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Consumption Dynamics of the Adult Piscivorous Fish Community in Spirit Lake, Iowa

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Abstract

At Spirit Lake, one of Iowa's most important fisheries, walleye Sander vitreus (formerly Stizostedion vitreum) is one of the most popular species with anglers. Despite a century of walleye stocking and management in Spirit Lake, walleye growth rate, size structure, and angler harvest continue to decline. Our purpose was to determine the magnitude and dynamics of walleye population consumption relative to those of other piscivorous species in Spirit Lake, which would allow managers to judge the feasibility of increasing the abundance, growth rate, and size structure of the walleye population.We quantified food consumption by the adult piscivorous fish community in Spirit Lake over a 3-year period. Data on population dynamics, diet, energy density, and water temperature from 1995 to 1997 were used in bioenergetics models to estimate total consumption by walleye, yellow perch Perca flavescens, smallmouth bass Micropterus dolomieu, largemouth bass Micropterus salmoides, black crappie Pomoxis nigromaculatus, and northern pike Esox lucius. Estimated annual consumption by the piscivorous community varied roughly fourfold, ranging from 154,752 kg in 1995 to 662,776 kg in 1997. Walleyes dominated total consumption, accounting for 68, 73, and 90% (1995–1997, respectively) of total food consumption. Walleyes were also the dominant consumers of fish, accounting for 76, 86, and 97% of piscivorous consumption; yellow perch followed, accounting for 16% of piscivorous consumption in 1995 and 12% in 1996. Yellow perch were the predominant fish prey species in all 3 years, accounting for 68, 52, and 36% of the total prey consumed. Natural reproduction is weak, so high walleye densities are maintained by intensive stocking. Walleye stocking drives piscivorous consumption in Spirit Lake, and yearly variation in the cannibalism of stocked walleye fry may be an important determinant of walleye year-class strength and angler success. Reducing walleye stocking intensity, varying stocking intensity from year to year, and attempting to match stocking intensity with the abundance of prey species other than walleye may improve the walleye fishery in Spirit Lake.

Keywords

Iowa, walleye, population consumption, bioenergetics, fish prey, animal ecology

Disciplines

Aquaculture and Fisheries | Environmental Monitoring | Natural Resources Management and Policy

Comments

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Abstract.—At Spirit Lake, one of Iowa's most important fisheries, walleye *Sander vitreus* (formerly *Stizostedion vitreum*) is one of the most popular species with anglers. Despite a century of walleye stocking and management in Spirit Lake, walleye growth rate, size structure, and angler harvest continue to decline. Our purpose was to determine the magnitude and dynamics of walleye population consumption relative to those of other piscivorous species in Spirit Lake, which would allow managers to judge the feasibility of increasing the abundance, growth rate, and size structure of the walleye population. We quantified food consumption by the adult piscivorous fish community in Spirit Lake over a 3-year period. Data on population dynamics, diet, energy density, and water temperature from 1995 to 1997 were used in bioenergetics models to estimate total consumption by walleye, yellow perch *Perca flavescens*, smallmouth bass *Micropterus dolomieu*, largemouth bass *Micropterus salmoides*, black crappie *Pomoxis nigromaculatus*, and northern pike *Esox lucius*. Estimated annual consumption by the piscivorous community varied roughly fourfold, ranging from 154,752 kg in 1995 to 662,776 kg in 1997. Walleyes dominated total consumption, accounting for 68, 73, and 90% (1995–1997, respectively) of total food consumption. Walleyes were also the dominant consumers of fish, accounting for 76, 86, and 97% of piscivorous consumption; yellow perch followed, accounting for 16% of piscivorous consumption in 1995 and 12% in 1996. Yellow perch were the predominant fish prey species in all 3 years, accounting for 68, 52, and 36% of the total prey consumed. Natural reproduction is weak, so high walleye densities are maintained by intensive stocking. Walleye stocking drives piscivorous consumption in Spirit Lake, and yearly variation in the cannibalism of stocked walleye fry may be an important determinant of walleye year-class strength and angler success. Reducing walleye stocking intensity, varying stocking intensity from year to year, and attempting to match stocking intensity with the abundance of prey species other than walleye may improve the walleye fishery in Spirit Lake.

Consumption is the process by which energy is transferred up the food web, and thus the nature, rates, and dynamics of consumption have effects not only on consumers but also on prey species (Kitchell 1992; Carpenter and Kitchell 1993). Consumption estimates are necessary to evaluate the food requirements of consumer populations in relation to carrying capacities of the systems supporting these populations. Unfortunately, population-level and community-level consumption information is difficult to obtain (Ney 1990).

Quantifying consumption by all the potentially important species is crucial in understanding food web dynamics and evaluating consumption demand in relation to the carrying capacity of systems where several species exploit the same prey community (Kempinger and Carline 1977; LaBar 1993; Kershner et al. 1999). Most consumption studies to date have focused on single species, but several authors have recognized the need to account for all major piscivorous species in a system (Kempinger and Carline 1977; Stewart et al. 1981; Johnson et al. 1992b; LaBar 1993; Hartman and Brandt 1995a; Kershner et al. 1999). A few recent studies have attempted to quantify consumption by several species, allowing comparisons of their trophic effects as well as evaluation of past and future management actions (Johnson et al. 1992a; Raborn et al. 2002; Raborn et al. 2003).

Spirit Lake is one of Iowa's most important fish-

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eries and has been a popular destination for commercial fishing, recreational angling, boating, and shoreline development for over a century (Hofsommer 1975). Angling pressure is high, and walleye *Sander vitreus* (formerly *Stizostedion vitreum*) and yellow perch *Perca flavescens* are among the most sought-after species. The predominant piscivorous fish species are yellow perch, walleye, black crappie *Pomoxis nigromaculatus*, largemouth bass *Micropterus salmoides*, smallmouth bass *Micropterus dolomieu*, and northern pike *Esox lucius*, which together account for 99% of the density and 97% of the biomass of all piscivorous fish in Spirit Lake (Pierce et al. 2001b). Despite over a century of regular stocking and length and bag limits, walleye growth rate and size structure in Spirit Lake have declined from historical levels, resulting in reduced harvest and angler satisfaction (Rose 1955; Jennings 1970; Larscheid 1994). Our purpose was to determine the magnitude and dynamics of walleye population consumption relative to other piscivorous species in Spirit Lake, which along with prey production estimates would allow managers to judge the feasibility of increasing the abundance, growth rate, and size structure of the walleye population. Our objectives were to (1) determine the taxonomic composition, magnitude, and temporal dynamics of prey consumption by the piscivorous community as a whole; (2) determine the taxonomic composition, magnitude, and temporal dynamics of prey consumption by the major piscivorous species; (3) compare walleye consumption with that of the rest of the piscivorous community; and (4) explore potential consequences of piscivorous consumption dynamics for Spirit Lake and similar fisheries.

Study Site

Spirit Lake (43°28′N, 95°06′W) is Iowa's largest natural lake, having a surface area of 2,229 ha, a mean depth of 5 m, and a maximum depth of 7 m (Bachmann et al. 1995). In 1999–2001, summer Secchi transparency averaged 1.8 m and summer chlorophyll-*a* concentrations averaged 15 mg/m^3 (S. Fisher, Iowa Lakeside Laboratory, personal communication). Spirit Lake is ice covered from early December to early April in most years, and summer temperature maxima of 24–26°C occur in late July without thermal stratification.

Methods

Data Collection

Field.—Yellow perch, walleye, black crappie, largemouth bass, smallmouth bass and northern pike were collected in Spirit Lake in 1995–1997. Our primary sampling methods were boat electrofishing and beach seining; supplemental samples were obtained using gill nets and fyke nets.

We typically electrofished 5 nights/week from early May to late October, covering most of the ice-free season in Spirit Lake. During each week, a different area was electrofished each night, weather conditions dictating choice of locations on any particular night. We began electrofishing after sunset, and continued for 30–120 min depending on catch rate. Electrofishing catch per unit effort (CPUE) was recorded as number of fish per minute for each night.

We beach-seined the littoral zone in July and September of 1995 and May, July, and September of 1996 and 1997. All beach seining was done at night. Because of closely spaced private cottages and docks along most of the shoreline, we used eight fixed sampling stations that are used by the Iowa Department of Natural Resources for monitoring, as well as in other recently published studies (Pierce et al. 2001a, 2001b). We sampled each station once during a 4–5-d period near the new-moon phase of each sampling month. During each sampling period stations were sampled in haphazard order, with weather conditions often dictating the number and order of stations sampled on a particular night.

We used 6-mm (bar) mesh, lampara-style beach seines (Hayes et al. 1996). Seine dimensions were 333 m × 4 m in July 1995 (sample area, 1.76 ha), 133 m × 4 m in September 1995 and all of 1996 and 1997 (0.28 ha), and 152 m × 4 m in all of 1998 (0.37 ha). Seines had weighted bottom lines, floats along the top lines, and were deployed from a boat in a semicircle extending out from the shoreline. Both ends of the seines were pulled to shore simultaneously.

We sampled the offshore zone with gill nets for 5 nights in May of each year when water temperatures were 15°C or less. Gill nets were checked every hour to minimize fish mortality. We sampled with fyke nets in eight littoral zone locations for 10 d in June of 1995 and 2 d in July of 1996. Fyke nets were checked every 24 h. Catch rates were low in both gill nets and fyke nets; neither of these gears made significant contributions to population estimation or stomach content samples.

We focused on consumption by fish 150 mm or more in total length; consumption by fish less than 150 mm in Spirit Lake is reported by Pelham (2000). Fish were measured (total length) to the nearest 2.5 mm and weighed (wet weight) to the nearest 14 g in the field and then fin-clipped for mark–recapture analysis. A unique fin clip was used for each year. Stomach contents were flushed out using a water pump (Baker and Fraser 1976), immediately put on ice in a cooler, and frozen within a few hours for later identification in the laboratory. Most of the stomach content samples were obtained from electrofishing and beach seining, which minimized potential digestion of prey after capture. Fish were maintained in tubs with fresh lake water, processed quickly to minimize stress, and released alive.

Subsamples of fish were anesthetized and sacrificed for estimating energy density in May, July, and September of 1995. Specimens were measured to the nearest 1 mm and weighed to the nearest 0.1 g.

Water temperatures were measured hourly (nearest 0.1°C) by means of temperature loggers located at depths of 1 and 3 m at various sites in Spirit Lake. The temperature loggers were deployed after ice-out in mid-April and retrieved before ice-up in late October each year.

Laboratory.—Prey fish from stomach content samples were identified to species and invertebrates were identified either to phylum, class, or order. Other vertebrate prey were identified to class. All prey items found in stomachs were counted. When possible, total length of prey fish was measured directly (nearest 1 mm). When a prey fish was partially digested, its total length was estimated using equations developed from this study as follows:

$$BL = NV_t(BL_p/NV_p) \tag{1}$$

and

$$TL = BL \cdot R, \tag{2}$$

where BL is backbone length, TL is total length, NV_t is the total number of vertebrae on the backbone (as found in Scott and Crossman 1973), R is the ratio of the total length to the backbone length for a particular prey fish species, and BL_p and NV_p are the partial backbone length and number of vertebrae remaining on the partial backbone for a prey fish specimen with such a backbone. When the standard length (SL) of a prey fish could be measured, it was converted to total length using equations either developed in this study or found in Carlander (1969).

Body lengths of crayfish were either measured directly (nearest 1 mm) or estimated from a body–claw length equation developed in this study. Body lengths of other invertebrates were measured (nearest 0.01 mm) using a video image analysis system with a dissecting microscope. Wet weights of prey fish and crayfish were estimated using length–weight equations developed in this study. Wet weights of invertebrates other than crayfish were assumed to be 5 times the dry weight (Morin and Dumont 1994); dry weights of these invertebrates were estimated using length–weight equations from the literature (Smock 1980; Meyer 1989).

For estimating energy density, we dried the sacrificed fish at 70°C in a drying oven until a constant dry weight (nearest 0.01 g) was reached. Calculation of energy density estimates is described below.

Data Analysis

Population dynamics.—We used data from Pelham (2000) and Pelham et al. (2001) to determine within-lake distributions of the six piscivorous species in Spirit Lake, which in turn determined our approach for estimating population sizes from beach seining. Pelham (2000) sampled the offshore zone at night from May to September 1998 using a semiballoon otter trawl (Hayes et al. 1996) with a 7.9-m headrope, a 38-mm-mesh body, and a 6-mm-mesh cod end. Trawling was done during the same weeks as littoral zone beach seining (Pierce et al. 2001b), allowing a direct comparison of relative densities in the littoral zone versus offshore. Pooled over the entire 1998 study period, mean offshore densities of black crappie, largemouth bass, northern pike, and smallmouth bass were less than 1 fish/ha and 95% confidence intervals (CIs) all included zero. In contrast, offshore walleye densities averaged 211 fish/ha (95% CI, ±61), and yellow perch densities averaged 2,042 fish/ha (±530). These estimates are similar to the littoral averages (M.E. Pelham, Minnesota Department of Natural Resources, unpublished data) of 242 walleye/ha (95% CI, ±55) and 1,566 yellow perch/ha (±486). From these comparisons of 1998 data we assumed that black crappie, largemouth bass, northern pike, and smallmouth bass populations were confined to the littoral zone in Spirit Lake, whereas walleye and yellow perch populations were distributed lakewide at similar littoral and offshore densities.

Beach seining was one of three approaches to population estimation we used. Black crappie, largemouth bass, smallmouth bass, and northern pike population estimates were obtained by first multiplying each individual beach seining density estimate by the area of the littoral zone (303 ha). Walleye and yellow perch population estimates were obtained by first multiplying each individual beach seining density estimate by the whole lake area. Annual population estimates and 95% CIs were then obtained from annual means and standard deviations of the expanded individual estimates. These annual means were assumed to represent midyear (July 1) population sizes.

In addition to beach seining, we used mark–recapture techniques to estimate population sizes of largemouth bass, northern pike, and smallmouth bass. Mark–recapture estimates were not attempted for the other three species because of low proportions of fish marked. We considered each year as a single mark–recapture period, and pooled marks, captures, and recaptures from all sampling gears within each year. Using the Jolly–Seber model (Krebs 1989) and data from 1995 to 1997, we estimated 1996 population sizes and 95% CIs. To estimate population sizes in 1995 and 1997, we first calculated mean electrofishing CPUE and 95% CIs separately for each of the 3 years. We then estimated population sizes in 1995 and 1997:

$$P_i = \mathrm{CPUE}_i(P_{1996}/\mathrm{CPUE}_{1996}), \tag{3}$$

where P_i is population size, CPUE_i is electrofishing CPUE in either 1995 or 1997, P_{1996} is the population size for 1996, and CPUE_{1996} is the electrofishing CPUE value for 1996. The lower and upper 95% CIs of population size in 1995 and 1997 were calculated similarly, using the appropriate CIs in place of population sizes. Both the Jolly–Seber and electrofishing CPUE annual estimates were assumed to represent midyear (July 1) population sizes. These estimates were averaged with the corresponding beach seining estimates for each year for largemouth bass, northern pike and smallmouth bass.

We used the Fraser–Lee method (DeVries and Frie 1996) to backcalculate lengths at age for the six piscivorous species from hard structures collected from subsamples of fish captured in 1995. For aging and back-calculations we used anal fin spines for yellow perch, dorsal fin spines for walleyes, pectoral fin rays for northern pike, otoliths for black crappies, and scales for largemouth bass and smallmouth bass. We constructed age–length keys (DeVries and Frie 1996) to estimate age frequency distributions for each year by using electrofishing catch data for largemouth bass, smallmouth bass, and northern pike and beach seining catch data for yellow perch, walleyes, and black crappies.

We used the age frequency distributions for each species to estimate annual survival rate by using the catch curve method (Van den Avyle 1993). We reduced biases by first eliminating the youngest and oldest age-classes present and then calculated linear regressions of $\log_{10}$ transformed age-class catches versus age for each species in each year. Using these regression equations and the annual population estimates, we generated smoothed age-frequency distributions for each species in each year by solving the regressions for each age-class. These smoothed age-frequency distributions provided the yearly age-class estimates used in bioenergetics models to generate age-class and population consumption estimates.

Diet composition.—Diet composition was determined from stomach content samples collected from May through October in each year. Samples were grouped by season: spring (May and June), summer (July and August) and fall (September and October). To account for size-related differences in diet, we divided each piscivorous species into two size classes. Threshold lengths for assigning fish to small or large size-classes were 203 mm for black crappies and yellow perch; 305 mm for largemouth bass, smallmouth bass, and walleyes; and 560 mm for northern pike.

Diet composition was expressed as percent weight, which we calculated for each prey taxon as

$$\%W_i = 100 \cdot \left(W_i \middle/ \sum_{i=1}^{n} W_i \right), \tag{4}$$

where n is the total number of prey taxa and W_i is the wet weight (g) of prey taxon i.

Energy density.—We used the relationship of Hartman and Brandt (1995b) to estimate predator and prey fish energy density from ratios of dry weight to wet weight, that is,

$$\mathrm{ED} = a + b(\mathrm{DW}), \tag{5}$$

where ED is energy density (J/g wet weight), DW is the ratio of dry weight to wet weight, and a and b are species-specific parameters. We used Hartman and Brandt's species-specific parameters whenever possible. Exceptions were as follows: muskellunge *Esox masquinongy* parameters were used for northern pike; cyprinid parameters were used for common carp, golden shiners *Notemigonus crysoleucas* and spottail shiners *Notropis hud-*

sonius; sciaenid parameters were used for freshwater drum; and perciform parameters were used for walleyes, largemouth bass, smallmouth bass, black crappies, bluegills *Lepomis macrochirus*, johnny darters *Etheostoma nigrum*, and logperch *Percina caprodes*. To account for size-related differences in energy densities of the six piscivorous species, we divided each into two size-classes, using the same threshold lengths as used for diet composition. Energy densities of invertebrates and other vertebrates were obtained from Cummins and Wuycheck (1971).

Water temperature.—We calculated daily mean temperatures from hourly measurements. We then developed a polynomial regression for each year to extrapolate daily mean temperatures on dates for which no measurements were taken. Extrapolated daily mean temperatures lower than 4°C were adjusted to 4°C, which we assumed to be the temperature under ice cover. Because Spirit Lake does not thermally stratify, our mean daily temperatures accurately reflected the thermal environment experienced by all fish. Daily mean temperatures were used in bioenergetics models.

Bioenergetics Modeling of Consumption

We used Fish Bioenergetics model 3 (FBM3; Hanson et al. 1997) to estimate consumption based on age-class data, annual mortality rates, diet composition, predator and prey energy densities, and water temperatures. Annual mortality rates were converted from annual survival rates. Because lengths at age were backcalculated from annuli formed in early spring on hard structures, we used April 1 as the first day of modeling in each year. We backcalculated population estimates on April 1 for each species from the July 1 population estimates and monthly mortality rates. Monthly mortality rates were obtained from annual mortality rates using the program SURVIVAL (Krebs 1989). Age-class size estimates for April 1 were generated by multiplying April 1 population size estimates by the proportional composition of each age-class. Length-weight equations were used to convert length-at-age to weight-at-age. The weights at age t and age $t + 1$ served as starting and final weights for modeling annual consumption by age t fish in each year.

Diet composition during spring (May 1 to June 30), summer (July 1 to August 31), and fall (September 1 to October 31) was estimated directly from stomach content samples taken during those seasons. The remainder of the year (November 1 to April 30) was classified as winter for bioenergetics modeling. Diet composition during winter, when no stomach content samples were taken, was assumed to be similar to that in fall (November 1–April 15) and spring (April 16–30). For modeling consumption by black crappies, largemouth bass, smallmouth bass, walleyes, yellow perch younger than age-4, and northern pike younger than age 3, we used diet composition and energy densities for the small size-class. Diet composition and energy density for the large size-classes were used for modeling consumption by older fish. Because of the narrow length range of the majority of prey fish consumed in Spirit Lake (Liao et al. 2002), we assumed that size variation in energy density of prey fish species was negligible. Small predator energy density estimates were used for black crappie, northern pike and yellow perch consumed as prey. Because FBM3 does not include a model for black crappies, the model for adult bluegills was used to estimate consumption by black crappies.

Bioenergetics models were run for each age-class of each species from April 1 to March 31 in each year. Population consumption was calculated by summing age-class consumption within species. Seasonal population consumption was calculated by summing daily FBM3 population consumption output within seasons. Annual consumption was calculated by summing seasonal consumption within years. Community consumption was calculated by summing consumption for all six piscivorous species.

Results

Population Dynamics

We obtained two population estimates each year for largemouth bass, northern pike, and smallmouth bass using beach seining data and either the Jolly–Seber model (1996) or electrofishing CPUE (1995, 1997; Table 1). Because of low proportions of fish marked, population estimates for black crappies, walleyes, and yellow perch were based solely on beach seining in all 3 years. Yellow perch and walleyes were the most abundant piscivorous species in Spirit Lake, averaging roughly two orders of magnitude greater in abundance than the other species. The other four species made minor contributions to abundance of the total piscivorous community in Spirit Lake during the study.

Annual population mortality rates ranged from 23% to 61%. Annual mortality rates in each year (1995–1997) were 31, 42, and 51% for black crappie; 32, 25, and 25% for largemouth bass; 53, 58, and 38% for northern pike; 39, 37, and 33% for

TABLE 1.—Population estimates for black crappies, largemouth bass, northern pike, smallmouth bass, walleyes, and yellow perch in Spirit Lake, Iowa, 1995–1997. Beach seining, Jolly–Seber, and electrofishing catch per unit effort (CPUE) estimates and confidence intervals (in parentheses) are for July 1. April 1 estimates were backcalculated from the mean of July 1 estimates using monthly mortality rates. All estimates include only fish 150 mm or longer. April 1 estimates were used to generate starting population sizes for bioenergetics modeling of consumption.

Estimate type	Black crappies	Largemouth bass	Northern pike	Smallmouth bass	Walleyes	Yellow perch
			1995			
Beach seining	7,049 (0–19,290)	3,057 (0–8,376)	1,736 (897–2,575)	2,578 (561–4,594)	100,187 (0–27,487)	174,737 (0–386,154)
Electrofishing CPUE		2,033 (1,418–2,628)	1,177 (850–1,504)	8,149 (6,367–9,932)		
April 1 estimate	7,735	2,797	1,748	6,056	106,873	206,009
			1996			
Beach seining	12,949 (8,238–17,661)	3,366 (3,131–3,602)	3,787 (2,727–4,847)	5,446 (3,221–7,672)	520,668 (159,360–881,976)	599,517 (0–1,391,348)
Jolly–Seber		4,984 (3,642–8,149)	1,175 (495–5,740)	6,529 (3,867–14,801)		
April 1 estimate	14,841	4,489	3,072	6,711	561,757	720,653
			1997			
Beach seining	4,929 (2,211–7,647)	17,043 (0–44,085)	3,066 (1,791–4,349)	5,951 (2,863–9,040)	692,771 (440,919–944,624)	236,483 (53,611–419,356)
Electrofishing CPUE		7,225 (4,845–9,606)	989 649–1,329)	8,797 (6,590–11,004)		
April 1 estimate	5,889	13,012	2,280	8,137	774,766	298,991

smallmouth bass; 23, 27, and 36% for walleyes; and 49, 53, and 61% for yellow perch.

Using our field estimates of July 1 population size and monthly mortality rates, we backcalculated estimates of population size on April 1 of each year (Table 1). These April 1 population estimates were used to generate April 1 age-class estimates, which were used as starting age-class sizes for bioenergetics modeling of consumption.

Energy Density

Predator energy densities ranged from 4,368 J/g wet weight for small walleyes in summer to 6,759 J/g for large black crappies. Prey energy densities ranged from 2,520 J/g wet weight for common carp to 6,280 J/g for logperch (Table 2).

Water Temperature

Water temperatures followed similar seasonal patterns each year, although the mean temperature on any given day varied by as much as 4°C among years. The highest daily mean temperature was 25.3°C on July 29, 1996; the lowest spring and fall daily mean temperatures were 4.1°C on April 16, 1997, and 5.4°C on October 31, 1997.

Community Consumption

Total estimated annual consumption by the adult piscivorous community was 154,752 kg in 1995, 637,643 kg in 1996, and 662,776 kg in 1997. Of the total annual food consumed (by weight), fish prey accounted for 90% in 1995, 85% in 1996, and 81% in 1997, a relatively constant proportion of fish to total consumption by the piscivorous community despite wide variation in the absolute amount of fish consumed. The large increase in community consumption between 1995 and 1996 was due to walleye and yellow perch population increases (Table 1).

Nineteen fish species were consumed by the piscivorous community (Liao et al. 2002). Yellow perch, logperch, walleyes, and bluegills were the four most predominant prey fish species over the 3 years (Figures 1–6). Yellow perch were the most-consumed fish species in all 3 years, although their percentage of total fish weight consumed declined from 68% in 1995 to 36% in 1997.

Population Consumption

As the dominant predators in Spirit Lake, walleyes accounted for 68% (by weight) of the estimated total community consumed in 1995, 73% in 1996, and 90% in 1997. Walleyes were also the dominant piscivorous predators, accounting for nearly 90% of fish community consumption over the 3 years. Walleyes consumed primarily yellow perch, which accounted for 76% of fish that walleyes consumed in 1995, 59% in 1996, and 36% in 1997. The decline in the yellow perch fraction of fish consumed by walleye was balanced by in-

TABLE 2.—Mean energy densities (J/g wet weight) for predator and prey fish in Spirit Lake, Iowa. Energy densities were calculated from dry weight : wet weight ratios by means of models in Hartman and Brandt (1995b). Size ranges of large and small predators varied by species (see text); prey are less than 150 mm.

Species	Large predators Mean	Large predators *N*	Small predators Mean	Small predators *N*	Prey Mean	Prey *N*
Black crappie	6,759	5	5,812	5		
Largemouth bass	6,089	14	5,479	17	4,306	10
Northern pike	4,928	4	5,111	5		
Smallmouth bass	6,292	13	5,475	19	3,856	13
Walleye					3,680	6
Spring	6,140	17	5,222	15	1	
Summer	5,794	18	4,368	15		
Fall	6,010	12	4,557	8		
Yellow perch	5,897	8	5,097	8		
Black bullhead					3,694	13
Bluegill					3,807	13
Common carp					2,520	1
Freshwater drum					5,786	1
Golden shiner					5,078	3
Johnny darter					6,108	10
Logperch					6,280	10
Spottail shiner					5,218	6
White bass					6,222	11

creases in consumption of logperch, walleyes, largemouth bass, and bluegills (Figure 1).

Yellow perch accounted for 23% of the estimated total community consumption in 1995, 24% in 1996, and 7% in 1997. Although yellow perch was the most abundant piscivorous species, fish accounted for much smaller fractions of their diet than for walleyes in Spirit Lake (Liao et al. 2002),

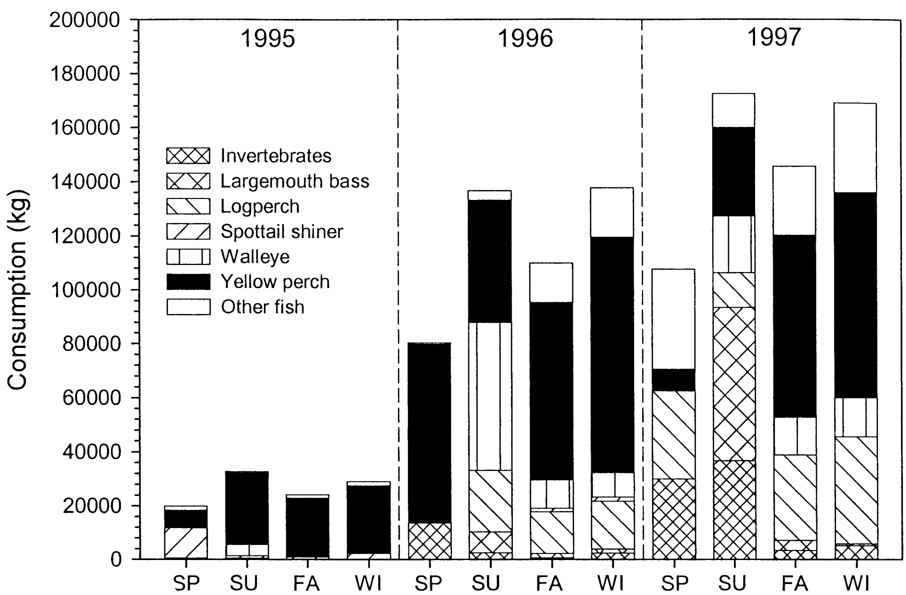

FIGURE 1.—Estimated seasonal consumption (by weight) of prey taxa by walleyes in Spirit Lake, Iowa, 1995–1997. Seasons included spring (SP; May 1 to June 30), summer (SU; July 1 to August 31), fall (FA; September 1 to October 31), and winter (WI; November 1 to April 30). Only the prey taxa accounting for 10% or more of the total prey consumed in any single year are identified; other taxa are pooled and labeled as ''other.'' Seasonal consumption is grouped within years for simplicity. Actual seasonal consumption values shown for a given year (1995, 1996, or 1997) are from May 1 of that year to April 30 of the following year.

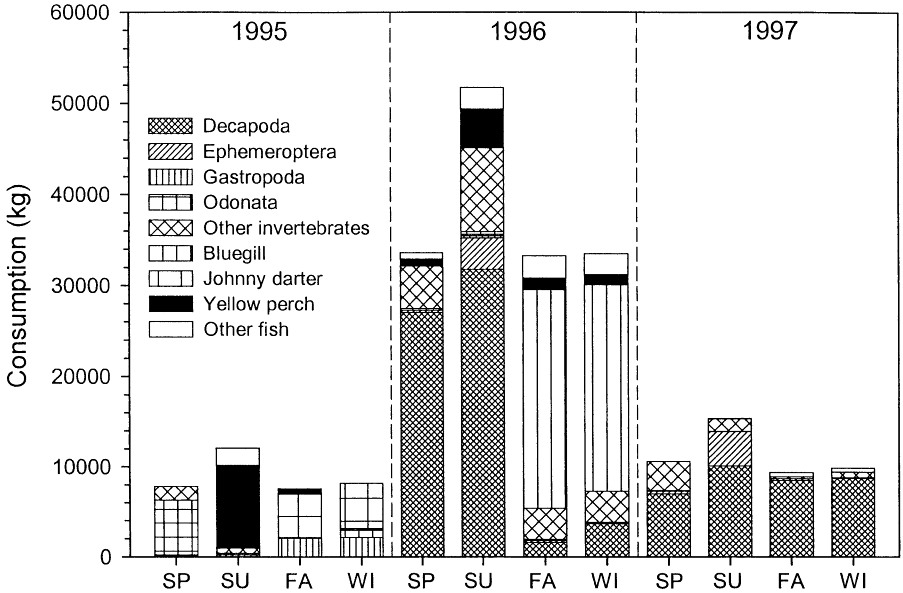

FIGURE 2.—Estimated seasonal consumption (by weight) of prey taxa by yellow perch in Spirit Lake, Iowa, 1995–1997. Other details are given in Figure 1.

and thus, the yellow perch population accounted for far less fish consumption than walleye (Figures 1, 2). Fish consumed by yellow perch were generally small-bodied species such as johnny darters, logperch, bluegills and small yellow perch (Figure 2).

Consumption of fish by black crappies, largemouth bass, northern pike, and smallmouth bass together accounted for small proportions of the community consumption of fish in Spirit Lake, largely because of their low abundance compared with walleyes and yellow perch. Black crappies consumed primarily fish in 1995, bluegills (66%) and yellow perch (12%) predominating in their total consumption (Figure 3). However, in 1996 and 1997 black crappies switched their consumption to primarily invertebrates, predominantly amphipods, ephemeropterans, dipterans, and decapods. Largemouth bass and northern pike consumed primarily fish in all 3 years (Figures 4, 5). Largemouth bass switched from consuming primarily yellow perch in 1995 to consuming primarily black bullhead *Ictalurus melas* in 1997 (Figure 4). Northern pike consumption included several fish species in 1995 but was predominated by yellow perch in 1996 and 1997 (Figure 5). Smallmouth bass fish consumption concentrated mainly on yellow perch (Figure 6). Decapods accounted for over 70% of the invertebrates consumed by smallmouth bass.

Discussion

Our results demonstrate dramatic variation over time in food consumption by the adult piscivorous fish community in Spirit Lake. Estimated annual community consumption increased roughly fourfold from 1995 to 1996. Because there are few comparable studies, it is difficult to speculate whether this level of annual variation in community-level consumption is typical. Estimated annual consumption of four species (walleye, northern pike, largemouth, and smallmouth bass) comprising the majority of the piscivorous community in Lake Mendota, Wisconsin, increased more than threefold from 1987 to 1989, although virtually all of this increase was due to dramatic increases in stocking of walleyes and northern pike in 1987 (Johnson et al. 1992a). Large fluctuations in abundance are well documented in many species (Mills and Mann 1985; Townsend 1989), including walleyes in Spirit Lake (Rose 1955; J. Larscheid, unpublished data). Because of the strong relationship of population consumption with population abundance (H. Liao, unpublished data), it is reasonable to expect considerable annual variation in community consumption in other systems.

Walleyes were the dominant piscivorous consumers in Spirit Lake, accounting for nearly 90% (by weight) of fish consumption over 3 years. Again, because there are few comparable studies,

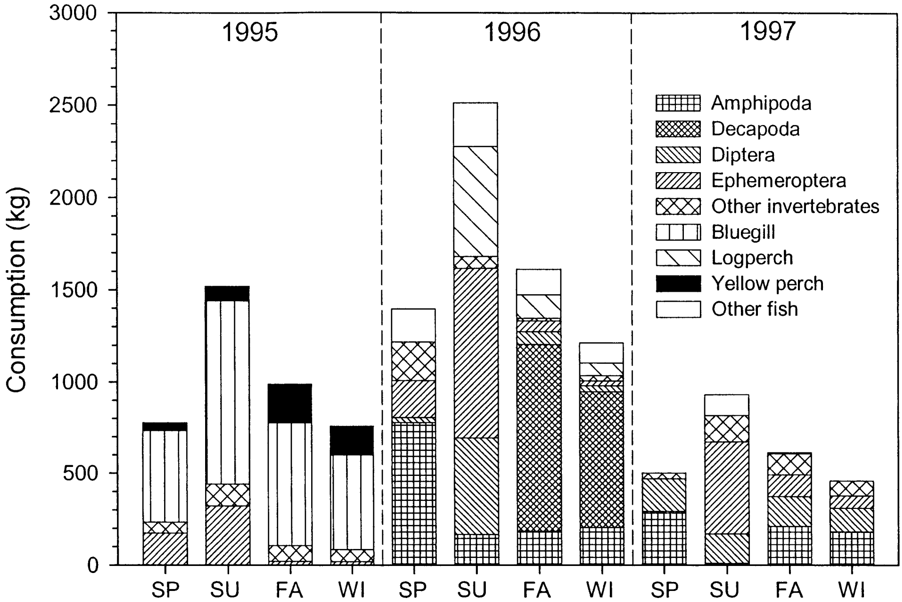

FIGURE 3.—Estimated seasonal consumption (by weight) of prey taxa by black crappies in Spirit Lake, Iowa, 1995–1997. Other details are given in Figure 1.

it is difficult to speculate whether this level of dominance by one species over communitywide consumption is typical. Piscivorous consumption in the late 1980s in Lake Mendota was dominated by two species stocked intensively in an attempt to improve sport fishing and reduce densities of planktivorous fish (Johnson et al. 1992a). Walleyes accounted for 69% and northern pike for 28% of piscivorous consumption in 1987. Interestingly, the relative proportions flip-flopped in 1989, walleyes accounting for only 32% and northern pike 60% of consumption in 1989. Raborn et al. (2003)

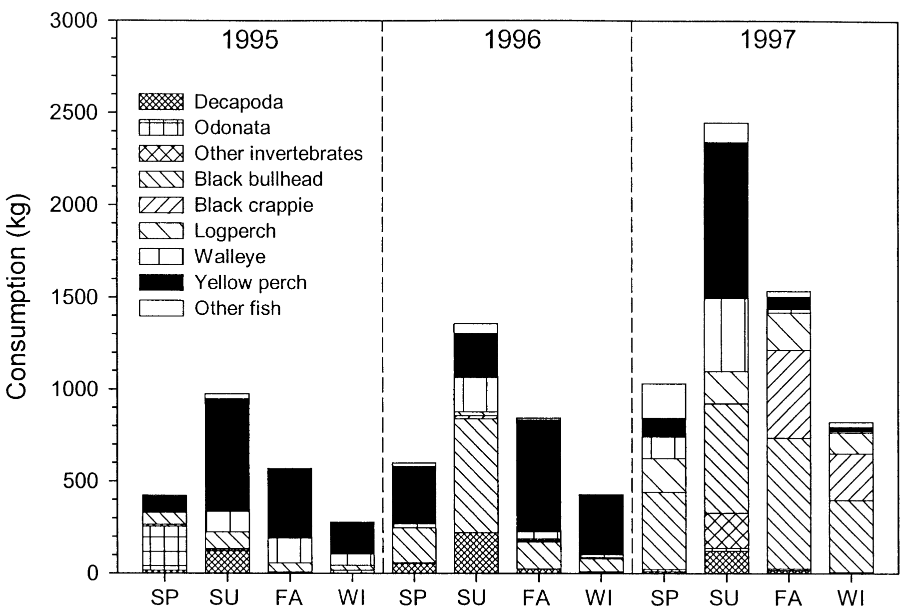

FIGURE 4.—Estimated seasonal consumption (by weight) of prey taxa by largemouth bass in Spirit Lake, Iowa, 1995–1997. Other details are given in Figure 1.

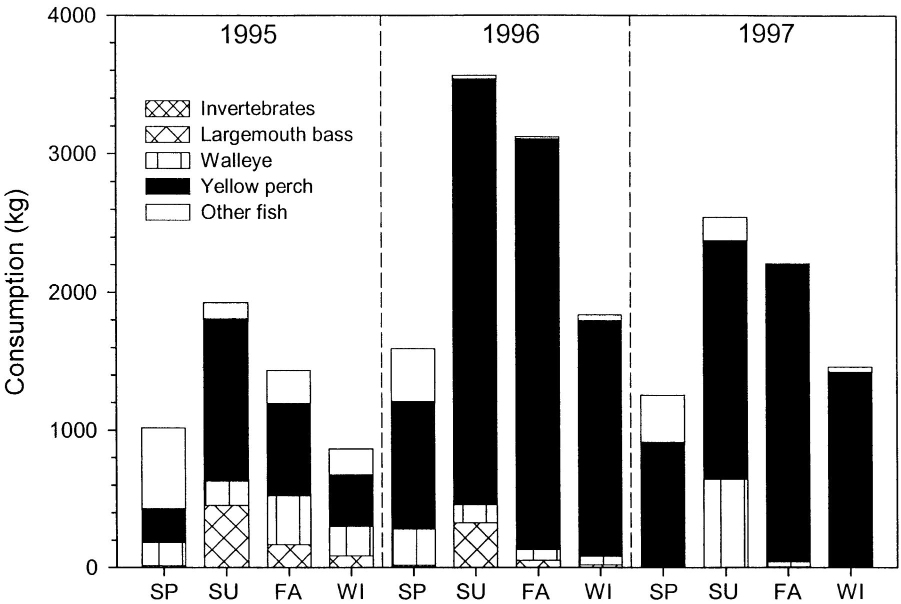

FIGURE 5.—Estimated seasonal consumption (by weight) of prey taxa by northern pike in Spirit Lake, Iowa, 1995–1997. Other details are given in Figure 1.

reported annual consumption of black basses (largemouth bass, smallmouth bass, and spotted bass *M. punctulatus*) by black basses, which accounted for 97% of the piscivorous fish community in Norris Reservoir, Tennessee (Raborn et al. 2002). Two of the three species accounted for the majority of consumption and in relatively equivalent proportions; spotted bass consumed 52% and largemouth bass consumed 39% of the black basses eaten. The collective evidence from Spirit Lake and elsewhere, although scant, suggests that piscivorous community consumption is likely to be dominated by one or two species.

Walleyes are more abundant in Spirit Lake than in most other systems where walleye density has been reported. We compiled data on walleye abundance from the literature (Lyons and Magnuson 1987; Johnson et al. 1992b; Mitzner 1992; Beard et al. 1997; Carlander 1997; Kershner et al. 1999; Nate et al. 2000) to compare with walleye abundance in Spirit Lake. Abundance estimates from 63 lakes (age-classes greater than age 0) averaged 27.2 fish/ha, compared with a 3-year average of 196.4 fish/ha (≥150 mm) in Spirit Lake. Estimates from 222 lakes for age-classes greater than age 2 averaged 6.8 fish/ha, compared with a 3-year average of 14.3 fish/ha (≥age 3) in Spirit Lake.

Walleye stocking drives piscivorous consumption in Spirit Lake. Natural reproduction of walleyes is limited (Rose 1955; McWilliams 1990), and thus, the population is sustained largely by stocking. Annual walleye stocking is intense in Spirit Lake: about 10,000 sac fry/ha stocked during the last decade (J. Larscheid, unpublished data). This stocking rate is on the high side of the range of stocking rates reported elsewhere (Ellison and Franzin 1992). Because walleyes accounted for nearly 90% of the piscivorous consumption during our study, it is clear that stocking ultimately accounts for the vast majority of piscivorous consumption in Spirit Lake.

Stocked fish are highly vulnerable to predation by resident piscivores, which may result in significant predation mortality (Wahl et al. 1995). Thus, in addition to depletion of resident prey resources, high piscivorous consumption rates can also result in poor survival of stocked game fish. Because nearly 90% of piscivorous consumption in Spirit Lake can be attributed to walleye predation, cannibalism may be a significant source of mortality of stocked walleye. In Oneida Lake, New York, cannibalism is a significant source of mortality in age-0 walleye cohorts, especially when yellow perch and other alternative prey are scarce (Chevalier 1973; Mills and Forney 1988). In Lake Mendota, cannibalism is an important source of mortality in age-1 walleye cohorts (Johnson et al. 1992a). The large variation in walleye population abundance we documented in just 3 years of study could be due, in part, to annual variation in sur-

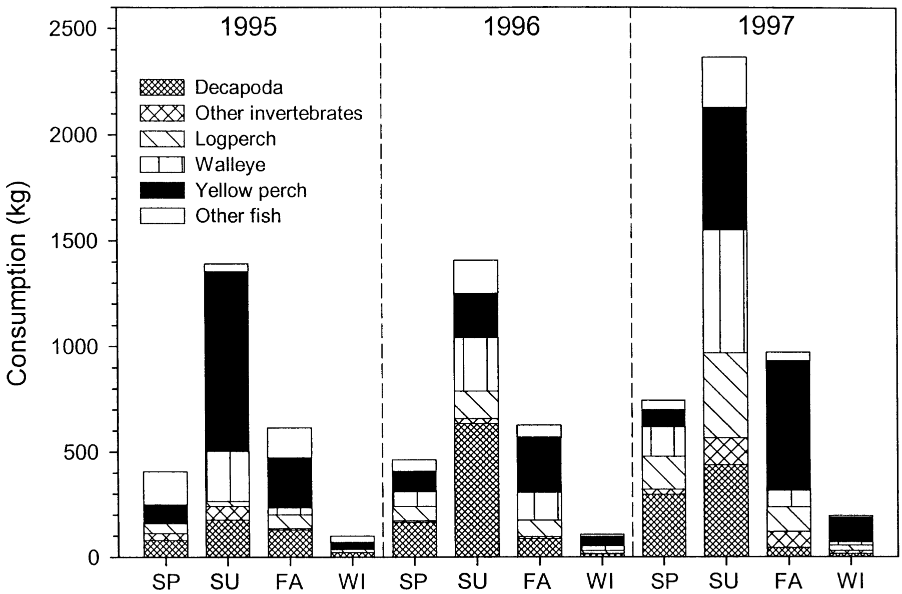

FIGURE 6.—Estimated seasonal consumption (by weight) of prey taxa by smallmouth bass in Spirit Lake, Iowa, 1995–1997. Other details are given in Figure 1.

vival of stocked age-0 fish resulting from annual variation in cannibalism. Angler catch rates are positively correlated with population abundance of walleyes (Isbell and Rawson 1989; Beard et al. 1997), and thus, annual variation in cannibalism of stocked walleye could ultimately be a major determinant of annual variation in success of walleye anglers in Spirit Lake.

Management Implications

Our study is one of the few providing complete accounting of the consumption demand of a diverse piscivorous community and the first to report this over three successive years. By examining all the major piscivorous species consumption simultaneously in Spirit Lake, we were able to identify walleye and yellow perch as the dominant consumers, and show that the other four species played relatively minor roles in overall community consumption. Walleye stocking drives piscivorous consumption in Spirit Lake, and yearly variation in cannibalism of stocked walleye fry may be a major determinant of walleye year-class strength and, ultimately, angler success. Clearly, managers will be challenged to tailor stocking and harvest regulations to this dynamic system; the relative abundance and resulting consumption dynamics of species probably change much faster than management policies can respond. However, by gaining a better understanding of the range of natural dynamics, more realistic expectations should be possible. Our analysis suggests that it may be desirable to reduce walleye stocking intensity in Spirit Lake, vary stocking intensity from year to year, and perhaps attempt to match walleye stocking intensity with abundance of prey species other than walleyes, perhaps through the use of models forecasting prey fish year-class strength (e.g., Shroyer and McComish 1998).

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