierce et al. (1980), based upon wet weight : dry weight ratios from Hartman (1989).
Cladocerans and other invertebrates	917.0	Cummins and Wuycheck (1971)

^a Energy density on 15 May 1986–1988.
^b Energy density on 1 November 1986–1988.

currently with walleye collections and diet was estimated as above. Annual temperature cycles varied little among study years (Figure 2). Growth of walleye cohorts was divided into several growing periods and a separate proportion of maximum consumption (*P*-value) was fitted to each interval based upon the observed growth over that period for the cohort. Growth for each cohort was estimated as the mean weight at age.

Data on energy density were obtained from the literature for most species; with others, values were assigned from fish of closely related species and morphology (Table 3). All energy density values are presented in joules per gram wet weight. We assumed an ontogenetic change in energy density of age-0 walleye from 4,186.8 J/g on 15 May to 4,605.5 J/g on 1 November, whereas age-1 and older walleyes were assigned a density of 4,605.5 J/g (Kelso 1972). Energy densities of clupeids (Pierce et al. 1980), emerald shiner (Kelso 1972), rainbow smelt, yellow perch (Hurley 1986), and *Morone* spp. (white bass *M. chrysops*: Wissing 1974) ranged from 4,101.8 to 5,700.0 J/g. Energy densities of trout-perch and freshwater drum were

TABLE 4.—Estimated abundances (N , millions of fish), annual mortality rates (M) at the beginning of the modeling period on 15 May 1986–1988, and annual growth (g /individual) of walleyes in western Lake Erie (from Lake Erie Committee 1990a). Age-classes without displayed estimates were not used in modeling exercises because of poor representation in our collections and low population estimates (<4 million fish) by the Lake Erie Committee (1990a).

Age-class	1986			1987			1988		
	N	M	Growth	N	M	Growth	N	M	Growth
Age 0	432.3	92.4	76.8	80.4	92.4	48.3	41.3	92.4	80.0 ^a
Age 1	17.0	22.0	312.8	29.9	22.0	241.1	5.6	22.0	274.5
Age 2	11.0	28.3	383.1	12.9	28.4	374.8	22.4	30.3	344.4
Age 3				7.6	35.6	429.0	8.7	38.7	487.7
Age 4	18.0	36.3	206.4				4.8	40.5	535.2
Age 5				11.4	37.2	568.8			
Age 6							7.0	40.5	691.4
Total	478.3			142.2			89.8		

^a Final weight projected from September 1988 data.

not available; they were estimated from that of clupeids (Pierce et al. 1980) as modified by relationships of wet to dry weight (Hartman 1989). Energy density of spottail shiner (which was pooled with emerald shiner as “shiners” for diet analysis) was assumed to be equal to that of emerald shiner (Table 3).

We used the bioenergetics model to estimate the cumulative annual consumption (g /individual) per walleye within a cohort and the total annual consumption of the walleye population from 1986 to 1988. In addition to the variables previously listed, estimates of walleye abundance and mortality rates were necessary to predict population consumption. Estimates of abundance for age-2 through age-6 and mortality for age-1 through age-6 walleyes in western Lake Erie were obtained from the Lake Erie Committee (1990a) of the Great Lakes Fishery Commission (Table 4). The Lake Erie Committee estimates of abundance and mortality were derived with the CAGEAN model (see Deriso et al. 1985); more specific methodological detail on the population estimation is contained in a Statistics and Modeling Task Group report (Lake Erie Committee 1990b).

We estimated abundances of age-0 and age-1 walleye by back-calculation from the numbers of age-1 and age-2 fish, respectively, in the following year's abundance estimates. For example, we applied an annual mortality rate of 22.00% for age-1 walleyes and Lake Erie Committee (1990a) estimates of age-2 walleye abundance in 1988 to estimate the number of age-1 walleyes in 1987. We then estimated the number of age-0 walleyes in 1986 from our estimate of age-1 abundance in 1987 after applying the annual mortality rate of 92.416% reported for age-0 walleyes in Oneida

Lake, New York (Forney 1980). Low sample sizes for growth estimation of walleyes over age 6 restricted modeling of total annual consumption to fish of ages 0–6. In some years, certain cohorts (age 3 in 1986, age 4 in 1987, age 5 in 1986 and 1988, and age 6 in 1986 and 1987) were not sufficiently sampled to estimate growth, so we did not model these. Cohorts not modeled were less than 8% of the total walleye abundance in a year.

Modeling of Increased Harvest

We also used the bioenergetics model to evaluate the effects of increased fishing mortality on prey availability by re-running the bioenergetics simulation with different walleye mortality rates. We chose to model 1987 because growth of cohorts was reduced and two strong year-classes were present in the population that year. Consumption by the walleye population was estimated at initial levels of mortality (Table 4) and with increases in fishing mortality of 5%, 10%, and 20% above initial levels. Because only walleyes age 2 or older are commonly harvested by Ohio anglers (ODW 1989), we modeled only those cohorts.

Results

Walleye Year-Class Strength

The production of a large year-class in 1986 permitted us to evaluate the effect of changing cohort density on diet, growth, and food consumption. The 1986 cohort was two or three times more abundant than the 9-year mean in both the summer and autumn young-of-year indices (Figure 3). Relative abundances of age-0 walleyes in 1987 and 1988 were generally much lower than in 1986. Recent gillnetting surveys and angler catches have

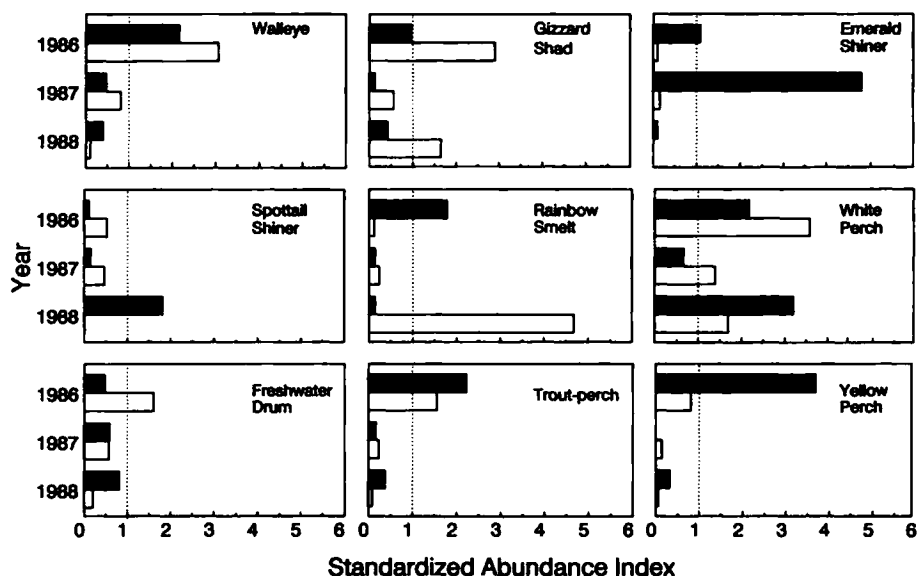


FIGURE 3.—Standardized relative abundances of age-0 walleyes and potential prey fishes as assessed in summer (dark bars) and autumn (open bars) of 1986–1988 by the U.S. Fish and Wildlife Service at their East Harbor sampling station. The 9-year mean seasonal trawl catches forming the reference standards are (numbers of fish in summer, autumn): alewife (72.1, 43.2); emerald shiner (117.9, 380.3); freshwater drum (881.3, 301.3); gizzard shad (1,208.2, 578.0); rainbow smelt (40.2, 19.1); spottail shiner (87.5, 101.7); trout-perch (102.2, 82.1); walleye (93.0, 38.7); white perch (3,847.5, 1,420.7).

substantiated these determinations of relative year-class strength (ODW 1990).

Prey Abundance

Relative abundances of preferred prey varied among years and seasons. The index for age-0 gizzard shad was nearly three times the 9-year mean in the autumn of 1986 and slightly above mean in autumn 1988 (Figure 3). In all seasons in 1987 and in summer 1988, gizzard shad abundances were only half or less of the 9-year mean. Emerald shiner abundance was average or greater in the summers of 1986 and 1987, but well below average in the autumn assessments of 1986–1988 (Figure 3). Abundances of spottail shiner were well below the 9-year mean except in summer 1988. Rainbow smelt abundances were above average in summer 1986 and autumn 1988, but well below average otherwise.

Age-0 white perch were the second most common prey fish collected in 1986–1988 (ODW 1989; USFWS, Sandusky, Ohio, unpublished data). Relative abundances of age-0 white perch were 1.7–3.5 times the 9-year average in 1986 and 1988 but only around average in 1987 (Figure 3). Relative abundances of other “nonpreferred” age-0 fish such as freshwater drum, trout perch, and yellow perch

were generally average or better in 1986 and below average in 1987 and 1988.

Walleye Growth

Growth of walleyes differed considerably among cohorts and years, but appeared to be density-dependent, particularly among age-0 to age-2 walleyes (Table 4; Figure 4). Growth of age-0 walleyes was best in 1988 (through September), intermediate in 1986, and poorest in 1987. The large 1986 year-class was estimated at 432 million fish on 15 May 1986 (compared with age-0 cohort sizes of 80.4 million and 41.3 million on 15 May 1987 and 1988, respectively). Annual growth of age-0 walleyes was lowest in 1987, perhaps because of competition with the abundant 1986 year-class. The 1986 year-class had the lowest incremental annual growth at age 1 in 1987 and age 2 in 1988. Between-year changes in growth of age-3 or older walleyes were not assessed because of small sample sizes.

Diet Composition

Walleyes were predominantly piscivorous, consuming 11 primary prey species—alewife, emerald shiner, freshwater drum, gizzard shad, rainbow smelt, spottail shiner, trout-perch, walleye, white

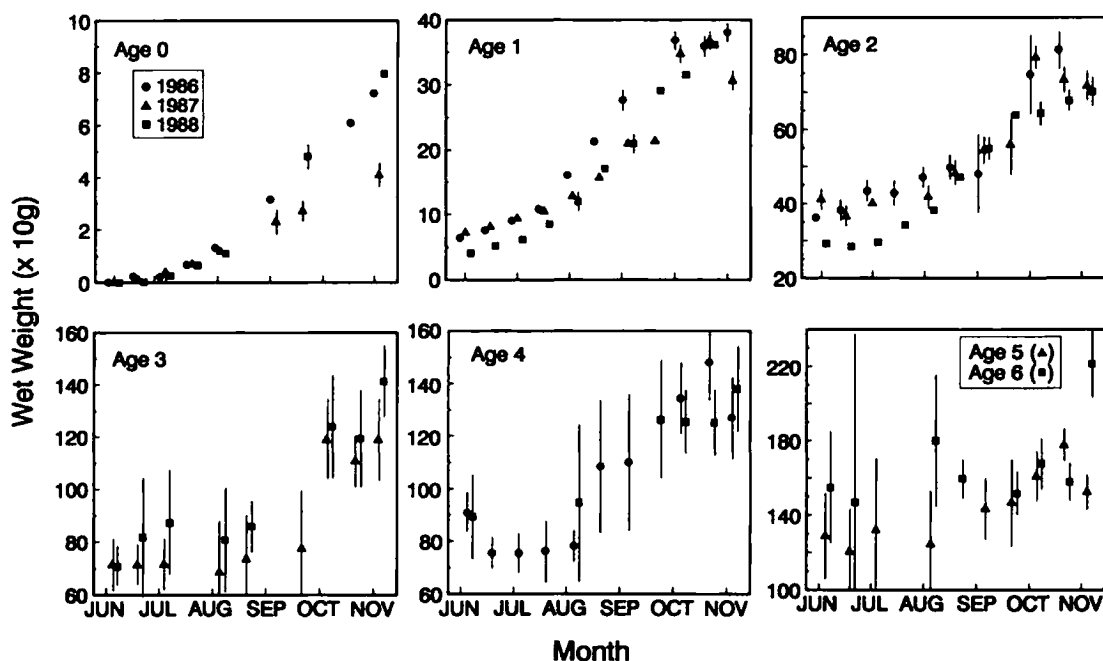


FIGURE 4.—Growth (mean wet weight \pm 95% confidence interval) of age-0 through age-6 walleyes in western Lake Erie between 1986 and 1988. Wet weight is in 10-g units (note different scales).

bass, white perch, and yellow perch. Of the species consumed, age-0 fish were eaten most frequently; however, age-1 and older shiners, trout-perch, and yellow perch were also eaten. Prey fish that were age 1 and older were most often encountered in stomachs of age-2 and older walleyes, particularly in spring and early summer.

Because of difficulties in identifying partially digested prey, we lumped several species within the same genus or family into the same diet category (Tables 5, 6). The diet grouping "clupeids" represented both gizzard shad and alewife. However, 96% of identified clupeids were gizzard shad. The "*Morone* spp." grouping encompassed both white perch and white bass, but 97% of the individuals in this grouping that could be identified to species were white perch. The final grouped diet category was "shiners," both emerald and spottail shiner. Of those identified to species in this group, 51% were emerald shiners and 49% spottail shiners.

Monthly diets of age-0 walleyes were dominated by four prey groups (Table 5). The main prey of age-0 walleyes was age-0 *Morone* spp., which constituted 27–94% of the monthly diet composition from June through September 1986–1988 and 37%–44% of the cumulative individual consumption over the 3 years (Table 7). Cumulative consumption of *Morone* spp. was highest in 1987,

when use of two other nonpreferred prey, trout-perch (10% of cumulative individual consumption) and freshwater drum (13%), was also high. Clupeids also were important to age-0 walleyes, especially in 1988 when growth of age-0 walleyes was highest (Figure 4). Cumulative individual consumption of clupeids ranged from 12% in 1986 to 43% in 1988 (Table 7).

Other prey species were used seasonally by age-0 walleyes (Table 5). Rainbow smelt were eaten most frequently in spring and early summer. Shiners were eaten in late summer and autumn, when most clupeids were too large for age-0 walleyes. Consumption of shiners and rainbow smelt was much higher in 1986 than in other years, mirroring the high trawl catches for age-0 emerald shiners and rainbow smelt reported in 1986. Trout-perch, freshwater drum, and yellow perch constituted as much as 18% of the monthly diets, but rarely for longer than 1 month in any year. The high use of these nonpreferred prey in 1987 occurred at a time when age-0 walleyes were growing significantly less well than in other years (Figure 4).

Age-1 walleyes ate the same species as age-0 walleyes. Clupeids were by far the dominant prey type in all years, accounting for 23–100% of the monthly diet after June each year (Table 5). Rel-

TABLE 5.—Diets (percentages of undigested wet stomach content weight) of age-0 and age-1 walleyes in western Lake Erie, 1986–1988. *N* = number of walleyes containing food.

Prey type, sample size	Age-0						Age-1					
	Jun	Jul	Aug	Sep	Oct	Nov	Jun	Jul	Aug	Sep	Oct	Nov
1986 samples												
Clupeids	0	47	12	6	12		1	78	95	93	94	75
<i>Morone</i> spp.	70	45	61	46	12		11	6	5	6	3	0
Shiners	0	0	3	48	64		82	8	0	1	1	25
Rainbow smelt	30	8	19	0	12		0	0	0	0	0	0
Freshwater drum	0	0	5	0	0		0	0	0	0	0	0
Yellow perch	0	0	0	0	0		4	3	0	0	2	0
Trout-perch	0	0	0	0	0		2	5	0	0	0	0
<i>N</i>	12	125	71	22	13	0	33	82	91	31	31	17
1987 samples												
Clupeids	11	2	21	22			7	23	60	74	100	89
<i>Morone</i> spp.	53	94	59	27			2	32	28	7	0	0
Shiners	0	0	5	23			67	39	10	10	0	7
Rainbow smelt	36	3	1	0			21	1	0	7	0	4
Freshwater drum	0	1	7	13			0	2	0	0	0	0
Yellow perch	0	0	6	0			2	2	1	0	0	0
Trout-perch	0	0	1	15			1	1	1	2	0	0
<i>N</i>	51	86	130	52	0	0	156	196	201	76	45	19
1988 samples												
Clupeids	25	22	28	60			0	31	60	92	96	
<i>Morone</i> spp.	50	72	50	28			3	55	40	8	1	
Shiners	0	1	2	12			0	4	0	0	3	
Rainbow smelt	7	5	10	0			2	0	0	0	0	
Freshwater drum	0	0	0	0			0	0	0	0	0	
Yellow perch	18	0	10	0			95	10	0	0	0	
Trout-perch	0	0	0	0			0	0	0	0	0	
<i>N</i>	124	70	262	48	0	0	133	98	78	40	87	0

ative use of clupeids by age-1 walleyes mirrored annual abundance indices for age-0 gizzard shad; gizzard shad made the highest sustained contribution to walleye diets in 1986 when their abundance indices were up to three times the 9-year mean (Figure 3). Clupeid use by age-1 walleyes was delayed and reduced in July and August 1987–1988, when gizzard shad indices were less than half the 9-year mean. Highest cumulative individual consumption occurred in 1986 (869 g, 85% of total consumption) when gizzard shad trawl catches were highest (Table 7). Conversely, cumulative individual consumption was lowest in 1987 (486 g, 62%) when trawl catches of gizzard shad were low and walleye cohort size was largest. Shiners were frequently eaten by age-1 walleyes, particularly in June and November 1986 and through much of 1987 (Table 5). Shiner use was low in 1988, less than 5% in any month. Use of nonpreferred prey by age-1 walleyes was highest in 1987 and 1988, when gizzard shad indices were lowest and age-1 walleye densities were highest. *Morone* spp. made up most of the nonpreferred prey eaten, accounting for 2–55% of the diet from

June through September 1987–1988. Age-0 yellow perch were rarely eaten by age-1 walleyes in 1986 or 1987, but were frequently eaten in June and July 1988.

Clupeids dominated diets of age-2 walleyes in all years (Table 6), representing 31–99% of the July–October diet. Reduced abundance of gizzard shad in 1987 was reflected in the diet of age-2 walleyes by a 40% or more reduction in clupeid use in the July monthly diet. The contribution of clupeids to cumulative individual consumption of age-2 walleyes was similar between 1986 and 1988, but was lowest in 1987 when age-0 gizzard shad abundance indices were low (Table 7). Shiners also were important, particularly in June (Table 6). Nonpreferred species averaged just 5% and 2% of monthly diets in 1986 and 1987. Use of non-preferred species was highest in 1988 (17%), when age-2 walleyes were most abundant.

Diet patterns of age-3 and older walleyes were similar to those of age-2 walleyes. Clupeids represented 66–100% of the August–November diets (Table 6). In 1986, when gizzard shad abundances were high, age-0 clupeids formed 83% of the July

TABLE 6.—Diets (percentages of undigested wet stomach content weight) of age-2 and older walleyes in western Lake Erie, 1986–1988. *N* is number of walleyes containing food.

Prey type, sample size	Age-2						Age-3 and older					
	Jun	Jul	Aug	Sep	Oct	Nov	Jun	Jul	Aug	Sep	Oct	Nov
1986 samples												
Clupeids	3	94	98	99	96		7	83	95	100	98	90
<i>Morone</i> spp.	0	4	1	1	4		39	17	2	0	0	0
Shiners	97	1	1	0	0		29	0	3	0	2	10
Rainbow smelt	0	0	0	0	0		0	0	0	0	0	0
Freshwater drum	0	0	0	0	0		0	0	0	0	0	0
Yellow perch	0	1	0	0	0		25	0	0	0	0	0
Trout-perch	0	0	0	0	0		0	0	0	0	0	0
<i>N</i>	52	288	118	21	26	0	35	181	64	22	73	16
1987 samples												
Clupeids	39	31	90	97	96	96	0	28	66	99	98	97
<i>Morone</i> spp.	0	12	3	1	4	0	80	4	23	0	0	1
Shiners	56	57	7	2	0	2	20	15	2	0	1	2
Rainbow smelt	0	0	0	0	0	2	0	0	0	0	1	0
Freshwater drum	0	0	0	0	0	0	0	0	0	0	0	0
Yellow perch	0	0	0	0	0	0	0	53	9	0	0	0
Trout-perch	5	0	0	0	0	0	0	0	0	1	0	0
<i>N</i>	26	24	51	20	46	24	20	11	17	21	129	20
1988 samples												
Clupeids	17	71	95	98	99		0	3	94	100	95	
<i>Morone</i> spp.	13	27	4	1	0		22	12	6	0	3	
Shiners	32	0	0	1	1		0	0	0	0	1	
Rainbow smelt	0	0	0	0	0		0	0	0	0	1	
Freshwater drum	0	0	0	0	0		0	0	0	0	0	
Yellow perch	37	2	1	0	0		78	85	0	0	0	
Trout-perch	1	0	0	0	0		0	0	0	0	0	
<i>N</i>	152	163	236	55	185	0	30	42	63	31	195	0

diet. Unlike consumption by age-2 or younger walleyes, cumulative individual consumption by older walleyes apparently was not coupled strongly to relative shad abundance (Table 7). In 1987 and 1988, diets in July were primarily of age-1 and older yellow perch (Table 6). Use of *Morone* spp. was highest in spring and early summer, particularly in 1987 when they represented 80% of the June diet. Shiners were eaten in spring and autumn of 1986 and 1987, but were virtually absent from the diets in 1988. As the large 1986 walleye cohort increased in age, the use of non-preferred prey by age-3 and older walleyes increased—from 17% in 1986 to 34% in 1987 to 41% in 1988.

The growth of age-1 and older walleyes was coupled to ingestion of clupeids in all years. Significant growth (*t*-test, $P < 0.05$) did not occur in any year until clupeids dominated the diets (Figure 4; Tables 5, 6). In 1987, the proportions of clupeids in diets of age-1 and older walleyes were reduced or the dominance of clupeids in diets was delayed. The reduced or delayed contributions of clupeids to the diets of age-1 and older walleyes in 1987

was coupled with reduced annual walleye growth (Figure 4; Table 4) and low abundance of age-0 gizzard shad (Figure 3).

Walleye Consumption

The bioenergetics model predicted that from May 15 through November 6, the total consumption of the walleye population (age 6 and younger) was similar in the three study years (Figure 5; Table 8). Total consumption was highest in 1986 (94,300 tonnes) and lowest in 1987 (83,700 tonnes). Clupeids were the most common prey, ranging from 63 to 68% of the total population consumption in a year. In 1986 and 1987, *Morone* spp. and shiners were the next most important prey types (13–15% of total population consumption), except in 1988 when shiners represented only 2% of the consumption (1,630.4 tonnes) and appeared to be replaced by yellow perch (19% of the total annual consumption).

The total annual consumption by an individual cohort varied directly with cohort size (Table 8). In 1986, age-4 (1982 year-class) walleyes ate nearly half of the total amount eaten by the entire

TABLE 7.—Average prey consumption (cumulative grams per individual) by walleyes and percent contributions to the annual diet (in parentheses) by year and prey type for individual walleyes of six age-classes in western Lake Erie, modeled between day 135 and day 310 of the years 1986–1988. (Based on Hewett and Johnson’s 1987 bioenergetics model.)

Year	Clupeids	<i>Morone</i> spp.	Shiners	Yellow perch	Trout-perch	Rainbow smelt	Fresh-water drum	Invertebrates	Total
Age-0 walleyes									
1986	19.9 (11.7)	62.3 (36.7)	69.4 (40.9)	0.0 (0.0)	0.0 (0.0)	16.3 (9.6)	1.7 (1.0)	0.2 (0.1)	169.8
1987	19.7 (16.3)	53.2 (43.9)	18.5 (15.3)	1.7 (1.4)	12.1 (10.0)	2.6 (2.1)	13.2 (10.9)	0.1 (0.1)	121.1
1988	80.0 (42.6)	70.3 (37.5)	24.9 (13.3)	4.9 (2.6)	0.0 (0.0)	7.5 (4.0)	0.0 (0.0)	0.1 (0.0)	187.7
Age-1 walleyes									
1986	869.3 (84.6)	52.9 (5.1)	87.0 (8.5)	10.6 (1.0)	8.2 (0.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1,028.0
1987	486.4 (61.8)	108.8 (13.8)	141.4 (18.0)	5.6 (0.7)	8.4 (1.1)	33.6 (4.3)	2.7 (0.3)	0.0 (0.0)	786.9
1988	540.5 (65.1)	211.8 (25.5)	13.1 (1.6)	63.4 (7.7)	0.0 (0.0)	0.9 (0.1)	0.0 (0.0)	0.0 (0.0)	829.7
Age-2 walleyes									
1986	1,411.5 (82.2)	36.4 (2.1)	266.7 (15.6)	2.3 (0.1)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	1,716.9
1987	1,304.4 (77.2)	58.0 (3.4)	315.2 (18.6)	0.0 (0.0)	10.0 (0.6)	2.6 (0.2)	0.0 (0.0)	0.0 (0.0)	1,690.2
1988	1,257.7 (82.8)	128.4 (8.5)	58.9 (3.9)	70.1 (4.6)	4.1 (0.2)	0.3 (0.0)	0.0 (0.0)	0.0 (0.0)	1,519.5
Age-3 walleyes									
1987	1,571.7 (69.9)	323.5 (14.4)	116.9 (5.2)	226.6 (10.1)	6.7 (0.3)	2.1 (0.1)	0.0 (0.0)	0.0 (0.0)	2,247.5
1988	1,404.5 (60.8)	185.9 (8.0)	4.0 (0.2)	711.6 (30.8)	0.0 (0.0)	3.4 (0.2)	0.0 (0.0)	0.0 (0.0)	2,309.4
Age-4 walleyes									
1986	2,200.0 (84.0)	206.6 (7.9)	139.9 (5.4)	71.2 (2.7)	0.0 (0.0)	1.2 (0.0)	0.0 (0.0)	0.0 (0.0)	2,618.9
1988	1,533.5 (59.1)	216.6 (8.4)	3.2 (0.1)	838.7 (32.3)	0.0 (0.0)	2.8 (0.1)	0.0 (0.0)	0.0 (0.0)	2,594.8
Age-5 walleyes									
1987	1,403.7 (58.6)	508.8 (21.2)	166.5 (7.0)	310.0 (12.9)	5.9 (0.3)	1.1 (0.0)	0.0 (0.0)	0.0 (0.0)	2,396.0
Age-6 walleyes									
1988	2,432.5 (69.8)	233.5 (6.7)	9.1 (0.3)	802.6 (23.0)	0.0 (0.0)	7.8 (0.2)	0.0 (0.0)	0.0 (0.0)	3,485.5

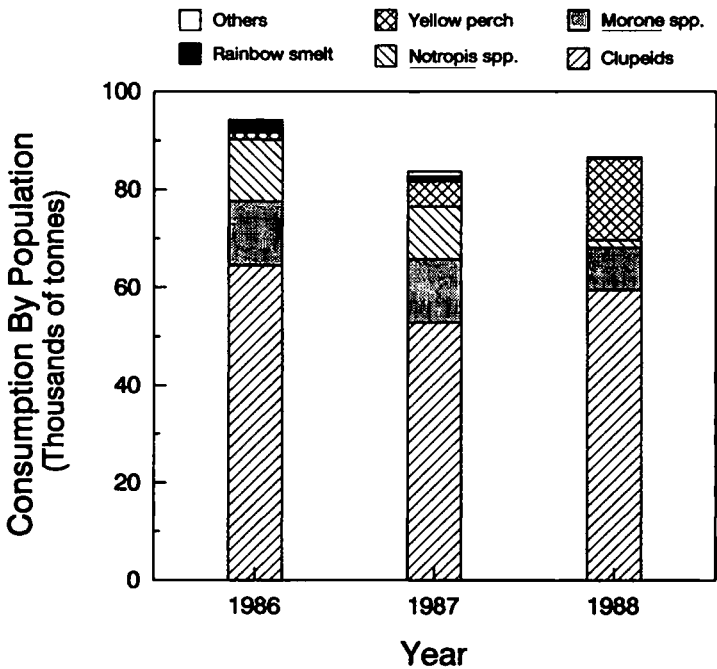


FIGURE 5.—Total consumption of prey by age-0 through age-6 walleyes (combined) in western Lake Erie between 15 May and 6 November 1986–1988.

TABLE 8.—Total prey consumption (thousands of tonnes) by walleye cohorts and percentages (in parentheses) of population consumption by year and prey type for walleyes in the western basin of Lake Erie, modeled between day 135 and day 310 of the years 1986–1988. (Based upon Hewett and Johnson's 1987 bioenergetics model.) Percentages sum vertically for age-groups and horizontally for totals.

Cohort	Clupeids	<i>Morone</i> spp.	Shiners	Yellow perch	Trout-perch	Rainbow smelt	Fresh-water drum	Invertebrates	Total
1986 estimates									
Age-0	2.6 (4.0)	8.5 (64.4)	6.0 (47.6)	0.0 (0.0)	0.0 (0.0)	2.2 (100)	0.2 (100)	0.1 (100)	19.6 (20.8)
Age-1	13.6 (21.1)	0.8 (6.1)	1.4 (11.1)	0.2 (14.3)	0.1 (100)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	16.1 (17.1)
Age-2	13.9 (21.6)	0.4 (3.0)	2.8 (22.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	17.1 (18.1)
Age-4	34.4 (53.3)	3.5 (26.5)	2.4 (19.1)	1.2 (85.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	41.5 (44.0)
Total	64.5 (68.4)	13.2 (14.0)	12.6 (13.4)	1.4 (1.5)	0.1 (0.1)	2.2 (2.3)	0.2 (0.3)	0.1 (0.1)	94.3 (100)
1987 estimates									
Age-0	0.4 (0.8)	1.5 (11.5)	0.3 (2.8)	0.0 (0.0)	0.2 (33.3)	0.1 (10.0)	0.2 (66.7)	0.0 (0.0)	2.8 (3.3)
Age-1	13.3 (25.1)	3.0 (23.1)	4.0 (37.0)	0.2 (4.0)	0.2 (33.3)	0.9 (90.0)	0.1 (33.0)	0.0 (0.0)	21.7 (25.9)
Age-2	15.1 (28.5)	0.7 (5.4)	3.9 (36.1)	0.0 (0.0)	0.1 (16.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	19.8 (23.7)
Age-3	10.3 (19.4)	2.3 (17.7)	0.8 (7.4)	1.6 (32.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	15.0 (17.9)
Age-5	13.9 (26.2)	5.5 (42.3)	1.8 (16.7)	3.2 (64.0)	0.1 (16.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	24.4 (29.2)
Total	53.0 (63.3)	13.0 (15.5)	10.8 (12.9)	5.0 (6.0)	0.6 (0.7)	1.0 (1.2)	0.3 (0.4)	0.0 (0.0)	83.7 (100)
1988 estimates									
Age-0	0.8 (1.3)	0.9 (10.5)	0.2 (11.7)	0.1 (0.6)	0.0 (0.0)	0.1 (100)	0.0 (0.0)	0.0 (0.0)	2.1 (2.5)
Age-1	2.7 (4.6)	1.1 (12.8)	0.1 (5.9)	0.3 (1.8)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.2 (4.9)
Age-2	25.3 (42.6)	2.7 (31.4)	1.3 (76.5)	1.5 (9.0)	0.1 (100)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	30.8 (35.5)
Age-3	10.3 (17.4)	1.5 (17.4)	0.0 (0.0)	5.8 (34.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	17.7 (20.4)
Age-4	6.2 (10.4)	0.9 (10.5)	0.0 (0.0)	3.7 (22.2)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	10.8 (12.5)
Age-6	14.1 (23.7)	1.5 (17.4)	0.1 (5.9)	5.3 (31.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	21.0 (24.2)
Total	59.4 (68.6)	8.6 (9.9)	1.7 (2.0)	16.7 (19.3)	0.1 (0.1)	0.1 (0.1)	0.0 (0.0)	0.0 (0.0)	86.6 (100)

walleye population. Age-0 walleyes were the next largest consumers in 1986 (19,600 tonnes), followed closely by age-2 (17,100 tonnes) and age-1 walleyes (16,100 tonnes). Consumption in 1987 was more evenly distributed among walleye cohorts. Age-5 walleyes (1982 year-class) accounted for 29% of the consumption, followed by age-1 (26%), age-2 (24%), and age-3 (18%) walleyes. Total consumption by age-0 walleyes (2,800 tonnes) was substantially less in 1987 than in 1986. In 1988, consumption was again dominated by the 1982 and 1986 year-classes. Age-2 walleyes (1986 year-class) had the highest consumption (30,800 tonnes), followed by age-6 (21,000 tonnes) and age-3 (17,700 tonnes) cohorts. Consumption by the age-0 and age-1 cohorts was 7% of the total population consumption, lowest of the 3 years.

Sizes of Prey Consumed

Sizes of prey eaten by western Lake Erie walleyes did not vary significantly (χ^2 , $P = 0.05$) within months or walleye size-classes (across years) except for large walleyes (≥ 400 mm TL) in autumn (Figure 6). Clupeids consumed by large walleyes in autumn 1987 were significantly larger (χ^2 , $P < 0.05$) and of a wider range in total lengths than in 1986 or 1988.

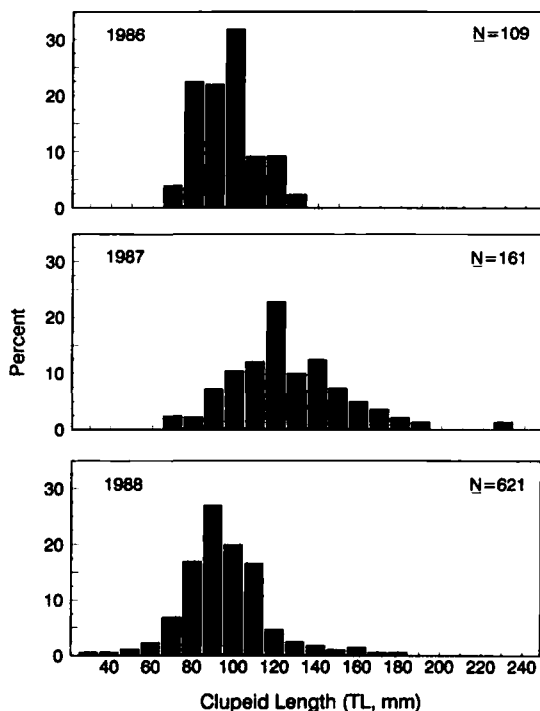


FIGURE 6.—Size distributions (total length, mm) of clupeids consumed by large walleyes (≥ 400 mm total length) in autumn 1986–1988.

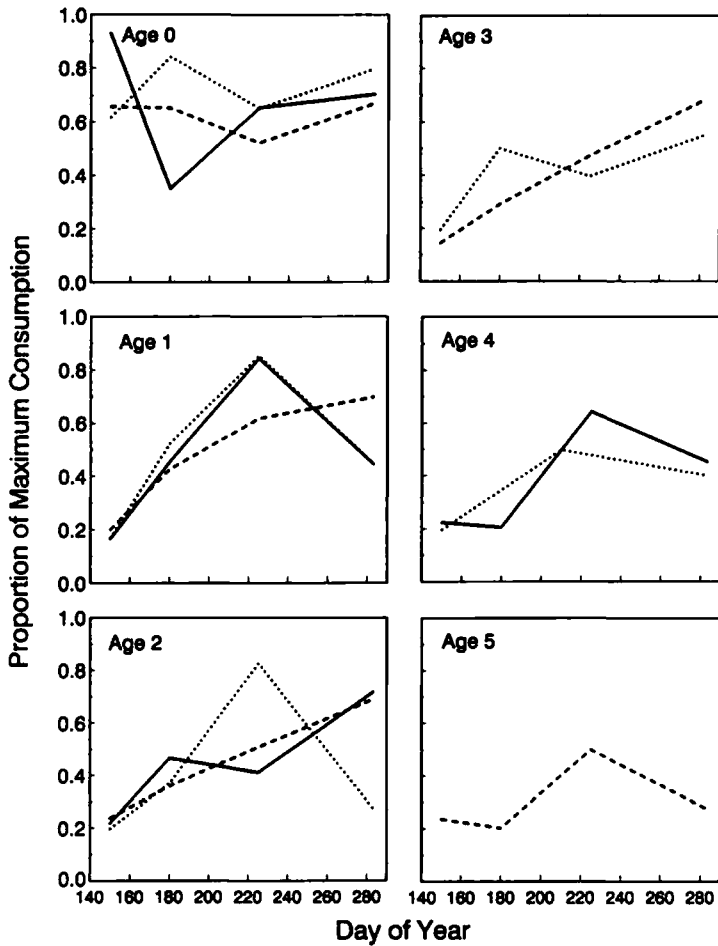


FIGURE 7.—Proportions of maximum consumption (P-value) for six age-classes of walleye from western Lake Erie in 1986 (solid lines), 1987 (broken lines), and 1988 (dotted lines).

Predation Success

The P-values generated by the bioenergetics models may provide a more detailed measure of prey availability than trawling indices. Annual or seasonal differences in predator and prey behavior or in relative abundances may cause P-values to vary within a cohort. If we assume that differences in P-values are not due to behavioral changes, then P-values are directly related to prey abundance. Two seasonal trends in P-values were consistent across years and age-classes. First, P-values from October 1988 were lower than those in 1986–1987 for walleyes of ages 2–4, despite generally higher 1988 P-values for ages 1–3 (Figure 7). Second, as walleyes increased in age, seasonal P-values became more consistent across years. The

P-values were highest in months when suitable-sized age-0 prey species were most numerous. For example, P-values of age-1 walleyes were highest in July, corresponding to high relative abundances of gizzard shad and white perch (Figure 7). The P-values of age-1 and older walleyes were lowest in late spring and early summer, likely reflecting low prey availability at that time.

Annual differences in the relative abundance of prey were reflected in the diets and growth of walleyes, particularly among younger cohorts. Annual growth (g/individual) of age-0 and age-1 walleyes was positively related to the standardized relative abundance of gizzard shad (Figure 8). The percent contributions of clupeids to annual consumption of age-1 and age-2 walleyes also were positively related to relative abundances of gizzard shad. Re-

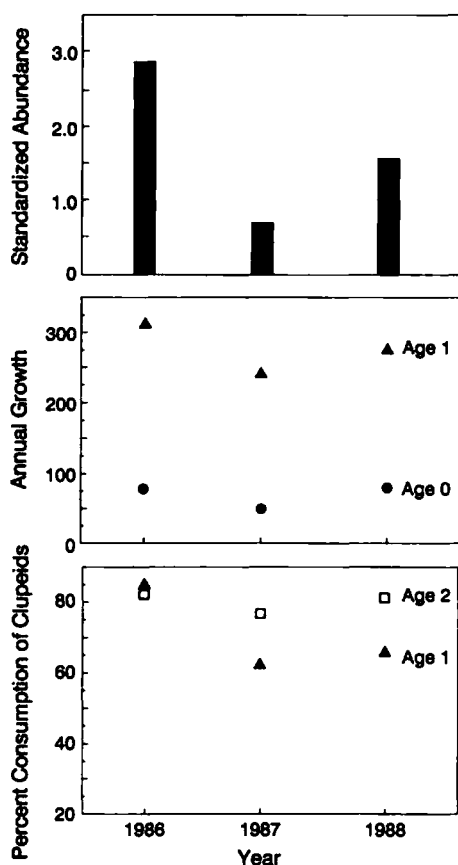


FIGURE 8.—Relationship between standardized abundance of gizzard shad during autumn and the annual growth (g/individual) and diet (annual percentage of clupeids in diet) of young walleyes (age 0 through age 2).

relationships between other prey species or older walleye cohorts were not as clear, due in part to the small number of observations (3 years).

Modeling Increased Harvest

Increasing annual mortality by 5, 10, and 20% over 1987 levels would release 2,870, 5,820, and 12,240 tonnes, respectively, of prey biomass from predation by age-2 and older walleyes, according to our model (Figure 9). The ultimate fate of the prey that would be conserved by these increased-mortality scenarios is unknown: the prey could be reallocated to growth of age-0 and age-1 walleyes, it could be used by the remaining age-2 and older walleyes or other piscivores, or it could be unused. If all conserved prey were used by age-0 and age-1 walleyes, these three scenarios represent potential biomass reallocations of 12, 24, and 50% of the total consumption by age-0 and age-1 walleyes in

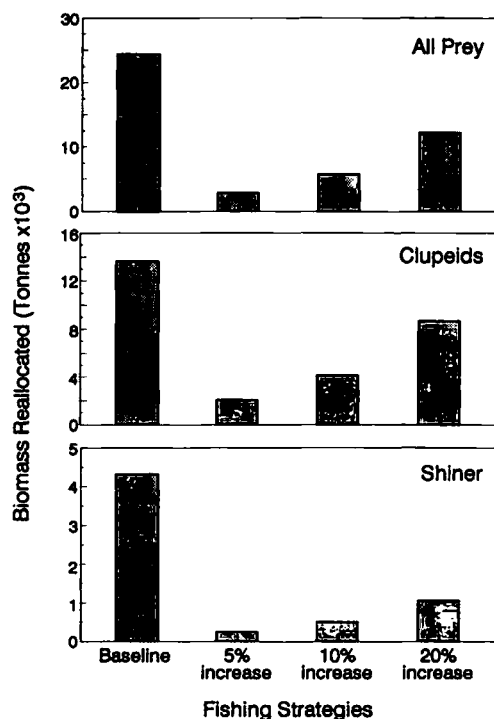


FIGURE 9.—Potential reallocation of prey with modeled increases in fishing mortality rates of 5, 10, and 20% in relation to prey consumption by age-0 and age-1 walleyes combined in 1987 ("baseline" values are those of Table 8 for 1987).

1987. Clupeids account for most of the potential reallocation; their release would augment the present clupeid consumption by age-0 and age-1 walleyes by 15, 30, and 64%. The reallocation potential of shiners would be only 6–24% of the baseline consumption by age-0 and age-1 walleyes combined.

Discussion

In periods of high piscivore biomass, the supply of prey may be the factor that limits walleye production. Despite relatively large variations in abundance of walleyes between 1986 and 1988, the total prey consumption by the walleye population was constant. The lowest total consumption occurred in 1987, when abundances of age-1 and older walleyes were highest, walleye growth was poorest, and abundances of nearly all age-0 prey fish species were low. The reduced growth of walleyes and low abundances of prey fish in 1987, in conjunction with the stable total consumption between 1986 and 1988, suggest that the annual sup-

ply of prey to western Lake Erie walleyes may be relatively constant.

Abundances of prey fish were reflected in patterns of prey use by walleyes. In years when gizzard shad and shiners were abundant, these species were the dominant prey. In years when preferred species (Forney 1974; Knight et al. 1984), especially gizzard shad, were not abundant, walleyes fed extensively on white perch, usually a non-preferred prey (Forney 1974). Perhaps as a consequence, annual incremental growth for age-0, age-1, and age-3 walleyes was lowest in 1987.

The positive relationship between gizzard shad abundance and age-1 walleye growth is understandable given the large contribution clupeids make to age-1 walleye diets. However, the positive relationship between gizzard shad abundance and age-0 walleye growth is surprising because clupeids represent only 12–43% of annual diets (Table 7). The positive relationship between age-0 walleye growth and gizzard shad abundance may be due to intraspecific competition for non-clupeid prey between age-0 and age-1 walleye when clupeid abundance is low. Relationships between older walleyes and older prey are understandably less clear. Other factors such as walleye size may tend to diminish noticeable relationships between relative prey abundance and diet or growth by enabling larger, older walleyes to feed more effectively upon larger age-0 gizzard shad, as they apparently did in 1987.

Length at age (growth) of walleyes in Lake Erie declined from 1965 to 1984 (Hatch et al. 1987), but growth appears to have stabilized since then, at least for age-1 and age-2 fish (ODW 1989). The reduction in growth of walleyes from 1965 to 1984 was likely linked to declining prey fish availability in spring and early summer. Water temperatures reach the optimal temperature for adult walleye growth (22°C: Kitchell et al. 1977) by mid-June in western Lake Erie, but prey consumption and growth by adults has been low, which is reflected in low P-values (typically <0.25). Metabolic costs are high for walleyes at temperatures above the optimum for consumption (Kitchell et al. 1977), and because western Lake Erie does not generally stratify thermally in summer, compensatory residence in thermal refuges by adult walleyes is not possible. Further evidence of poor growing conditions for adult walleyes comes from the use by adults of nonpreferred prey in June and July. Historically, shiners were important prey in spring and early summer (Parsons 1971; Knight et al. 1984). Shiners were eaten in June by age-1 and

age-2 walleyes in our study as well, but growth rates were slow and P-values (which integrate temperature and growth rate, providing a measure of predation success) were low. Thus, the low predation success observed during June and July and the reduced growth of walleyes between 1965 and the present may be due to a decline in shiner abundance.

In recent years gizzard shad have been the most important prey of western Lake Erie walleyes. Gizzard shad have been in Lake Erie since at least the mid-1800s (Trautman 1981), but did not become abundant until the 1960s and 1970s (ODW 1989). Their increase coincided with an increase in their contribution to walleye diets since 1959–1960 (Parsons 1971). Gizzard shad represented most of the biomass consumed by walleyes during our study on both individual (cumulative individual consumption) and population (total population consumption) levels. The effect of reduced availability of gizzard shad on walleye diet, growth, and consumption was evident in 1987, when growth of walleyes was poor. In that year, the contribution of gizzard shad to monthly diets was delayed or reduced, and large walleyes fed on a larger range and mean size of gizzard shad than in other years, perhaps because large walleyes became less size-selective or because gizzard shad grew faster. Further evidence of the reliance of walleyes upon gizzard shad is that significant growth by age-1 and older walleyes did not occur in any year until after age-0 gizzard shad predominated in the diet.

The reliance of walleyes on gizzard shad may be a problem for fisheries managers. In the event of a year-class failure of gizzard shad, the walleye population could dramatically alter the Lake Erie community. A hungry walleye population could reduce already declining populations of emerald and spottail shiners, as well as yellow perch, to low levels. A decline in yellow perch abundance could further depress the sagging fishery for this species. Alternatively, the ability of walleyes to eat white perch may reduce the numbers of age-0 fish of that species, enhancing conditions for other species.

Management efforts to enhance the prey fish community of Lake Erie are impractical. However, growth of walleyes could be maintained or improved by reducing intraspecific competition among walleyes through density reductions. Our modeling exercise showed that population manipulation through flexible harvest regulations could be used to improve prey availability and presum-

ably growth of the fishable stock. However, increased harvest would not be successful at improving growth of age-0 and age-1 walleyes because of differences in diet between small and large walleyes and the susceptibility of released prey to predation by other piscivore species.

An increase in exploitation (fishing mortality) of age-2 and older walleyes by 5% would result in only a 3% reduction in the total consumption by the walleye population. Even a rise of 20% in the annual fishing mortality would bring only a 14% reduction in consumption by the walleye population. Much of the uneaten prey resulting from increasing walleye mortality would be available to the remaining walleyes in the fishable stock, because 80% of the prey conserved would be clupeids—which grow so rapidly that they are generally available only to larger (age-2 and older) walleyes. Shiners would represent only a small amount of the newly available prey. Because shiners have a small terminal size, they are vulnerable to other piscivorous species such as smallmouth bass *Micropterus dolomieu*, white bass, channel catfish *Ictalurus punctatus*, white perch, and yellow perch, as well as to walleyes. Therefore, very little of the prey made available for reallocation by increasing annual walleye mortality would likely be translated into the production of small (age-0 and age-1) walleyes.

Intraspecific competition is apparent in western Lake Erie's walleye population, particularly among large year-classes and cohorts formed within a year of large year-classes. On a strictly biological basis, it would be best to improve conditions for growth by reducing intraspecific competition of very large walleye year-classes at a younger age. However, small walleyes (age 0 and age 1) are not acceptable products to resource users and no other reasonable means of control are available. Therefore, it seems that high walleye biomass, reduced growth, and strong pressure on the prey fish community are factors that must be endured by managers when large year-classes are produced.

Acknowledgments

We thank J. Bohne for technical assistance, B. Vondracek for support, the Ohio Division of Wildlife's Lake Erie Fishery Unit for technical assistance in the collection of specimens, and the Lake Erie Fishery Unit and the USFWS Sandusky Biological Station staff for the use of their trawling index data. We also thank E. Houde and three anonymous reviewers for comments on earlier

versions of this manuscript, F. Younger for graphical support, and the Maryland Sea Grant Institute for the use of computer facilities. The study was funded through Federal Aid in Sport Fish Restoration, projects F-57-R, study 13, and F-61-R, study 1, by contract from the Ohio Department of Natural Resources to the Ohio Cooperative Fish and Wildlife Research Unit and the Ohio State University Research Foundation.

References

- Chevalier, J. R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. *Transactions of the American Fisheries Society* 102:739–744.
- Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitteilungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 18.
- Deriso, R. B., T. J. Quinn II, and P. R. Neal. 1985. Catch-age analysis with auxiliary information. *Canadian Journal of Fisheries and Aquatic Sciences* 42:815–824.
- Forney, J. L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. *Transactions of the American Fisheries Society* 103:15–24.
- Forney, J. L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. *New York Fish and Game Journal* 27:105–141.
- Hartman, K. J. 1989. Western Lake Erie walleye: predation, prey utilization, and the relationship with somatic growth. Master's thesis. The Ohio State University, Columbus.
- Hartman, W. L. 1973. Effects of exploitation, environmental changes, and new species on the fish habits and resources of Lake Erie. Great Lakes Fishery Commission Technical Report 22.
- Hatch, R. W., S. J. Nepszky, K. M. Muth, and C. T. Baker. 1987. Dynamics of the recovery of the western Lake Erie walleye (*Stizostedion vitreum vitreum*) stock. *Canadian Journal of Fisheries and Aquatic Sciences* 44(Supplement 2):15–22.
- Hayward, R. S., F. J. Margraf, C. J. Knight, and D. J. Glomski. 1989. Gear bias in field estimation of the amount of food consumed by fish. *Canadian Journal of Fisheries and Aquatic Sciences* 46:874–876.
- Hewett, S. W., and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin, Sea Grant Technical Report WIS-SG-87-245, Madison.
- Hokanson, K. E. F., and W. M. Koenst. 1986. Revised estimates of growth requirements and lethal temperature limits of juvenile walleyes. *Progressive Fish-Culturist* 48:90–94.
- Hurley, D. A. 1986. Growth, diet, and food consumption of walleye (*Stizostedion vitreum vitreum*): an application of bioenergetics modeling to the Bay of Quinte, Lake Ontario, population. *Canadian Spe-*

- cial Publication of Fisheries and Aquatic Sciences 86:224-236.
- Jearld, A. 1983. Age determination. Pages 301-324 in L. A. Nielsen and D. L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.
- Kelso, J. R. M. 1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet, and temperature. Journal of the Fisheries Research Board of Canada 29: 1181-1192.
- Kitchell, J. F., D. J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*). Journal of the Fisheries Research Board of Canada 34:1922-1935.
- Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Transactions of the American Fisheries Society 113:677-693.
- Lake Erie Committee. 1990a. Report of the Lake Erie Walleye Task Group. Minutes of the Lake Erie Committee (meeting), March 22-23, 1990. Appendix XI:121-134. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- Lake Erie Committee. 1990b. Report of the Statistics and Modeling Task Group. Minutes of the Lake Erie Committee (meeting), March 22-23, 1990. Appendix X:61-120. Great Lakes Fishery Commission, Ann Arbor, Michigan.
- Leach, J. H., and S. J. Nepszy. 1976. The fish community in Lake Erie. Journal of the Fisheries Research Board of Canada 33:622-638.
- ODW (Ohio Division of Wildlife, Lake Erie Fisheries Unit). 1989. Status and trend highlights Ohio's Lake Erie fish and fisheries. Ohio Department of Natural Resources, ODW, Columbus.
- ODW (Ohio Division of Wildlife, Lake Erie Fisheries Unit). 1990. Status and trend highlights Ohio's Lake Erie fish and fisheries. Ohio Department of Natural Resources, ODW, Columbus.
- Parsons, J. W. 1970. Walleye fishery of Lake Erie in 1943-62 with emphasis on contributions of the 1941-61 year classes. Journal of the Fisheries Research Board of Canada 27:1475-1489.
- Parsons, J. W. 1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. Transactions of the American Fisheries Society 100:474-485.
- Pierce, R. J., T. E. Wissing, J. G. Jaworski, R. N. Givens, and B. A. Megrey. 1980. Energy storage and utilization patterns of gizzard shad in Acton Lake, Ohio. Transactions of the American Fisheries Society 109: 611-616.
- Schaeffer, J. S., and F. J. Margraf. 1986. Population characteristics of the invading white perch (*Morone americana*) in western Lake Erie. Journal of Great Lakes Research 12:127-131.
- Smith, L. L., Jr., and W. M. Koenst. 1975. Temperature effects on eggs and fry of percoid fishes. U.S. Environmental Protection Agency Ecological Research Series, EPA-660/3-75-017, Duluth, Minnesota.
- Trautman, M. B. 1981. The fishes of Ohio. The Ohio State University Press, Columbus.
- Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian University, Minsk. Translated from Russian: the Fisheries Research Board of Canada. Translation Series 164, 1960, Ottawa.
- Wissing, T. E. 1974. Energy transformations by young-of-the-year white bass *Morone chrysops* (Rafinesque) in Lake Mendota, Wisconsin. Transactions of the American Fisheries Society 103:32-37.

Received February 28, 1990

Accepted October 28, 1991