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Abstract

We examined stomach contents of 906 age-0 and older walleyes *Stizostedion vitreum vitreum* and 1,575 age-2 and older yellow perch *Perca flavescens*, collected from western Lake Erie in 1979–1981, to measure preferences for prey type and size and diet overlap among different size groups of these two percids. Seasonal diets closely followed changes in forage-fish availability. Walleyes ate age-1 shiners *Notropis atherinoides* and *N. hudsonius* in spring, but switched to age-0 clupeids *Dorosoma cepedianum* and *Alosa pseudoharengus* in summer and autumn. Diet selection was governed by abundance of appropriate-size prey and preferences for forage species. Yellow perch ate invertebrates in spring but clupeids and shiners thereafter; electivity values for prey were low compared with those of walleyes, indicating that yellow perch were the more opportunistic feeders. Diet overlap was greatest among walleye age groups (0, 1, and 2-and-older) and least between walleyes and yellow perch. We hypothesize that density-dependent processes within the percid community probably will occur during years of low shiner and clupeid abundance and that they will be most intense for walleyes. Walleyes were less size-selective and grew more slowly in 1979–1981 than in 1959–1960, suggesting that forage-fish availability has declined in the presence of increased walleye stocks. Yellow perch should be less affected by forage-fish reductions if invertebrates are plentiful.

Abundant stocks of walleyes *Stizostedion vitreum vitreum* and yellow perch *Perca flavescens* support valuable sport and commercial fisheries in western Lake Erie. Commercial harvest of walleyes, which was as great as 6,985 t in 1956, reached an historic low of 213 t in 1969, pre-sumably because of overfishing and poor recruitment (Hartman 1973; Busch et al. 1975; Schneider and Leach 1977). However, the closure of the walleye fishery in 1970 due to mercury contamination and exclusion of commercial fishing for walleyes in United States waters since 1972 have allowed the population to recover (Kutkuhn et al. 1976). Annual commercial harvest of yellow perch averaged 2,600 t from 1915 through the 1950s, peaked at 15,286 t in 1969, and declined to about 9,000 t in the early 1970s (Leach and Nepszy 1976). Fluctuating recruitment, declining catch per unit of effort, and increasing exploitation in recent years suggest that the population is unstable. Because of these changes in the fish community,

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it is likely that walleye and yellow perch diets have changed as well. In this study, we examined the interactions among walleyes, yellow perch, and forage fishes to determine diet selection by these predators and the limitations of forage fishes as prey.

The capacity of the forage fish community in western Lake Erie to support large predator populations is unknown. Because walleyes become piscivorous early in life (Smith and Pycha 1960; Mathias and Li 1982), forage fishes in Lake Erie are preyed upon by almost the entire walleye population throughout the year. White bass *Morone chrysops* and large yellow perch (>200 mm long) in western Lake Erie also are piscivorous (Price 1963) and exert additional pressure on forage fishes. If forage populations cannot sustain predator demands, density-dependent mechanisms might act to reduce growth rates of predators through competition for food and to increase predation on their young. Additionally, predators might move from western Lake Erie to other areas of greater prey availability, thereby increasing predation pressure in nearby waters.

To quantify the capacity of the forage-fish community to support percids in western Lake Erie, one must examine the availability of forage fishes to predators. Although food habits of most predators in Lake Erie are known (Price 1963), only Wolfert (1966) and Parsons (1971) related food selection to prey availability. However, they studied only young (age-0 and age-1) walleyes during years when adult walleye abundance was low. No work relates yellow perch predation to forage fish availability in western Lake Erie. We used data obtained in cooperation with United States Fish and Wildlife Service (USFWS) personnel from the Sandusky Biological Station of the Great Lakes Fishery Laboratory to determine selection for types and sizes of prey by yellow perch and walleyes of different sizes, and to document diet overlap within and among walleye and yellow perch size groups.

Methods

Data were collected at six offshore trawling stations used for many years by the USFWS to index fish abundance. Sampling areas (Fig. 1) were about 1 km offshore from East Harbor State Park and 2 km offshore from the city of Bono, which is about 10 km east of Toledo,
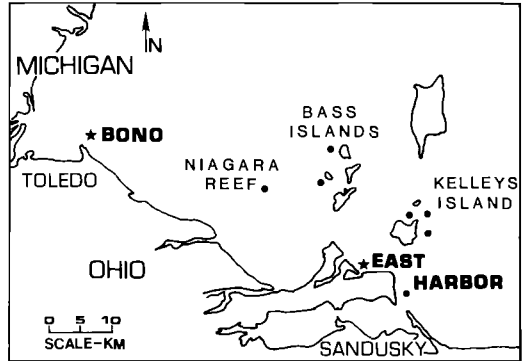

FIGURE 1.—*Primary sampling areas off Bono and East Harbor, Ohio (stars) for walleyes, yellow perch, and forage fishes in western Lake Erie. Solid circles show supplementary collection sites.*

Ohio. Trawling stations were established at the 3.0-, 4.6-, and 6.1-m bottom contours in each area. All stations had soft bottoms of mud, sand, and detritus.

Sampling Procedure

Sampling cruises consisted of 1 day each at East Harbor and Bono trawling stations. Samples were collected every 3 weeks during 1979 and 1980, and monthly in 1981 from late April through early November. Stations were sampled three times per day: morning (0700–1200 hours), afternoon (1300–1700), and evening (1800–2400). A 7.9-m (headrope) semiballoon bottom trawl (3.2-mm mesh in the cod) was used to capture forage fishes, yellow perch, and small (age-0 and age-1) walleyes. Trawls were towed at 3.2 km/hour for 10 minutes and strained about 2,000 m^3 of water. Standard experimental gill nets were set for 3-hour intervals at each trawling station—in the morning, afternoon, and evening. Gill nets were used to collect age-1 and older walleyes and sometimes to supplement yellow perch collections.

We collected additional monthly samples of walleyes and yellow perch with gill nets at stations on Kelleys Island Shoal, near the Bass Islands, and on Niagara Reef (Fig. 1). Two or three nets were set three times per day for 3 hours, though not always at the same station throughout the day. We also trawled to capture predators when soft bottom areas could be located near gill-net sites.

TABLE 1.—*Common and scientific names of fishes caught with bottom trawls and gill nets in western Lake Erie, 1979–1981.*

Common name	Scientific name
Alewife	*Alosa pseudoharengus*
Black crappie	*Pomoxis nigromaculatus*
Brown bullhead	*Ictalurus nebulosus*
Channel catfish	*Ictalurus punctatus*
Common carp	*Cyprinus carpio*
Common carp × goldfish hybrid	*C. carpio × C. auratus*
Emerald shiner	*Notropis atherinoides*
Freshwater drum	*Aplodinotus grunniens*
Gizzard shad	*Dorosoma cepedianum*
Golden redhorse	*Moxostoma erythrurum*
Golden shiner	*Notemigonus chrysoleucas*
Goldfish	*Carassius auratus*
Johnny darter	*Etheostoma nigrum*
Lake whitefish	*Coregonus clupeaformis*
Largemouth bass	*Micropterus salmoides*
Logperch	*Percina caprodes*
Mimic shiner	*Notropis volucellus*
Mooneye	*Hiodon tergisus*
Mottled sculpin	*Cottus bairdi*
Pumpkinseed	*Lepomis gibbosus*
Quillback	*Carpiodes cyprinus*
Rainbow smelt	*Osmerus mordax*
Sauger	*Stizostedion canadense*
Shorthead redhorse	*Moxostoma macrolepidotum*
Silver chub	*Hybopsis storeriana*
Smallmouth bass	*Micropterus dolomieui*
Spottail shiner	*Notropis hudsonius*
Stonecat	*Noturus flavus*
Trout-perch	*Percopsis omiscomaycus*
Walleye	*Stizostedion vitreum vitreum*
White bass	*Morone chrysops*
White crappie	*Pomoxis annularis*
White perch	*Morone americana*
White sucker	*Catostomus commersoni*
Yellow perch	*Perca flavescens*

time (hour and day). Total abundance was the sum of age-specific CPUEs across all species for a given month. These estimates included only fish of ages considered vulnerable to percid predators, as determined from stomach analyses. Relative abundance was calculated for three categories of forage: soft-rayed fishes (emerald shiners, spottail shiners, and rainbow smelt), spiny-rayed fishes (white bass, yellow perch, freshwater drum, and walleyes), and clupeids (gizzard shad and alewives). These categories were chosen because of morphological similarities (body depth and presence of spines). Trout-perch were examined separately, because they were rarely eaten by walleyes or yellow perch.

Percid Food Habits

Stomachs were removed from 10 yellow perch (age-2 and older) and 10 walleyes (age-1 and older) at each collecting time and date in 1979 and 1980, from 15 yellow perch (age-2 and older) and 15 each of age-0 and age-1 or older walleyes in 1981. For yellow perch in 1981, stomachs were removed from five fish for each of three total length intervals (150–175, 176–200, and >200 mm). Stomachs were preserved (aboard ship) in 10% buffered formalin soon after their removal. Food items observed in predator mouths were discarded unless regurgitation was obvious. Additionally, we removed scales from areas above the lateral line and below the dorsal fin to age individual predators and we recorded total lengths.

Stomach contents were sorted and examined under a dissecting microscope. Each prey item was blotted dry, and its displacement volume was measured in a graduated cylinder. Fish were identified to species when possible (73% of specimens) and measured for total length. Partly digested fishes often were identified on the basis of backbone and gut morphology, as established from preserved collections. We estimated total length of some prey from backbone or standard lengths by regression equations developed from preserved specimens (Table 2). Invertebrates were identified to order when possible (95% of specimens), but their volumes were summed for the food-habit analyses. We calculated the mean percent volume (Wallace 1981) for each prey type, summarizing data by month and year of capture.

Forage Fishes

Trawl catches were processed to estimate forage-fish abundance and length distribution. Fish of each species (Table 1) were sorted into three age groups (0, 1, and 2 or older), based on a long series of length-at-age measurements made by USFWS. Age-specific abundance within each species was estimated by transformation of numbers to catch per hour of trawling (catch per unit effort—CPUE). Total lengths from randomly selected samples of each age were recorded to the nearest millimeter from preserved specimens of each species in 1981.

To estimate monthly total and relative abundance, forage-fish samples were pooled across

TABLE 2.—*Equations that relate backbone (BB) and standard (SL) lengths to total length (TL) for some fish species from western Lake Erie.*

Species	Equation	Length range (mm)	N	r^2
Alewife	TL = 1.37BB + 8.10	35–130	44	0.98
	TL = 1.26SL − 1.01			0.99
Emerald shiner	TL = 1.45BB − 0.69	24–134	44	0.99
	TL = 1.23SL − 0.69			0.99
Freshwater drum	TL = 1.56BB + 3.19	21–98	50	0.99
	TL = 1.32SL − 0.53			0.99
Gizzard shad	TL = 1.45BB + 3.08	34–159	62	0.99
	TL = 1.26SL − 0.22			0.99
Rainbow smelt	TL = 1.38BB − 0.72	29–88	25	0.99
	TL = 1.20SL − 1.37			0.99
Spottail shiner	TL = 1.42BB + 3.78	32–144	55	0.99
	TL = 1.24SL + 1.17			0.99
Trout-perch	TL = 1.48BB + 3.78	43–121	38	0.99
	TL = 1.23SL + 1.08			0.99
White bass	TL = 1.54BB + 2.18	21–155	67	0.99
	TL = 1.29SL − 1.75			0.99
White crappie	TL = 1.49BB + 0.42	25–80	22	0.98
	TL = 1.25SL + 0.73			0.99
White perch	TL = 1.47BB + 4.97	37–170	38	0.99
	TL = 1.26SL − 0.35			0.99
Yellow perch	TL = 1.48BB + 0.96	38–144	51	0.99
	TL = 1.21SL + 0.02			0.99

Species Selection

Preferences by predators for various forage-fish species were determined with the Vanderploeg and Scavia (1979) electivity index E^*:

$$E_i^* = [W_i - (1/n)]/[W_i + (1/n)];$$

and

$$W_i = (r_i/p_i)/\sum_{i=1}^{n} (r_i/p_i);$$

the index is based on the relative proportions of food i of n total food items in the diet (r_i) and the environment (p_i). This index has desirable characteristics with regard to forage abundance and field use (Lechowicz 1982), but does share some of the biases (due to differential vulnerability of prey to predators and sampling gear, patchy distributions of fishes, et cetera) of other electivity indices. Therefore, trends in electivity values were considered more important than single values to determine selection for or against a prey taxon. Values may range from +1 (total selection for) to 0 (random feeding) to −1 (total selection against). Numbers of ingested prey were used to estimate stomach proportions (Hyslop 1980), and were compared with CPUE for forage. Only fish that were small enough for predators to eat (hereafter called vulnerable forage) were considered. Lengths of vulnerable prey were calculated with nonlinear regression equations that related maximum length of ingested prey to predator length (Table 3). These equations were derived with a method analogous to that used to estimate stomach capacity (Knight and Margraf 1982). Predators were grouped into length intervals (50 mm for walleyes, 20 mm for yellow perch) and prey into the three categories (clupeids, soft-rayed, and spiny-rayed) previously defined. We selected the largest ingested individual of each prey type for each predator length interval and regressed (by least squares) the maximum prey lengths on the lengths of the predators that ate them.

Regression equations were used to calculate the maximum length of prey that was vulnerable to predators from the maximum length of a predator within the four predator groups (age-0, -1, and -2 or older walleyes, and age-2 or older yellow perch) on a given sampling date. To estimate relative abundance of vulnerable

TABLE 3.—*Regression equations between maximum size of prey (Y) in predator stomachs and predator length (X) in western Lake Erie, 1979–1981. N represents number of prey in stomachs; n represents number of predator-size intervals used in regression (length intervals were 50 mm for walleyes and 20 mm for yellow perch).*

Predator	Prey type	N	n	Equation	r^2
Walleye	Clupeids[a]	427	8	$Y = -192.245 + 52.167 \log_e X$	0.99
	Soft-rayed[b]	287	6	$Y = -295.539 + 73.655 \log_e X$	0.97
	Spiny-rayed[c]	66	8	$Y = -215.785 + 55.941 \log_e X$	0.94
Yellow perch	Clupeids[a]	105	7	$Y = -207.333 + 56.548 \log_e X$	0.72
	Soft-rayed[b]	55	4	$Y = -1,284.938 + 265.540 \log_e X$	0.89
	Spiny-rayed[c]	57	5	$Y = -747.488 + 157.420 \log_e X$	0.86

[a] Includes gizzard shad and alewife.

[b] Includes emerald and spottail shiners and rainbow smelt.

[c] Includes yellow perch, white perch, white bass, and freshwater drum.

forage to each group, we multiplied the number of each species caught in trawls by the proportion (from a length-frequency distribution) of fish that was less than the species' calculated maximum vulnerable length. Thus, abundance of vulnerable prey was computed separately for each of the four predator groups. Because lengths of forage were similar (±10%) to those reported in past USFWS trawl data, we considered growth rates of forage species to be constant and therefore used proportions of vulnerable prey from 1981 to estimate proportions of 1979 and 1980 samples from the same month and area.

Prey-Size Selection

To evaluate size-selective predation by walleyes and yellow perch on forage fishes, we related predator food habits to length distributions and relative abundances of prey. Means and ranges were calculated for lengths of ingested prey (pooled species) grouped according to 50-mm walleye and 20-mm yellow perch length intervals. A nonlinear regression (least squares) was computed through mean prey lengths and means of predator length intervals. Because too few ingested prey were available from walleyes in 1979 and 1980, and differences among years for prey-size preferences were unknown, we used only data from 1981 for regression analysis. This regression line was then compared with that for the 1959 year class of walleyes in western Lake Erie (Parsons 1971). For yellow perch, we pooled data from all years to insure having sufficient data for regression analysis.

Preferences for prey size were computed with the electivity index E^*. Proportions of prey in

stomachs and in the environment were estimated with length-frequency data (10-mm total length intervals) from ingested prey and trawl collections, respectively, from 1981. Abundance of prey smaller than 30 mm probably was underestimated because of low vulnerability to trawls. Electivity values were calculated for predator groups for every sampling date on which 10 or more measurable fish were found in stomachs. When too few ingested prey were available for any sampling date, we pooled forage and stomach data from the same sampling area over time to develop monthly or seasonal electivity values.

Diet Overlap among Percid Groups

An index used by Schoener (1970) was computed to measure diet similarity among three age groups of walleyes (0, 1, and 2 or older), between two length groups of yellow perch (150–200 and >200 mm, hereafter labeled as small and large, respectively), and between walleyes and yellow perch. Because forage availability was unknown for invertebrates, Schoener's index was the most appropriate measure for diet comparisons (Wallace 1981):

$$\alpha = 1 - 0.5\left(\sum_{i=1}^{n} |P_{xi} - P_{yi}|\right) \quad \text{or}$$

$$= \sum_{i=1}^{n} \frac{\text{minimum}}{\text{values}} (P_{xi}, P_{yi});$$

n = number of food categories;

P_{xi} = proportion of food i in diet of species x;

P_{yi} = proportion of food i in diet of species y.

Values range from 0.0 (no overlap) to 1.0 (complete overlap) and represent proportions of diet overlap between two predator groups. There is no statistical basis for assigning significance to this index; hence, the values have utility only when they are substantially large or small, or differ greatly from one another.

We calculated the proportion of each prey species in the diet using mean percent volumes. Although many factors (such as partial digestion) can introduce biases, mean percent volumes were considered the least-biased estimators of dietary importance (Wallace 1981). Some prey types were sorted into general categories to increase sample sizes. For example, emerald and spottail shiners, alewives and gizzard shad, and invertebrates composed three categories of prey. The grouping of shiners and clupeids enabled us to include many food items that were unidentifiable to species. Diet similarities were compared for predators captured during the same season and from the same area.

Results

Forage Fishes

Forage-fish abundance changed seasonally at East Harbor and Bono in each of the three years, 1979–1981. Typically, abundance was lowest in spring, highest in summer (owing to recruitment of young of year), and intermediate in autumn (Fig. 2). The CPUE for most species often differed between East Harbor and Bono, reflecting the variability between locations and among catches with trawls (Taylor 1953).

Relative abundance changed seasonally for each forage category at both sampling areas. Soft-rayed fish (predominately shiners) were usually the most abundant species in spring as yearlings, but became relatively less abundant during summer when age-0 fish were recruited (Fig. 3). Shiner abundance in autumn was usually high (32–65% of trawl catches) at East Harbor but low (0–10%) at Bono. Spiny-rayed fishes composed 5–40% of catches in spring as yearlings and 10–80% as age-0 fishes in summer and autumn. Age-0 clupeids were abundant in trawl catches from August through November, particularly at Bono. However, yearling clupeids seldom were captured during any month. Trout-perch occasionally composed 20–40% of spring catches, but were relatively scarce (<10%) after June. Generally, shiners or clupeids were the most abundant forage species through the year.
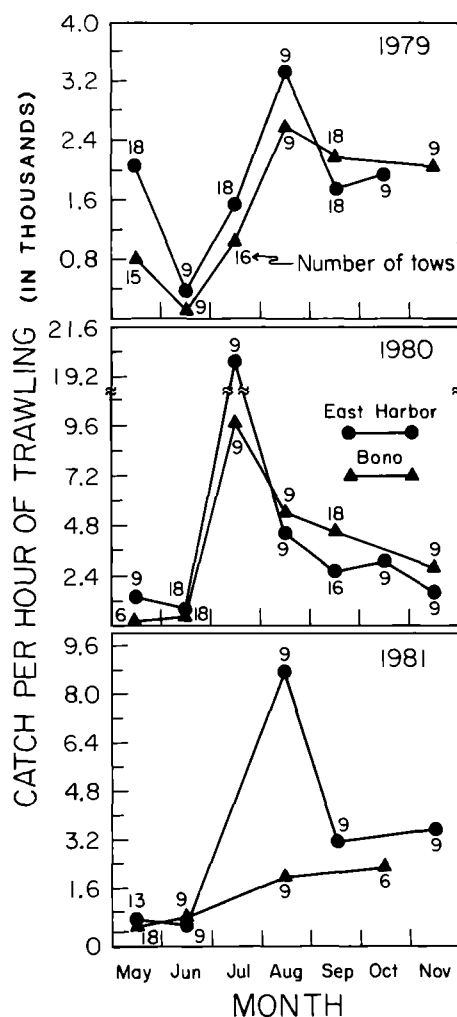

FIGURE 2.—*Monthly abundance of forage fishes (all species) at trawling stations off Bono and East Harbor in western Lake Erie, 1979–1981.*

Food Habits

Food of walleyes changed seasonally but was consistent among years. Age-1 or older walleyes were almost entirely piscivorous, eating 75–100% (mean percent volume) yearling shiners in spring, but switching to abundant age-0 clupeids (60–90%) in late July (Fig. 4). Age-0 clupeids and shiners composed 25–70 and 10–40%, respectively, of the diets of age-1 or older walleyes in autumn. Spiny-rayed fishes were the least important prey, contributing 0–40% to the diet of walleyes. None of the 736 walleye stomachs
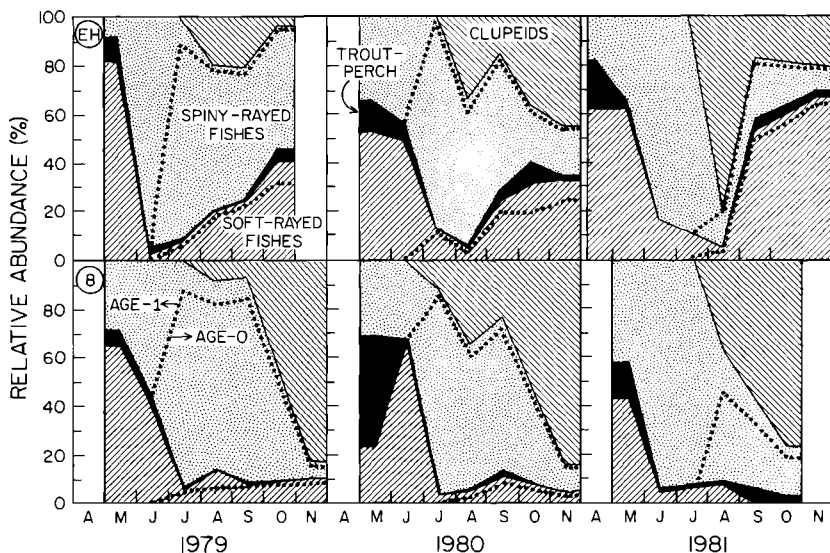
FIGURE 3.—*Monthly changes in relative abundance for age-0 clupeids and age-0 and age-1 soft-rayed fishes, trout-perch, and spiny-rayed fishes at East Harbor (EH) and Bono (B) trawling stations in western Lake Erie, 1979–1981. Dotted lines distinguish age-0 from age-1 soft-rayed and spiny-rayed fishes.*

with identifiable food contained walleyes. In-vertebrates (primarily immature chironomids) were observed mostly in stomachs from yearling walleyes and contributed an appreciable por-tion (about 25%) to the diet only in spring 1981. Age-0 walleyes were entirely piscivorous after July (Fig. 5), eating 20–70% young-of-year soft-rayed fishes and 25–80% age-0 clupeids. In gen-eral, walleyes of all sizes were piscivorous and ate clupeids and shiners in the greatest quan-tities.

Piscivorous yellow perch ate a variety of fish-es, but lesser volumes relative to walleyes. Shin-ers contributed 5–25% of the diet in spring and 35–40% in autumn (Fig. 4). Age-0 clupeids were major prey in summer and autumn, constituting 5–60 and 40–60% of the diet, respectively. In contrast to walleyes, cannibalism on young of year was evident; small yellow perch made up 5–20% of the summer diet of adult yellow perch. In general, yellow perch ate a greater propor-tion of spiny-rayed fishes than did walleyes.

Most yellow perch, however, ate similar vol-umes of invertebrates and fishes. Invertebrates constituted 80–100% of the diet from April to August, consisting mostly of pelecypods (40%) and immature chironomids (40%) in spring, and cladocerans (75%) in summer. Invertebrate consumption appeared to be highest in 1981,

owing to the presence of larger numbers of small (<200 mm) yellow perch than in 1979–1980. Yellow perch ate few invertebrates (0–20% of diet) in late summer and early autumn, when they switched to abundant age-0 gizzard shad and shiners. However, consumption of inver-tebrates increased again in late autumn when forage-fish availability declined. Overall, yellow perch were more opportunistic feeders than walleyes through the year; forage-fish avail-ability strongly influenced diet selection.

Foraging activity varied across months for all years (Table 4). On average, about 77% of wall-eye stomachs were empty from April through July (range 33–100%) compared to 38% of those from August through November (range 18–70%). Regurgitation was evident in less than 10% of walleye stomachs and was considered insignificant. About 72% of yellow perch stom-achs were empty through the year, ranging from 33 to 92% in April–July and 60 to 80% in Au-gust–November. Thus, walleyes seemingly fed most actively during summer and autumn when forage-fish abundance was high, whereas yellow perch feeding was more uniform across months.

Species Selection

Selection of species by walleyes and piscivo-rous yellow perch changed with season (Table
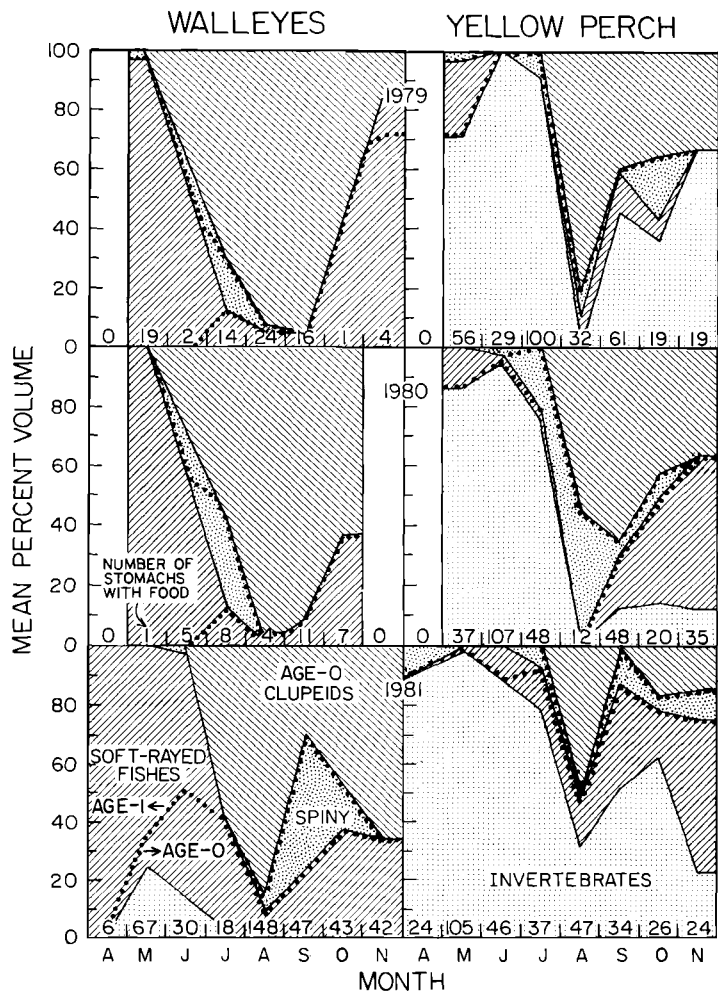
FIGURE 4.—*Monthly diet of age-1 or older walleyes and age-2 or older yellow perch from western Lake Erie, 1979–1981. Dotted lines distinguish age-0 from age-1 shiners and rainbow smelt and spiny-rayed fishes.*

5). Shiners were highly selected (+0.65 and +0.69) by age-1 and older walleyes in spring, but values varied during summer and autumn (−1.00 to +0.66) as walleyes switched to age-0 clupeids. Yellow perch also selected shiners, particularly in autumn 1980 and summer and autumn 1981. Clupeids were highly selected by both predators; positive electivity values (0.40 to 1.00) were evident on 10 of 11 occasions for walleyes and on 8 of 11 occasions for yellow perch (Table 5). Freshwater drum, white bass, and rainbow smelt were selected occasionally by both predators; typically, electivity values more closely approached 0.00 for yellow perch

than for walleyes. Trout-perch and yellow perch were selected against (−0.08 to −1.00, 45 of 46 occasions) by both percids.

Prey-Size Selection

The mean and range of lengths of ingested prey were related directly to walleye length (Fig. 6). Large walleyes (>250 mm) ate, on average, smaller prey in 1981 than did walleyes of similar size in 1959–1960. Walleyes less than 250 mm long ate prey of similar (mean) size among these years. Range of prey lengths in walleye stomachs was broader in 1981 than in 1959–1960,
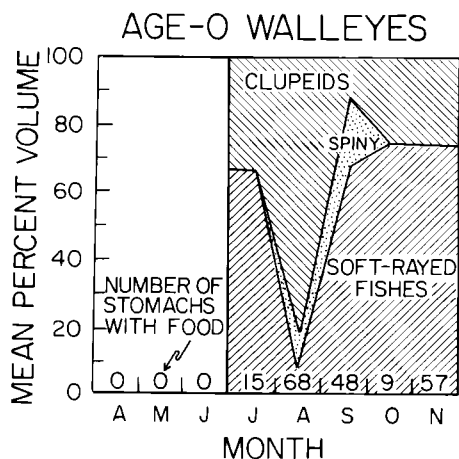
AGE-0 WALLEYES

FIGURE 5.—*Monthly diet of age-0 walleyes from western Lake Erie, 1981. All prey were age-0 fishes.*

TABLE 4.—*Number of stomachs examined (N) and percent with food for walleyes and yellow perch captured during April–November, 1979–1981, in western Lake Erie.*

Preda-tor	Month	1979		1980		1981	
		N	% with food	N	% with food	N	% with food
Walleye	Apr					13	46
	May	62	35	5	20	136	14
	Jun	6	17	14	0	40	30
	Jul	39	18	9	67	30	20
	Aug	43	67	10	30	213	65
	Sep	34	56	29	41	61	74
	Oct	1	0	11	82	67	51
	Nov	11	45			72	56
	Total	196	42	78	40	632	48
Yellow perch	Apr					45	18
	May	131	10	50	18	112	42
	Jun	49	21	119	28	89	67
	Jul	115	38	60	42	45	22
	Aug	60	30	60	12	90	22
	Sep	120	22	116	27	45	27
	Oct	30	33	30	40	75	21
	Nov	30	20	60	40	45	29
	Total	535	26	494	28	546	34

encompassing smaller prey for predators of comparable size.

Selection of prey lengths (10-mm intervals) was similar among months and ages of walleyes. For example, yearling walleyes (217–385 mm) from East Harbor selected prey 20–60 mm long in spring, 30–85 mm long in August, and 30–55 mm long in September (Fig. 7). Those from Bono selected prey 15–50 mm long during May and 30–80 mm long in late August (Fig. 8). Age-0 walleyes (61–221 mm long) selected prey 20–50 mm long in August, 20–40 mm long in September, and 30–70 mm long in November (Fig. 7). Age-2 or older walleyes (350–583 mm long) selected prey 40–90 mm long in August (Fig. 8).

In general, age-1 or older walleyes ate prey from a wider length range than did age-0 walleyes (Fig. 9), even though both selected small (<90 mm) fishes through the year. Typically, forage length frequencies were bimodal; age-0 walleyes were restricted largely to prey from the small size mode whereas older walleyes ate prey from both modes. Accordingly, forage fishes such as gizzard shad outgrew vulnerability to many age-0 walleyes by November and to most older walleyes by spring. Therefore, seasonal changes in forage-fish size distribution affected prey availability to walleyes.

Yellow perch and walleyes of similar sizes ate prey of similar sizes. For example, 200-mm walleyes ate, on average, 52-mm prey (Fig. 6), whereas 200-mm yellow perch ate 56-mm prey

(Fig. 10). The length range of ingested prey also was similar between walleyes and yellow perch of comparable size. Yellow perch (152–242 mm) selected 40–70 mm prey in August and 20–40 mm prey in September (Fig. 11), the only months for which electivity values could be calculated. In general, walleyes and yellow perch selected similar sizes of forage fishes at least during late summer and early autumn.

Diet Overlap

Diet similarities among the groups were influenced by season and predator size (Table 6). Diet overlap was great (0.68–0.80) between ages-1 and -2 or older walleyes for all seasons and between ages-0 and -1 walleyes in autumn. Age-0 and age-2 or older walleyes, however, had different diets in summer (0.47) and autumn (0.51). Low diet overlap was attributed largely to differing consumption of shiners and clupeids between these walleye groups. Shiners composed an average 51.2 and 73.3% of the diet of age-0 walleyes in summer and autumn, respectively, but only 15.2 and 26.2% of the diet of age-2 or older walleyes. Clupeids, however, constituted an average 63.3 and 53.3% of the diet of age-2 or older walleyes but only 31.4

TABLE 5.—*Values of Vanderploeg and Scavia's (1979) electivity index* E* *for walleyes and yellow perch collected during spring, summer, and autumn, 1979–1981, at offshore trawling stations in western Lake Erie.*

Year, season	Area[a]	Age (years)	N[b]	n[b]	Electivities[c] for fish prey[d]					
					Shiners	Clupeids	Freshwater drum	Rainbow smelt	White bass	Yellow perch
					Walleyes					
1979										
Spring	Bono	>2	18	30	0.69	+	−	−	−	−
Summer	EH	1	33	34	−0.58	0.72	−0.97	−0.28	−	−0.92
	Bono	1	10	76	−	0.75	−	−	−	−0.82
1980										
Summer	Bono	1	7	13	0.43	0.64	−	−	−	−
		>2	17	73	0.13	0.66	−	−	−	−0.08
1981										
Spring	EH	1	15	31	0.65		−	0.09	+	−
Summer	EH	0	78	127	−0.16	0.62	−	−0.02	0.03	−
		1	57	119	−0.49	0.65	0.29	−	−	−
	Bono	1	19	55	−	0.66	−	−	0.37	−
		>2	5	18	0.20	0.69	−	−	−	−
Autumn	EH	0	33	56	−0.11	0.68	−	−	−	−
	Bono	1	9	15	0.66	−0.79	−			−
					Yellow perch					
1979										
Summer	EH	>2	27	34	−0.33	0.65	−	0.06	−	−0.24
	Bono	>2	20	34	−0.36	0.72	−0.93	−	−	−0.60
Autumn	EH	>2	9	12	−0.96	0.75	−0.86	−	−	−
1980										
Summer	EH	>2	17	37	−0.52	0.71	−	−0.37	−0.94	−0.45
	Bono	>2	39	39	−0.13	0.40	−	0.56	−0.79	−0.60
Autumn	EH	>2	22	27	0.40	0.58	−0.09	−	−	−
	Bono	>2	13	22	0.75	−0.84	−	−	−	−
1981										
Summer	EH	>2	20	24	0.36	−0.62	−0.29	0.47	0.15	−
	Bono	>2	14	25	0.39	0.55	−	−	0.13	−
Autumn	EH	>2	14	16	−0.26	0.68	0.10	−	−	−
	Bono	>2	7	10	0.64	−0.34	−			−

[a] EH = East Harbor.
[b] N = number of stomachs with identifiable fish; n = number of identifiable fish in stomachs.
[c] Table conventions: − = −1.00 (prey occurred in trawl catches, but not in stomachs);
$\qquad$ + = +1.00 (prey occurred in stomachs, but not in trawl catches);
$\qquad$ blank space = prey occurred neither in trawl catches nor stomachs.
[d] Shiners = *Notropis* spp.; clupeids = gizzard shad and alewives. Trout perch had an electivity value of 0.24 for age-2 and older walleyes from Bono during spring 1979, but otherwise did not occur in stomachs of either predator (E^* = −1.00).

and 24.5% for age-0 walleyes during these seasons.

Diet overlap between small and large yellow perch followed similar seasonal trends across all years (Table 6). Diets usually were most similar (0.74–0.93) in spring because fish of both groups ate primarily invertebrates. In summer and autumn, diets were less similar (0.41–0.76) because large yellow perch ate mostly fish whereas small yellow perch ate both fish and invertebrates. In general, the index of diet overlap between small and large yellow perch was inversely related to the difference (D) between these groups in the mean percent volume of invertebrates. Correlations between seasonal overlap index values and D (independent variable) were highly significant ($P < 0.01$) for all years ($r = -0.92$ in 1979, −0.85 in 1980, and −0.99 in 1981).

Comparisons of diet overlap between walleyes and yellow perch indicated that their diets usually differed, with some exceptions (Table
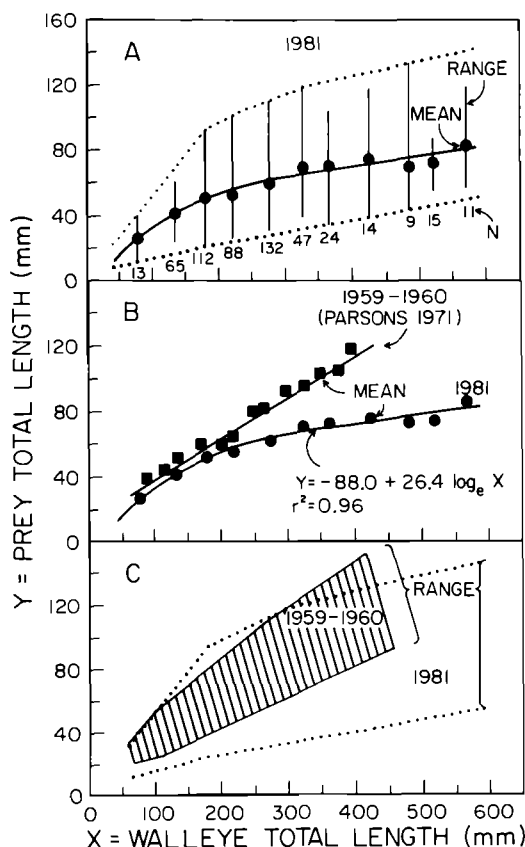
FIGURE 6.—*Mean and range of lengths for fishes eaten by walleyes of various sizes in western Lake Erie.* **A.** *1981. Solid line is a nonlinear regression through means of prey-size and 50-mm walleye length intervals; dotted lines were fitted by inspection across range extremes. N is the number of prey per walleye length interval.* **B.** *1981 regression compared with that for 1959–1960.* **C.** *Prey size ranges compared for 1981 and 1959–1960.*

6). Because diets of yearling and older walleyes were similar, we combined these age groups (hereafter labeled large walleyes) for comparison with yellow perch groups. Diet overlap between small yellow perch and large walleyes was low (0.10–0.36) for all seasons of all years except autumn 1980, when yellow perch ate more fish than in autumns 1979 and 1981. Diets of large yellow perch and large walleyes were most similar (0.55–0.86) in autumn because yellow perch were more piscivorous then than in other seasons. Overlap between age-0 walleyes and either large or small yellow perch always was

low (0.27–0.55); walleyes ate mostly shiners, whereas small yellow perch primarily ate invertebrates and large yellow perch ate clupeids.

In summary, diets of walleyes and yellow perch usually were similar within each species but differed between species, largely because walleyes were more piscivorous than yellow perch.

Discussion

Diet Selection by Walleyes

Seasonal shifts in the diet of walleyes were caused primarily by changes in size and abundance of preferred forage fishes. Parsons (1971), who demonstrated a progressive change to different prey species as each grew into the preferred size range of walleyes, concluded that abundance of appropriate-size prey was the primary factor affecting diet selection in 1959–1960. Our results also indicate that abundant, vulnerable species were eaten in the largest quantities; thus, walleyes ate mostly age-1 shiners in spring, age-0 clupeids in summer, and both age-0 shiners and clupeids in autumn.

However, diet selection was not related entirely to changes in abundance of vulnerable forage. Electivity values indicate that certain fishes (clupeids and shiners) were selected by walleyes. Other species (trout-perch, white bass, and freshwater drum) were selected against, even though they often were as abundant as preferred species. Perhaps escape tactics, morphology, and patchy distributions of prey made some species less vulnerable than clupeids or shiners to walleyes (Murdoch and Oaten 1975; Keenleyside 1979; Stein 1979).

Diet selection by walleyes in western Lake Erie has changed since the 1950s. Because walleyes are size-selective feeders (Parsons 1971; MacLean and Magnuson 1977), changes in size selection reflect changes in the diet. A comparison of size selection between walleyes from 1981 and 1959–1960 distinctly shows that walleyes were less selective in 1981.

We attribute this decline in size selection to the greater density of walleyes in 1981 than in 1959–1960. Annual commercial harvest of walleyes in Ontario waters declined precipitously from 2,436 t in 1956 to 365 t and 245 t in 1959 and 1960, respectively (Ontario Ministry of Natural Resources, Commercial Fish Industry, Statistics on Landings). Additionally, Parsons (1970) reported age-2 and older wall-
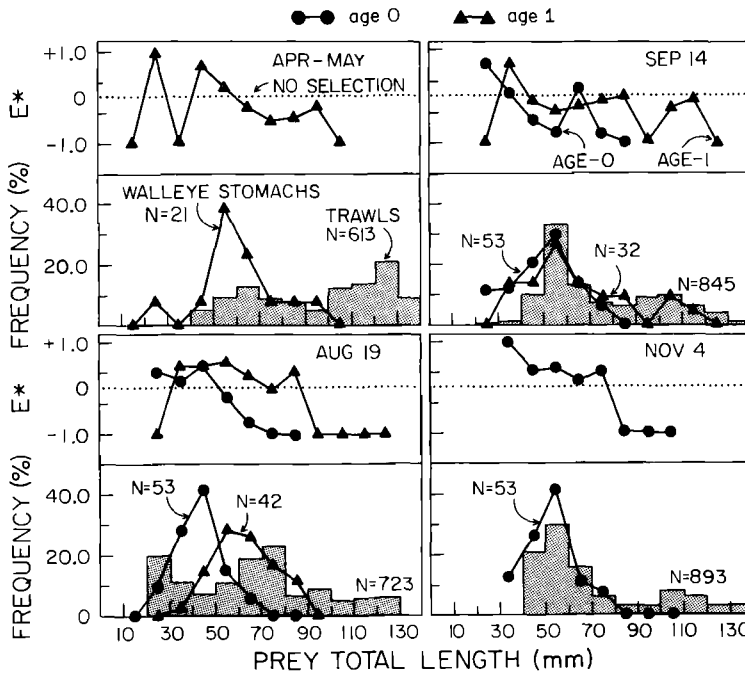
FIGURE 7.—*Monthly preference for prey size (electivity E*) by age-0 and -1 walleyes, based on prey-size distributions in walleye stomachs and trawl catches, East Harbor, western Lake Erie. N is number of prey.*

eyes composed 60–90% of October trap net catches in Ohio waters during 1950–1958, but only 2–3% of those in 1959. Thus, the numbers of adult walleyes in western Lake Erie had decreased substantially by 1959. Ontario commercial harvest remained low throughout much of the 1960s and 1970s but increased to 516 t in 1979 and 619 t in 1980 as individuals from a strong 1977 year class recruited into the fishery. Although comparisons of commercial catch per unit effort between these time periods were not possible, harvest data do provide a measure of population density and indicate walleyes were more abundant in 1979–1981 than in 1959–1960.

Density-dependent mechanisms probably accounted for the reduction in size selectivity by walleyes in 1981. Trawling indices of the USFWS suggest that forage-fish abundance has not increased in proportion to walleye abundance between these years; thus, the ratio of prey biomass to predator biomass was reduced. Diet breadth of predators typically increases as prey availability decreases (Werner and Hall 1974); thus, walleyes became less size-selective.

Similarly, largemouth bass in a Tennessee reservoir ate prey of a wider length range during a year of low gizzard shad abundance than during a year of greater abundance (Adams et al. 1982).

Additionally, growth rates of walleyes were lower in 1981 than in 1959–1960. In August, September, and November, respectively, age-0 walleyes measured, on average, about 140, 168, and 199 mm (total length) in 1981, and 152, 213, and 254 mm in 1959 (Parsons 1971). Age-1 walleyes in August, September, and October, respectively, measured 272, 312, and 345 mm in 1981, and 333, 356, and 366 mm in 1960. Mean lengths were not available for age-2 or older walleyes in 1959–1960. Although differences in mean length could not be tested statistically, they were substantial in some instances. These differences suggest that prey density in 1981 was insufficient to sustain the higher growth rates of walleyes in 1959–1960.

The lack of walleye cannibalism, which serves as a feedback mechanism to control walleye density in Oneida Lake (Chevalier 1973; Forney 1974), seemingly contradicts our conclu-
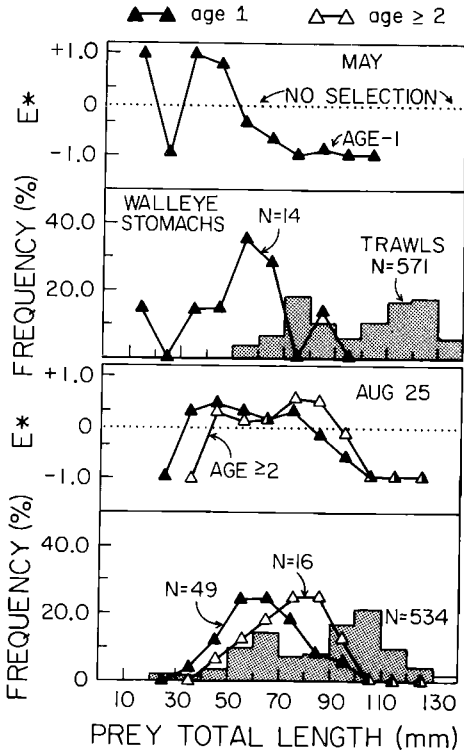
FIGURE 8.—*Monthly preferences for prey size (electivity E*) by age-1 and -2 or older walleyes based on prey size distributions in walleye stomachs and trawl catches, Bono, western Lake Erie. N is number of prey.*
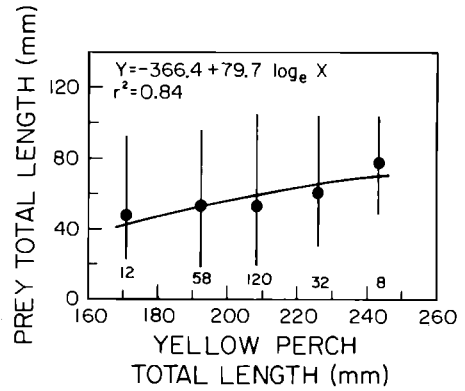

FIGURE 10.—*Mean and range of lengths (Y) for fishes eaten by yellow perch of various sizes (X) in western Lake Erie, 1979–1981. Solid line represents a nonlinear regression through means across 25-mm yellow perch length intervals.*

sions. However, CPUE of age-0 walleyes averaged roughly 28, which was substantially lower than that of nearly all other fishes. Thus, walleyes ate abundant prey rather than their own

young. Similarly, Swenson (1977) reported cannibalism by walleyes in Shagawa Lake, Minnesota, only at some offshore areas of low prey availability.

In summary, density of preferred forage fish species strongly affected size selection and, hence, diet selection by walleyes in western Lake Erie. A density-dependent response by abundant walleyes to changes in forage-fish availability was apparent and suggests that growth of walleyes was food-limited.

Diet Selection by Yellow Perch

Seasonal shifts in the diet of piscivorous yellow perch were caused by changes in forage-
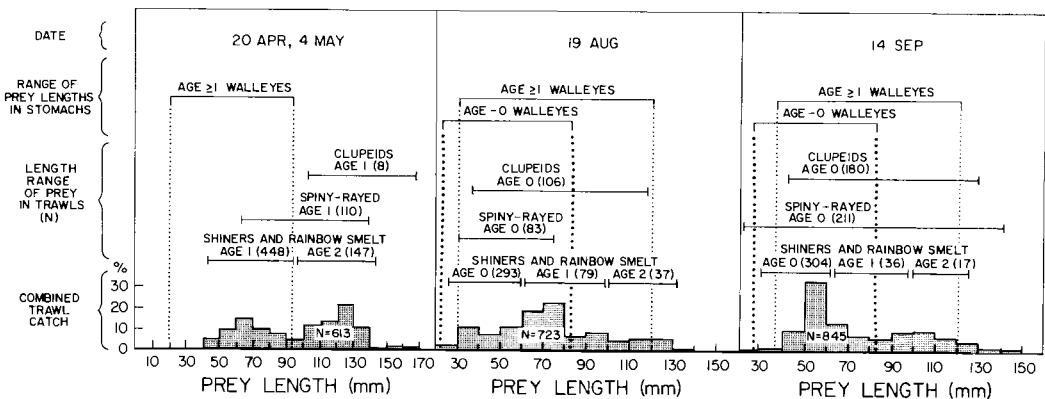

FIGURE 9.—*Range of lengths for prey fishes (in three categories) in walleye stomachs and trawl catches during 1981, East Harbor, western Lake Erie.*
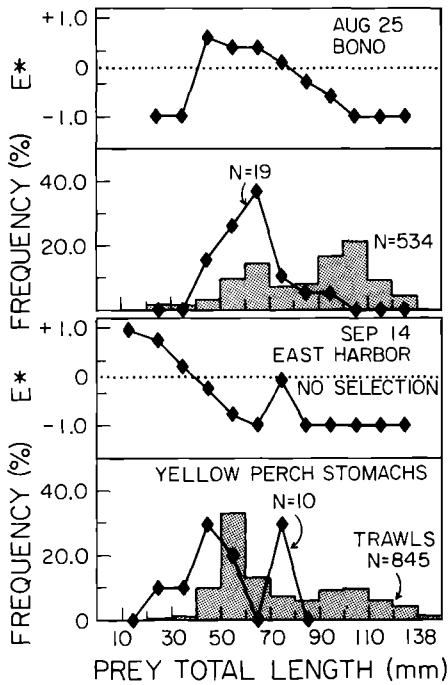
FIGURE 11.—Preference for prey size (electivity E*) by yellow perch based on prey-size distributions in yellow perch stomachs and trawl catches, Bono and East Harbor, western Lake Erie. N is number of prey.

fish availability. Invertebrates were eaten in greater quantities than fish during spring by all sizes of age-2 or older yellow perch, probably because abundance of vulnerable forage fishes was low relative to that in other seasons. During summer and autumn, many yellow perch (>180 mm long) switched to age-0 fishes because these prey were more abundant than in spring. However, some yellow perch (150–180 mm long) ate similar volumes of fish and invertebrates in summer and autumn. Either forage fishes were too large for these predators or invertebrates were more readily available than fish. Thus, diet selection by yellow perch was influenced mostly by abundance of vulnerable forage fishes and the size of the yellow perch.

Selection for prey type by piscivorous yellow perch was less intense than by walleyes. Yellow perch electivity values were near zero for most prey species whereas walleye values more closely approached the positive and negative extremes. This supports work from other lakes that sug-

gests yellow perch are more opportunistic than walleyes, because prey abundance strongly influences the former's diet selection (Tarby 1974; Clady 1976; MacLean and Magnuson 1977).

Limitations of Forage Fishes as Prey

The capacity of the forage-fish community to support walleyes and yellow perch in western Lake Erie probably is determined by the abundance of clupeids and shiners, the preferred forage fishes. Because walleyes and yellow perch eat predominantly age-0 fishes, they are susceptible to fluctuations in recruitment of prey. Most of the variation of forage-fish CPUE among years (Fig. 2) was attributed to changes in shiner and clupeid abundance (Fig. 3). Clupeid recruitment, in particular, fluctuates widely in both marine and freshwater systems (Murphy 1977; Griffith 1978). Thus, predators that select shiners and clupeids likely will experience years of low prey abundance. Large walleyes seemed especially susceptible to food shortages because of their strong preference for age-0 clupeids from August through November. A similar situation exists in Oneida Lake, where growth and survival of walleyes are limited by recruitment of their primary prey, yellow perch (Forney 1965, 1977). Yellow perch in Lake Erie appear less susceptible to forage-fish recruitment failures because they readily switch to invertebrates.

Walleyes also could switch to alternative fishes if shiner or clupeid availability declines. Potential prey are spiny-rayed fishes (Morone spp., freshwater drum, and yellow perch) and trout-perch. Most white bass and freshwater drums, however, are vulnerable to walleyes only from late July to October. White perch, a recent invader into Lake Erie (Busch et al. 1977), might become major prey because they are smaller than white bass and are becoming abundant. However, walleyes may not be effective predators on spiny-rayed fishes in general; work with esocids (Mauck and Coble 1970; Weithman and Anderson 1977; Gillen et al. 1981) suggests that spines reduce capture success by piscivores. This effect may be less pronounced for yellow perch, which are more fusiform than most other spiny-rayed fishes and are eaten by walleyes in Oneida Lake. Trout-perch seldom are eaten by Lake Erie walleyes and are not highly abundant; thus, they probably would not provide an alternative food source. Therefore, prey availability to

TABLE 6.—*Schoener's index of seasonal intra- and interspecific diet overlap between groups of walleyes and yellow perch in western Lake Erie. Numbers of stomachs with food are indicated in parentheses, in the species order of the main comparison.*

Comparison[a]	Year	Season		
		Spring	Summer	Autumn
W0, W1	1981		0.53 (102,110)	0.73 (44,28)
W0, W2+	1981		0.47 (70,24)	0.51 (44,13)
W1, W2+	1979		0.76 (42,9)	0.68 (6,4)
	1980		0.75 (7,21)	
	1981	0.73 (57,18)	0.80 (110,24)	0.77 (28,13)
YP1, YP2	1979	0.74 (64,21)	0.51 (62,31)	0.67 (57,42)
	1980	0.93 (75,71)	0.76 (28,32)	0.62 (32,71)
	1981	0.81 (121,54)	0.67 (59,25)	0.41 (62,22)
YP1, W1+	1979	0.10 (40,19)	0.18 (117,51)	0.36 (34,10)
	1980		0.27 (110,28)	0.67 (15,7)
	1981	0.27 (86,75)	0.32 (118,134)	0.34 (38,41)
YP2, W1+	1979	0.63 (16,19)	0.40 (81,51)	0.55 (38,10)
	1980		0.48 (109,28)	0.77 (40,7)
	1981	0.32 (43,75)	0.46 (46,134)	0.86 (12,41)
YP1, W0	1981		0.27 (118,70)	0.30 (38,44)
YP2, W0	1981		0.54 (46,70)	0.55 (12,44)

[a] Walleyes   Yellow perch
W0 = age 0   YP1 = 150–199 mm
W1 = age 1   YP2 = 200–290 mm
W1+ = age 1 and older
W2+ = age 2 and older

walleyes decreases substantially when clupeid or shiner abundance is low.

We hypothesize that density-dependent processes within the percid community are likely to occur during years of poor shiner or clupeid recruitment and will be most intense among different sizes of walleyes. Intraspecific competition among walleyes for food is more likely than competition between walleyes and yellow perch, because diet similarities are greatest among different age groups of walleyes and least between yellow perch and walleyes. Although partitioning of food by prey size would reduce competition among walleyes (Werner and Hall 1974), this phenomenon may not occur because walleyes of different ages select small (<90 mm) prey throughout the year. Intraspecific competition is not likely to be intense among yellow perch of different sizes because they are food generalists; foraging on different types and sizes of prey should reduce competitive interactions.

In summary, the capacity of the forage-fish community to support percids in western Lake Erie appears to be limited by (1) variable re-

cruitment of shiners and clupeids and (2) competition for these prey among abundant walleyes.

Management Implications

We can now readily divide forage-fish samples into prey groups that are vulnerable and invulnerable to walleyes and yellow perch. Likewise, we can predict which species might provide alternative prey for various sizes of walleyes and yellow perch if primary forage is scarce. Thus, with early-summer indices of forage-fish recruitment, forecasting of potential food shortages is possible. Short-term harvest regulations then could be applied as needed, to adjust predator densities before density-dependent, biological responses occur in the community.

If the walleye population expands or recruitment fails for shiners and clupeids, walleyes might experience further reductions in prey-size selectivity and growth rates, and might shift predation to the young of valuable game fishes, such as yellow perch. In view of the predatory

success by walleyes on yellow perch in Oneida Lake (Nielsen 1980), results could be disastrous to the unstable yellow perch population in Lake Erie. A remedial management action is to increase fishing mortality of walleyes. Indeed, low forage availability may increase vulnerability of walleyes to angling (Kempinger et al. 1975), which could provide a negative feedback mechanism to lower the density of walleyes. Additionally, reduced forage may increase walleye movements (Schupp 1978) and, consequently, their susceptibility to commercial gear.

Historically, walleyes and yellow perch in western Lake Erie have not coexisted at high densities (Leach and Nepszy 1976). Yet, the demise of one population cannot be related entirely to the other. For example, yellow perch seldom were eaten by walleyes; thus, it is unlikely that walleye predation alone caused the fluctuating recruitment of yellow perch in recent years, unless overwinter predation (which we did not measure) was substantial. In fact, yellow perch probably ate more small yellow perch than did walleyes. Competition between walleyes and yellow perch for food also is not a limiting factor to either population. Additional research is needed to identify the functional link between walleyes and yellow perch in western Lake Erie, if indeed there is one.

In this study, we examined and quantified interactions among walleyes, yellow perch, and forage fishes in western Lake Erie. As data are obtained for other predators in this community, researchers can incorporate diet selections of all predators into yield models that forecast reactions of predator populations to management actions. A community approach to management of walleyes and yellow perch should promote more effective use of these resources than the single-species concept that has been used traditionally in western Lake Erie.

Acknowledgments

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