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Changes in Prey Fish Populations in Western Lake Erie, 1969–88, as Related to Walleye, *Stizostedion vitreum*, Predation

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Relative abundance of the total prey fish community in the western basin of Lake Erie varied little from 1969 to 1988, but species composition changed significantly. Soft-rayed fishes such as emerald shiner, *Notropis atherinoides*, spottail shiner, *N. hudsonius*, and alewife, *Alosa pseudoharengus*, declined significantly after 1977 whereas only one spiny-rayed species, white bass, *Morone chrysops*, declined over the same period. Trout-perch, *Percopsis omiscomaycus*, a relatively abundant species rarely eaten by piscivores in this system, experienced only minor shifts in abundance between 1969 and 1988. Although several factors could be responsible for the shift in species composition, predation by increasingly abundant walleye, *Stizostedion vitreum*, played a major role. Walleye prefer to eat soft-rayed fishes; thus, observed shifts in the community match expectations of selection noted in the diet. We suggest that management goals focusing primarily on walleye affected not only the targeted species but the entire fish community of western Lake Erie.

L'abondance relative de la communauté totale de poissons proies dans le bassin occidental du Lac Érié a peu varié de 1969 à 1988, mais la composition spécifique a changé de façon notable. Les poissons à nageoires rayonnées comme le méné émeraude, *Notropis atherinoides*, la queue à tache noire, *N. hudsonius*, et le gaspateur, *Alosa pseudoharengus*, ont nettement décliné après 1977, tandis qu'une seule espèce à nageoires épineuses, le bar blanc, *Morone chrysops*, marquait un recul pendant la même période. L'omisco, *Percopsis omiscomaycus*, espèce relativement abondante mais rarement consommée par les piscivores dans ce système, n'a présenté que des modifications mineures de l'abondance entre 1969 et 1988. Si les changements observés dans la composition spécifique peuvent être imputables à plusieurs facteurs, la prédation due à une population de plus en plus abondante de doré, *Stizostedion vitreum*, a joué un rôle de premier plan. Le doré préfère se nourrir de poissons à nageoires rayonnées, et les changements observés dans la communauté correspondent aux prévisions que permet le choix alimentaire de cette espèce. Nous pensons que les buts de la gestion, qui ont été axés avant tout sur le doré, ont affecté non seulement l'espèce visée, mais l'ensemble de la communauté ichthyologique de l'ouest du Lac Érié.

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Lake Erie provides a natural setting to evaluate the role of selective piscivory on a multispecies prey fish community in a large system. Walleye, *Stizostedion vitreum*, are the dominant piscivores in Lake Erie and their population characteristics have received considerable attention historically (Regier et al. 1969; Wolfert 1969; Parsons 1970, 1971; Kutkuhn et al. 1976; Muth and Wolfert 1986; Hatch et al. 1987). Walleye abundance declined during the 1960's, remained low through the mid-1970's, but increased rapidly after 1976 due to conservative fishery management and the production of strong year classes in 1977, 1982, and 1986 (Hatch et al. 1987; Ohio Department of Natural Resources, unpublished data). In the mid-1980's, walleye in the western basin may have exceeded historical levels and expanded into the central basin of Lake Erie and other connecting waters.

The substantial increase in predator abundance prompted concerns regarding system carrying capacity (Knight et al. 1984; Muth and Wolfert 1986). Walleye prefer soft-rayed fishes over spiny-rayed fishes in Lake Erie and are size selective, eating mostly small (<130 mm total length) prey even as adults (Knight et al. 1984). Because these predators depend on annual production of age-0 fishes in Lake Erie (Knight et al. 1984; Hartman and Margraf 1992), walleye predation could alter the fish species composition and size structure of the community. Although such shifts might be attributed to other factors such as a reduction in the rate of eutrophication (e.g., Leach et al. 1977) or the presence of an exotic species (e.g., white perch, *Morone americana*), effects due to predation should be magnified in the presence of abundant walleye and when viewed over a short time interval.

We examined differences in fish community structure between an earlier period (1969–77) of low walleye abundance in western Lake Erie and a later one (1978–88) of high walleye abundance to ascertain the effects of piscivory. Prey fish abun-

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FIG. 1. Sampling stations for ODNR bottom trawl surveys in western Lake Erie, 1969–88. Offshore index stations are designated at MS and KB, nearshore stations at ED, EH, JI, and CP, and supplemental stations as “+” (NR = Niagara Reef).

TABLE 1. Physical characteristics of western Lake Erie waters measured by ODNR during trawling surveys, 1969–88.

Year	<i>n</i> ^a				Mean water temperature (°C) ^b				Mean dissolved oxygen (mg·L ⁻¹) ^b				Median Secchi transparency (m) ^c			
	June	July	Aug.	Oct.	June	July	Aug.	Oct.	June	July	Aug.	Oct.	June	July	Aug.	Oct.
1969	3	6	7	2	18.0	23.5	25.1	19.5+	—	—	—	—	0.6	0.8	1.2	—
1970	12	12	18	0	21.9	23.2	24.7	—	9.6	8.3	7.9	—	0.6	0.8	0.6	—
1971	11	12	12	5	23.4	23.7	23.7	20.2	8.1	8.5	8.4	8.6	0.6	0.8	0.8	—
1972	12	12	12	5	20.8+	23.8+	22.2+	14.8+	10.3+	7.5+	8.2+	9.4	0.6	0.8	0.9	—
1973	3	5	2	7	21.0+	24.2+	25.0+	17.0+	10.0+	—	9.5+	10.0	0.6	0.6	—	—
1974	6	15	13	7	17.5+	24.0+	25.7+	14.0+	—	8.1+	8.0+	—	0.8	0.9	0.8	0.8
1975	10	14	12	7	22.2+	24.4+	23.4	14.4	—	—	—	10.0	0.8	1.2	0.9	0.9
1976	10	21	12	7	21.2	23.9	21.0	13.7	9.6	10.2	—	10.9	0.9	0.8	0.9	—
1977	12	8	13	2	19.5	23.8	24.1	10.5	11.0	11.2	10.1	—	0.6	0.9	0.9	0.9
1978	6	11	10	3	23.0	22.9	24.0	12.3	—	—	—	—	0.8	0.9	0.9	—
1979	6	14	9	6	20.2	22.4	22.5	13.2+	—	—	—	—	0.3	0.6	0.9	—
1980	11	9	6	2	19.3	23.3	19.8	—	—	—	—	—	0.3	0.9	0.8	0.6
1981	6	0	0	0	21.7	—	—	—	—	—	—	—	—	—	—	—
1982	18	16	18	7	19.3	23.4	21.3	17.9	8.5	7.8	8.6	9.3	0.6	0.9	0.9	—
1983	16	16	16	6	20.9	23.9	25.8	13.5	8.2	6.0	7.1	8.8	0.9	1.1	0.9	1.1
1984	16	16	16	6	19.8	21.8	23.3	15.7	7.9	7.7	6.7	9.0	0.6	0.8	1.1	0.3
1985	17	16	9	6	19.5	22.6	22.7	14.3	8.4	7.6	7.2	9.5	0.6	0.9	0.9	1.1
1986	21	14	18	7	21.5	24.7	24.6	13.4	7.5	6.6	7.5	8.9	0.6	1.2	0.6	0.6
1987	14	16	6	6	21.6	24.5	25.0	17.3	7.7	6.1	7.0	9.0	1.2	0.9	0.9	1.4
1988	8	11	8	6	21.9	24.5	22.4	18.8	8.3	6.6	5.0	8.3	0.9	1.1	0.9	0.8

^aNumber of stations where at least one variable was measured.

^bUnmarked data are from bottom waters; marked data (+) are from surface waters.

^cNearshore stations only.

dance data from bottom trawl assessment surveys in conjunction with previous studies of walleye diets were used to measure these changes. The early period was established as the time prior to the recruitment of the strong 1977 walleye year class

to the yearling–adult population whereas the later period reflected substantial increases in walleye abundance (Hatch et al. 1987). Our objectives were to examine annual abundance and species composition of prey fishes and prey composition

of the walleye diet in relation to the change in walleye abundance between these periods.

Materials and Methods

Study Area

Physical and limnological characteristics of the western basin of Lake Erie are well documented (Beeton 1963; Hartman 1972; Sly 1976; Boyce et al. 1987). Generally, the western basin is isothermal throughout the year due to mixing of its shallow waters and seldom becomes anoxic. Bottom substrates consist primarily of sand and clay, although dolomite limestone forms several major reef complexes. Stations were established in the western basin at several soft-bottomed areas (Fig. 1) amenable to trawling and were assumed to be representative of prey fish populations throughout the western basin, despite the lack of samples from reef habitats and from waters outside of Ohio's jurisdiction. Abiotic data collected during this study are summarized in Table 1.

Prey Fish Field Collections

Fish population data were collected biweekly from June through August (summer) and in October (fall) by the Ohio Department of Natural Resources (ODNR) at four nearshore (2–7 m depth) and two offshore (>9 m depth) index stations in the western basin of Lake Erie from 1969 to 1988 (Fig. 1). Fishes were collected with a semiballoon trawl (10.7-m head-rope, 6.4-mm bar mesh in cod end) towed on the lake bottom at about $0.8 \text{ m} \cdot \text{s}^{-1}$. Nearshore stations were sampled for 10 min and offshore stations were sampled for 15 min to provide adequate catches (catches generally were lower in offshore areas during summer). Paired tows were made in opposite directions at each station but were not considered independent samples because of overlapping tow swaths; thus, total effort was 20 min at nearshore stations and 30 min at offshore stations.

Summer surveys were designed to quantify relative abundance of age-0 walleye and yellow perch, *Perca flavescens*. Surveys began soon after age-0 walleye were first captured in preliminary tows in early June. Supplemental stations (Fig. 1) were established at offshore (depth >6 m) areas after 1977 to provide additional data on fish distribution patterns.

Fall trawl surveys consisted of single visits to the sampling stations (Fig. 1). Fall surveys began by early October and were completed within 3 wk. As in summer, supplemental stations were sampled after 1977 to provide additional data on fish distribution.

Catches were sorted and counted by species (Table 2) and size group aboard ship. If abundance of any species/size group was high (exceeding approximately 1000 fish), total numbers were estimated from random subsamples obtained either volumetrically ($\pm 0.5 \text{ L}$) or gravimetrically ($\pm 30 \text{ g}$) from the total volume or weight of that group. Rainbow smelt, *Osmerus mordax*, were not always counted in summer surveys; hence, we included them in relative abundance analyses for fall only.

Prey Fish Data Analyses

To estimate relative abundance, we first converted catch per tow to catch per hour of trawling (CPHT) at each index station. These data then were transformed as $\ln(\text{CPHT} + 1)$ to approximate a normal distribution (Sokal and Rohlf 1986) and to serve as a relative abundance index.

TABLE 2. Common and scientific names of fishes captured during bottom trawl surveys in western Lake Erie, 1969–88. Species regularly captured at every station are identified with a “+”. Prey of walleye are identified with a “p”.

	Common name	Scientific name
+ , p	Alewife	<i>Alosa pseudoharengus</i>
	Bigmouth buffalo	<i>Ictiobus cyprinellus</i>
	Black bullhead	<i>Ameiurus melas</i>
	Black crappie	<i>Poxomis nigromaculatus</i>
	Blackside darter	<i>Percina maculata</i>
	Bluegill	<i>Lepomis macrochirus</i>
	Bluntnose minnow	<i>Pimephales notatus</i>
	Bowfin	<i>Amia calva</i>
+	Brown bullhead	<i>Ameiurus nebulosus</i>
	Burbot	<i>Lota lota</i>
+	Channel catfish	<i>Ictalurus punctatus</i>
	Coho salmon	<i>Oncorhynchus kisutch</i>
+	Common carp	<i>Cyprinus carpio</i>
+ , p	Emerald shiner	<i>Notropis atherinoides</i>
	Fathead minnow	<i>Pimephales promelas</i>
+ , p	Freshwater drum	<i>Aplodinotus grunniens</i>
+ , p	Gizzard shad	<i>Dorosoma cepedianum</i>
	Golden shiner	<i>Notemigonus crysoleucas</i>
	Goldfish	<i>Carassius auratus</i>
	Northern hog sucker	<i>Hypentelium nigricans</i>
	Johnny darter	<i>Etheostoma nigrum</i>
	Lake whitefish	<i>Coregonus clupeaformis</i>
	Largemouth bass	<i>Micropterus salmoides</i>
	Longnose gar	<i>Lepisosteus osseus</i>
	Logperch	<i>Percina caprodes</i>
	Mooneye	<i>Hiodon tergisus</i>
	Muskellunge	<i>Esox masquinongy</i>
	Northern pike	<i>Esox lucius</i>
	Pumpkinseed	<i>Lepomis gibbosus</i>
+	Quillback	<i>Carpiodes cyprinus</i>
+ , p	Rainbow smelt	<i>Osmerus mordax</i>
	Rainbow trout	<i>Oncorhynchus mykiss</i>
	Rock bass	<i>Ambloplites rupestris</i>
	Sand shiner	<i>Notropis stramineus</i>
	Sauger	<i>Stizostedion canadense</i>
	Sea lamprey	<i>Petromyzon marinus</i>
	Shorthead redhorse	<i>Moxostoma macrolepidotum</i>
	Silver chub	<i>Macrhybopsis storeriana</i>
	Silver lamprey	<i>Ichthyomyzon unicuspis</i>
	Smallmouth bass	<i>Micropterus dolomieu</i>
	Spotfin shiner	<i>Cyprinella spiloptera</i>
+ , p	Spottail shiner	<i>Notropis hudsonius</i>
	Stonecat	<i>Noturus flavus</i>
+ , p	Trout-perch	<i>Percopsis omiscomaycus</i>
+ , p	Walleye	<i>Stizostedion vitreum</i>
+ , p	White bass	<i>Morone chrysops</i>
	White crappie	<i>Pomoxis annularis</i>
+ , p	White perch	<i>Morone americana</i>
	White sucker	<i>Catostomus commersoni</i>
+ , p	Yellow perch	<i>Perca flavescens</i>

Index values were calculated in two ways: as the arithmetic mean of the log-transformed CPHT across four nearshore stations (pooled species) in summer and as the mean transformed CPHT across offshore stations for each species in fall. Seasonal selection of near and offshore stations for index calculations was based on apparent offshore movements of many species in late summer and fall. Pooling of species into prey type categories (discussed below) was performed on CPHT values prior to transformation.

TABLE 3. Relative abundance statistics for all fish species caught in ODNR summer bottom trawl surveys in western Lake Erie, 1969–88.

Year	June			July			August		
	<i>n</i> ^a	Mean ^b	95% CI ^c	<i>n</i>	Mean	95% CI	<i>n</i>	Mean	95% CI
1969	4	1171.6	183, 7471	4	3747.1	420, 33356	4	1217.0	4, 18209
1970	8	781.9	217, 2800	8	3618.2	1082, 12090	12	2127.1	925, 4890
1971	6	83.7	19, 343	8	2701.7	388, 18749	8	2454.3	782, 7694
1972	7	177.0	27, 1129	8	520.7	115, 2336	8	4039.0	633, 25739
1973	4	135.0	30, 595	12	4998.0	1590, 15701	8	5983.9	1663, 21514
1974	4	278.5	6, 9960	11	2685.5	459, 15686	9	12518.0	3002, 52177
1975	6	1174.0	135, 10132	10	1129.0	247, 5132	8	4410.6	1864, 10434
1976	7	1297.5	404, 4162	8	11463.4	6346, 20707	8	11474.8	5917, 22252
1977	8	1261.7	226, 6997	8	2848.8	228, 35373	8	4203.9	946, 18656
1988	4	1338.4	56, 30965	8	4632.2	1251, 17134	8	3525.3	918, 13543
1979	4	146.2	8, 2294	8	1661.4	605, 4552	8	26956.0	15425, 41015
1980	7	400.8	101, 1581	8	8777.0	2306, 33397	4	13133.5	8019, 21508
1981	8	661.5	65, 6553	8	8094.0	917, 71310	8	8005.4	3085, 20766
1982	12	2015.3	1059, 3834	8	8945.3	3464, 23094	8	3046.3	1849, 5019
1983	8	198.7	89, 440	8	1890.3	905, 3946	8	2789.6	1032, 7534
1984	8	320.2	84, 1213	8	8750.7	3536, 21650	8	20069.4	7959, 50600
1985	8	613.6	145, 2570	8	1698.3	436, 6604	4	9995.6	520, 191548
1986	8	378.2	105, 1346	8	4933.5	1212, 20059	8	13959.7	7458, 26127
1987	7	153.6	34, 670	8	3669.2	1458, 9231	4	2696.3	737, 9848
1988	4	3546.5	896, 14025	8	18470.8	8604, 39651	4	43782.0	9595, 199748
Pooled									
1969–77	54	506.2	306, 837	77	2739.8	1703, 4407	73	4397.4	3040, 6361
1978–88	78	530.1	356, 788	88	4973.1	3571, 6925	72	8475.1	6197, 11591

^aNumber of trawl stations.^bGeometric mean of catch per hour of trawling.^cBack-transformed lower and upper limits of 95% CI.

Summer index values were used to monitor monthly changes in prey fish abundance and were assumed to directly reflect annual production. We estimated species composition of trawl catches during August (generally the month of highest prey fish availability) as the mean percentage of the CPHT among stations. Fall index values were assumed to reflect prey fish abundance after most of the annual predation by walleye had occurred (Hartman and Margraf 1992).

We designated “prey fishes” to include major species/size groups known to be vulnerable to walleye during the year (Knight et al. 1984). Prey fishes included all sizes of most soft-rayed fishes (e.g., emerald shiner, *Notropis atherinoides*, spot-tail shiner, *N. hudsonius*, rainbow smelt, and trout-perch, *Percopsis omiscomaycus*) but only age-0 clupeids (gizzard shad, *Dorosoma cepedianum*, and alewife, *Alosa pseudoharengus*). Spiny-rayed fishes were considered vulnerable only as age 0 and included walleye, white bass, *Morone chrysops*, white perch, yellow perch, and freshwater drum, *Aplodinotus grunniens*. Age-1 and older clupeid and spiny-rayed fishes were not vulnerable to most walleye because they generally exceed 130 mm (total length) in summer and fall (Knight et al. 1984; ODNR, unpublished data). Age-0 walleye also were too large (>200 mm) to be prey in fall and were excluded from analyses.

Species were grouped into clupeid, soft-, and spiny-rayed prey type categories to account for differences due to food selection by walleye (Knight et al. 1984). Clupeids were separated from other soft-rayed fishes because of their frequent consumption by walleye and because their fast growth allows them to outgrow vulnerability to most walleye. Other soft-rayed fishes remain at vulnerable sizes to walleye throughout their lives. Spiny-rayed fishes were separated from both clupeids and

other soft-rayed fishes because of their fast growth and low consumption by walleye.

Walleye Food Habits

A review of walleye food habits literature produced four sources of data from which we could determine seasonal composition of the three prey types to the diets of age-0 and age-1 or older walleye in western Lake Erie (Wolfert 1969; Parsons 1971; Knight 1982; Hartman and Margraf 1992). Published data were averaged (when necessary) across stations and/or ages (1 and older) to provide monthly composition percentages by prey type, year, and walleye age group (0 or older) from each study. Seasonal diet composition was measured for each walleye age group as the average and range of monthly percentages across spring (April–June), summer (July–August), and fall (September–November) of each year. Percentages were based on numbers (Parsons 1971), volumes (Wolfert 1969; Knight 1982), or wet weight (Hartman and Margraf 1992).

Results

Prey Fish Abundance and Size

Relative abundance (all species pooled) was similar between 1969–77 and 1978–88 for all summer months. In June, average total catch rates were low in both periods, probably because larval and early juvenile fishes were not fully vulnerable to the trawl. Total catches increased significantly (*t*-tests, $P < 0.05$) between June and July–August and typically were highest in August (Table 3; Fig. 2). However, differences in total catch rates were not significant (*t*-tests, $P > 0.05$) between periods

FIG. 2. Mean log-transformed catch per hour trawled (CPHT) with 95% confidence intervals for three types of prey fishes from ODNR bottom trawl catches at nearshore stations during summer, 1969–88.

FIG. 3. Mean percent contribution to total catch per hour trawled (CPHT) for three prey fish types collected from ODNR bottom trawl surveys at nearshore stations in western Lake Erie during August, 1969–88.

for any month. Likewise, differences in mean index values were apparent for each of the various prey types between periods but were significant ($P < 0.05$) only for spiny-rayed fishes in August (Fig. 2), which became more abundant during 1978–88.

Shifts in species composition were apparent between periods during August trawl surveys, consisting mostly of a decrease in the proportion of soft-rayed fishes and an increase in the proportion of spiny-rayed fishes (mostly white perch) after 1977 (Fig. 3). Gizzard shad and alewife fluctuated widely over the

FIG. 4. Relative abundance trends for three prey fish types during fall ODNR bottom trawl surveys at two offshore stations in western Lake Erie, 1969–88. Index values were calculated as the mean log-transformed catch per hour trawled (CPHT) across both stations for each year.

TABLE 4. Geometric mean of catch per hour of trawling for fishes caught in ODNR fall bottom trawl surveys at two offshore stations in western Lake Erie, 1969–88.

Year	Soft-rayed species ^a						Spiny-rayed species ^b				
	AW	GS	ES	SS	TP	RS	WB	WP ^c	YP	WA	FD
1969	162.2	56.0	994.6	351.6	4.9	40.6	112.9	—	163.7	0.0	607.5
1970	26.7	26.7	1564.3	56.2	43.3	25.9	59.2	—	1153.0	0.7	12.5
1971	37.0	12.1	434.5	176.2	59.2	41.8	5.9	—	625.4	0.0	213.6
1972	18.0	2.6	289.1	60.3	0.7	9.2	14.9	—	506.2	0.0	119.9
1973	95.3	12.1	103.8	244.2	12.0	1.8	0.0	—	43.9	0.7	17.7
1974	731.2	20.8	189.4	56.6	14.2	157.6	14.2	—	92.3	4.0	91.3
1975	20.1	4.0	172.4	60.7	17.9	19.7	19.6	—	692.0	46.5	186.7
1976	193.4	11.1	102.6	181.0	45.9	41.7	27.3	—	101.3	6.1	159.9
1977	25.5	13.3	39.8	170.9	198.5	56.1	8.0	0.0	1512.2	8.7	132.0
1978	5.7	53.7	20.2	253.9	35.2	2.6	2.3	0.0	329.3	14.0	345.9
1979	41.8	60.1	2.6	236.9	312.2	312.2	4.6	0.7	1877.1	13.0	184.9
1980	179.4	231.5	7.7	93.1	13.9	14.3	14.2	0.0	1799.8	20.3	24.2
1981	9.8	274.1	0.0	6.5	86.0	0.0	0.7	7.5	294.6	3.2	26.2
1982	0.0	3.4	4.2	5.1	156.4	11.2	2.6	48.7	1301.4	22.5	18.4
1983	1.6	3.6	14.6	17.1	72.5	3.6	0.0	182.3	15.5	0.7	139.2
1984	8.4	2.3	0.0	15.6	62.0	36.5	7.8	2017.3	246.4	7.8	30.8
1985	1.2	156.9	0.0	1.2	73.7	0.0	1.2	252.9	55.0	0.0	54.8
1986	10.1	140.2	3.1	6.4	73.2	37.3	5.7	250.9	35.1	42.7	22.8
1987	2.0	4.9	4.9	7.3	83.6	24.1	0.7	1019.5	28.5	3.6	87.9
1988	4.6	27.5	0.7	6.9	56.1	20.7	1.2	884.4	30.5	0.7	58.7
Pooled ^d											
1969–77	65.3	12.8	241.2	121.0	20.4	27.2	14.7	0.0	309.9	2.3	87.4
1978–88	6.7	32.2	2.8	17.5	71.4	11.0	2.5	54.6	168.4	6.1	136.4

^aAW = alewife, GS = gizzard shad, ES = emerald shiner, SS = spottail shiner, TP = trout-perch, RS = rainbow smelt.

^bWB = white bass, WP = white perch, YP = yellow perch, WA = walleye, FD = freshwater drum.

^cWhite perch were not observed in trawl catches until summer 1977.

^dGeometric mean per period ($N = 18$ observations during 1969–77 and 22 during 1978–88).

TABLE 5. Percent composition of three prey fish types to the seasonal diets of walleye of age 0 and ≥ 1 in western Lake Erie during 1959–60 (Parsons 1971), 1962 (Wolfert 1969), 1979–81 (Knight 1982), and 1986–88 (Hartman and Margraf 1992).

Season	Age	Year	<i>n</i> ^a	Prey fish type		
				Clupeids Mean (range)	Soft-rayed Mean (range)	Spiny-rayed Mean (range)
Spring (Apr.–June)	≥ 1	1960	2	0.0 (0–0)	100.0 (100–100)	0.0 (0–0)
		1979–81	7	1.8 (0–16)	91.4 (78–100)	6.8 (0–18)
		1986–88	3	8.2 (4–15)	46.1 (12–70)	45.7 (26–83)
Summer (July–Aug.)	0	1959	2	1.0 (0–2)	61.5 (50–73)	38.0 (26–50)
		1962	5	31.0 (0–86)	12.5 (0–50)	56.5 (7–100)
		1979–81	2	48.3 (40–57)	37.2 (34–40)	14.5 (9–20)
		1986–88	6	22.0 (2–47)	9.7 (3–22)	68.3 (45–95)
	≥ 1	1960	2	32.5 (5–60)	44.0 (0–88)	23.5 (7–40)
		1979–81	6	75.0 (69–100)	6.7 (0–20)	18.3 (0–80)
		1986–88	6	66.4 (27–96)	8.6 (0–38)	25.0 (3–64)
	0	1959	2	0.0 (0–0)	88.0 (76–100)	12.0 (0–24)
		1962	3	9.4 (0–28)	67.9 (11–100)	22.7 (0–61)
		1979–81	3	18.2 (5–33)	70.8 (50–95)	11.0 (0–33)
		1986–88	4	25.0 (6–60)	43.5 (12–76)	31.5 (12–46)
Fall (Sept.–Nov.)	≥ 1	1960	2	84.0 (68–100)	16.0 (0–32)	0.0 (0–0)
		1979–81	8	55.6 (0–95)	37.2 (5–100)	7.2 (0–49)
		1986–88	8	93.9 (83–97)	4.4 (0–18)	1.7 (0–3)

^aNumber of monthly percent values used in the calculation of mean and range.

20-yr period but generally composed a relatively constant fraction of trawl catches over the long-term trend. Alewife was the predominant clupeid in the early period, but gizzard shad became increasingly abundant after the mid-1970's. After 1977, age-0 gizzard shad and white perch composed more than 85% of August trawl catches.

In fall, substantial declines in relative abundance were evident after 1977 for alewife, emerald shiner, and white bass (Table 4). Spottail shiner declined after 1980 and yellow perch after 1982. Gizzard shad and trout-perch increased in relative abundance after 1977. As a group, spiny-rayed fishes maintained relatively constant densities over the 20-yr period, with some decline occurring after 1982 (Fig. 4). Clupeids, on average, were significantly less abundant (*t*-tests, $P < 0.05$) in the later period compared with the earlier period. Declines for other soft-rayed fishes during 1982–88 were the most substantial of any prey type.

Mean index values in fall declined significantly (*t*-tests, $P < 0.05$) between 1969–77 and 1978–88 for alewife, both shiner species, and white bass and were lower (although not significantly so) for all species except gizzard shad, trout-perch, freshwater drum, and walleye during the latter period (Fig. 5). For emerald shiner, this decline began early in the 20-yr period concurrent with the increase in the walleye population (Table 4). In contrast, spottail shiner maintained constant abundance until the early 1980's before they declined. Overall, relative abundance for four of six soft-rayed and two of four spiny-rayed fishes decreased in the period of high walleye abundance, which accounted for a significant ($P < 0.05$) decline in total fall catch rates (all species) relative to the early period of low walleye abundance.

Walleye Food Habits

Eleven of the 15 most commonly encountered fishes in trawl

surveys were eaten by walleye (Table 2) (Knight et al. 1984; Hartman and Margraf 1992). Walleye diets varied among years (studies) within seasons and age groups (Table 5). In spring, age-1 and older walleye ate mostly shiner in 1960 and during 1979–81, but spiny-rayed prey were more prevalent during 1986–88. In summer, age-0 walleye usually ate a higher proportion of spiny-rayed prey than did older walleye, which ate mostly clupeids or shiner in all years. There was evidence of higher shiner consumption during the summers of 1959–60 than in later years by both walleye age groups. Fall diets of age-0 walleye were dominated by shiner in all years whereas older walleye ate mostly clupeids. Spiny-rayed fishes were not the major prey of age-1 and older walleye in summer or fall from any period. Generally, walleye ate more shiner in early years than in later years and more spiny-rayed prey in later years, except for age-1 and older walleye, which ate mostly clupeids in summer and fall in all years.

Discussion

Walleye and Community Structure

We contend that predation by abundant walleye, the terminal piscivores in this system, played a large role in structuring the fish community from 1969 to 1988. Our conclusion is based on observed changes in annual prey abundance and species composition in western Lake Erie as walleye abundance increased over this period (Hatch et al. 1987). Walleye in Lake Erie are known to be selective for prey type (Knight et al. 1984; Francis 1992), exhibiting positive electivity values for most soft-rayed fishes (excluding trout-perch) and negative values for spiny-rayed prey. In this study, we show that significant declines in relative abundance occurred primarily for soft-rayed fishes (particularly shiner) but not for spiny-rayed fishes or trout-perch between 1969–77 and 1978–88.

FIG. 5. Differences in mean log-transformed catch per hour trawled (CPHT) between 1978–88 and 1969–77 for six soft-rayed and four spiny-rayed prey fishes from fall ODNR bottom trawl catches at offshore stations in western Lake Erie. Significant differences (*t*-tests, $P < 0.05$) are indicated with an asterisk. Species codes are defined in Table 4.

Implicit in our conclusion is the assumption that walleye feeding behavior did not change substantially between periods. A review of walleye diet studies in western Lake Erie produced no information from 1969 to 1977 but did provide data from 1959 to 1962 (Wolfert 1969; Parsons 1971) when walleye abundance was similarly low (Hatch et al. 1987) and from 1979 to 1988 (Knight 1982; Hartman and Margraf 1992) when their abundance was high. Diet shifts between 1959–62 and 1979–88 reflect major changes in the composition of the prey fish community between periods but not necessarily changes in walleye feeding behavior. For example, increased use of spiny prey in spring by walleye during 1986–88 (Hartman and Margraf 1992) coincided with high abundance of white perch and low abundance of shiner. However, walleye did not become entirely opportunistic, as soft-rayed prey were the prevalent item in stomachs despite their low abundance. Changes in summer and fall diets across periods also coincided with changes in abundance of soft-rayed prey, and walleye consistently switched to clupeids as opposed to spiny prey. Francis (1992) concluded that diet selection of Lake Erie walleye during 1990–91 was determined primarily by prey type as opposed to abundance, soft-rayed prey being selected over spiny prey. Therefore, we believe that walleye feeding behavior was consistent between 1959 and 1988 and, consequently, their selective predation on soft-rayed prey had a major influence on fish community structure.

Structuring of aquatic communities by predation has been well documented. Numerous studies on planktivore–plankton interactions have demonstrated community shifts in size structure and species composition as a result of size-selective predation (see Northcote 1988 for an excellent review). The effects of piscivory on prey fish populations also have received considerable attention. Using regression analyses on published

data, McQueen et al. (1986) determined that although food availability to any trophic level establishes the maximum level of attainable biomass, piscivore effects on planktivore biomass are strong in both oligotrophic and eutrophic systems. Robinson and Tonn (1989) concluded that piscivory was at least as important as abiotic factors in structuring fish communities of Alberta (Canada) lakes.

Although most field studies involving piscivory have occurred in small systems, there are examples in large systems as well. Mills and Forney (1988) summarized that nutrient/food availability regulates production at each trophic level but that piscivorous walleye control biological structure of the fish community in Oneida Lake. In Lake Michigan, Stewart et al. (1981) concluded that introduced salmonids consumed 20–30% of the annual alewife production, which in turn had major ramifications on the structure of an extensive planktivorous fish community. To our knowledge, no other studies exist concerning the effects of piscivory on the prey fish community in Lake Erie, but Makarewicz and Bertram (1991) attributed recent increases in the number of large-bodied cladocerans in Lake Erie to top-down control of planktivorous fishes by walleye.

Undoubtedly, some shifts in the Lake Erie fish community were caused by factors other than walleye predation. Changes in nutrient load (Leach et al. 1977; Hayward and Margraf 1987), loss of spawning habitat (Regier et al. 1969), fisheries exploitation (Hartman 1972), and interactions with exotic species (Schneider and Leach 1979) have been suggested as stressors on percid communities of the Great Lakes (Edwards and Ryder 1990).

Loading rates of phosphorus into Lake Erie peaked in the late 1960's (Sly 1976) and then declined (Rathke and McRae 1989). This reduction likely promoted recovery of the depressed

walleye population, as may have occurred in the Bay of Quinte (Hurley 1986), but effects on other members of the fish community are unknown. Annual prey fish production was similar from 1969 to 1988, as measured by summer index values. Reductions in nutrient loading should have lowered biomass at all trophic levels and increased the effect of top-down control (McQueen et al. 1986). Consistent production suggests that reductions in phosphorus loadings had not yet caused substantial declines in energy to secondary trophic levels, perhaps due simply to lagged responses. Because only age-0 abundance was measured for most species, however, it is possible that production shifted from older to younger age groups during 1978–88 relative to 1969–77 and masked any real differences in abundance between periods. If this did occur, it is plausible that walleye predation allowed more energy to be shunted to reproduction because of reduced intraspecific competition.

Effects of fisheries exploitation were substantial for percids historically (Parsons 1970; Hartman 1972; Hatch et al. 1987) but were negligible on adult forage fishes (e.g., gizzard shad), which have limited commercial or recreational value in Lake Erie. A small-scale commercial bait industry has existed on Lake Erie for several decades, primarily targeting on shiner, but harvests are believed to be insignificant relative to total population sizes (G. Emond, ODNR, personal communication).

With the exception of white perch, no exotic species flourished in the western basin from 1969 to 1988. Lake Erie white perch are zooplanktivorous at age 0 but become opportunistic as adults, eating fish when availability is high (Schaeffer and Margraf 1986; Parrish 1988; Parrish and Margraf 1990, 1991; Prout et al. 1990). Because of their feeding habits, white perch may influence fish community structure both through competition and predation. Hartman et al. (1992) examined diet overlap among several planktivorous fish species in Lake Erie and concluded that some level of competition occurred between white perch and native fishes. Studies in both Lake Erie (Parrish and Margraf 1990, 1991) and Oneida Lake (Prout et al. 1990) indicate high potential for competition between age-0 white perch and yellow perch. The effects of white perch as piscivores are unknown. We believe that white perch had a role in the declining population trends of many prey fishes (e.g., white bass, yellow perch, spottail shiner, emerald shiner) in Lake Erie after 1982, but had little effect prior to then due to their own low abundance (Boileau 1985).

Reductions of emerald and spottail shiner population in recent years have major ramifications on community stability. During years of low gizzard shad production, the availability of small (<100 mm) prey fishes during winter and spring may be limiting to juvenile walleye and other piscivores. Although spiny-rayed fishes have become more abundant in recent years, they are more difficult for small piscivores to capture and handle than are soft-rayed prey (Weithman and Anderson 1977; Gillen et al. 1981; Wahl and Stein 1990). Additionally, reductions in shiner populations may have increased food availability to other planktivores, such as gizzard shad and white perch, because shiner feed primarily on large zooplankton (Muth and Busch 1989; Hartman et al. 1992).

Management Implications

In western Lake Erie, interagency fisheries management traditionally has been directed at percid species. By implementing

conservative management actions to sustain walleye rehabilitation in Lake Erie, fishery managers probably have influenced fish community structure via the “top-down” effects of walleye predation. Hartman and Margraf (1992) suggested that current management techniques used by Lake Erie agencies are unlikely to affect walleye biomass when strong year classes are produced; hence, effects of predation on the fish community are simply endured. Additionally, several consecutive year-class failures may be necessary to reduce piscivory sufficiently to increase populations of prey fish (Stewart et al. 1981; Carpenter et al. 1985). Thus, continued single-species management to maintain high walleye abundance may result in unstable prey fish populations.

Shuter (1990) proposed that small, short-lived fish species are useful indicators of community stress. Significant reductions of key prey species (e.g., emerald and spottail shiner) may serve as an appropriate indicator that carrying capacity was exceeded. A loss of forage species diversity may equate to a loss in community stability (Elton 1958), particularly if remaining forage fishes are less preferred by predators and/or experience highly variable annual recruitment that translates into a variable food supply to walleye. Reductions in native fishes also may allow exotic species to become established or flourish.

Biological control of exotic fishes in Lake Erie by abundant walleye, as suggested by Hurley and Christie (1977) in the Bay of Quinte, may not be a realistic expectation for spiny-rayed invaders. Despite increased use of age-0 white perch by walleye in Lake Erie (Hartman and Margraf 1992), recruitment of white perch continued to increase throughout the 1980's. Even if walleyes contribute to significant overwinter mortality of age-0 white perch, competitive interactions between white perch and native species are probably most intense as age-0 individuals (Prout et al. 1990) and will have already occurred. In contrast, recruitment of soft-rayed exotics (alewife and rainbow smelt) in the western basin declined during 1978–88. We predict that of future exotic fishes introduced into Lake Erie, only spiny-rayed fishes will proliferate in pelagic areas. Soft-rayed fishes are unlikely to become established in the presence of intense walleye predation.

In summary, we provide evidence that walleye are influencing fish community structure in Lake Erie. It is evident from this study and from the literature that management of a top predator can indirectly affect the structure of the entire fish community, even in systems as large as Lake Erie. Hopefully, future studies will quantify prey supply (as suggested by Ney 1990), as well as further substantiate predator demand (e.g., Hartman and Margraf 1992) in Lake Erie, so that limits to carrying capacity can be included in risk analyses of management strategies available to resource managers. This should greatly assist agencies in establishing community as opposed to single-species management goals.

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