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Dynamics of the Littoral Fish Assemblage in Spirit Lake, Iowa, and Implications for Prey Availability for Piscivores

CLAY L. PIERCE,* MARK D. SEXTON,[1] MARK E. PELHAM,[2] AND
HONGSHENG LIAO

U.S. Geological Survey, Biological Resources Division,
Iowa Cooperative Fish and Wildlife Research Unit, Department of Animal Ecology,
11 Science II, Iowa State University, Ames, Iowa 50011, USA

JOE G. LARSCHEID

Iowa Department of Natural Resources, 611 252nd Avenue,
Spirit Lake, Iowa 51360, USA

Abstract.—We assessed the dynamics of the littoral fish assemblage in Spirit Lake, Iowa, and examined potential consequences of these dynamics for availability of prey fish for piscivores. Using beach seines, we quantified the annual, seasonal, and spatial variation in density and biomass of the entire assemblage and of component species over a 4-year period. Potential prey fish availability was inferred from the biomass of the cumulative total fish length groups and sizes of fish eaten by piscivores. Total fish density and biomass averaged 10,024 fish/ha and 276.3 kg/ha, respectively. Density and biomass of total fish varied among years and seasons, but seasonal patterns differed among years. Yellow perch *Perca flavescens*, bluegill *Lepomis macrochirus*, walleye *Stizostedion vitreum*, and common carp *Cyprinus carpio* were the predominant species overall, but the proportional species composition of both total density and total biomass varied highly. Changes in the fish assemblage resulted in dramatic changes in the potential availability of prey fish over time and with piscivore size. These dynamics could lead to variable growth and condition of resident piscivores as well as to variable success of stocking fingerling piscivores.

Animal populations are known to fluctuate widely in abundance (Begon et al. 1986), a characteristic well documented in both marine (Hjort 1914; Rothschild 1986) and freshwater fishes (Townsend 1989). Regular, cyclic fluctuations are often attributed to biotic factors such as predation, competition, or breeding cycles (Townsend 1989), whereas environmental factors often induce irregular, unpredictable fluctuations (Mills and Mann 1985). Long-term records of fish population abundance may even show evidence of two patterns of fluctuation operating at different frequencies, with high-frequency fluctuations reflecting biotic factors being superimposed on low-frequency fluctuations resulting from environmental factors or exploitation (Mills and Hurley 1990; Cyterski and Spangler 1996). Disentangling the driving mechanisms behind these fluctuations has been difficult and remains one of the challenges in understanding and managing fish populations.

An important consequence of fluctuations in fish populations is the resulting variation in the abundance of prey for piscivorous species, many of the latter being important to recreational or commercial fisheries (Noble 1981; Stewart et al. 1981). The dynamic balance between prey supply and predator demand is increasingly recognized as an important determinant of the quality of fisheries (Ney 1990). Thus, a key step in understanding and managing fisheries is quantifying the variation in abundance of exploited populations and their prey species.

The littoral zone fish assemblage is an important functional component of freshwater lakes (Northcote 1988). Abundance is often greater than in other areas, and in some lakes littoral species account for the majority of the entire fish community (Keast and Harker 1977; Werner et al. 1977). Habitat and food resources are more diverse in the littoral zone than in the pelagic zone, and littoral habitats are often crucial for spawning, feeding, and avoiding predation (Keast and Harker 1977; Savino and Stein 1982; Wiley at al. 1984; Carpenter and Lodge 1986; Rasmussen 1988). Because of the importance of the littoral zone to fish

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* Corresponding author: cpierce@iastate.edu

[1] Present address: Outdoor Technologies Group, 1900 18th Street, Spirit Lake, Iowa 51360, USA.

[2] Present address: Minnesota Department of Natural Resources, 7372 State Highway 25 SW, Montrose, Minnesota 55363, USA.

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assemblages and fisheries in lakes, fluctuations in the abundance and composition of the littoral assemblage can affect energy flow, food web interactions, and fishery yields from the entire ecosystem.

Spirit Lake, Iowa, supports one of the state's most important natural lake fisheries, which has attracted anglers and commercial fishers for over a century (Hofsommer 1975). Stocking walleye *Stizostedion vitreum* dates back to the late 1800s, and fishery research and management have been underway for several decades (Rose 1949; Larscheid 1997). Angling pressure is high for 10 months of the year, with as many as a dozen species being represented in the anglers' catch (J. Larscheid, unpublished data). In addition to angler harvest, common carp *Cyprinus carpio*, bigmouth buffalo *Ictiobius cyprinellus*, and freshwater drum *Aplodinotus grunniens* are harvested commercially.

Our goal was to quantify the dynamics of the littoral fish assemblage in Spirit Lake and to explore the potential consequences of these dynamics for the availability of prey for naturally occurring and stocked piscivorous fish. Our objectives were to (1) determine density and biomass of component species and the entire littoral assemblage; (2) determine the extent and significance of annual, seasonal, and spatial variation in density and biomass; (3) determine the size of prey fish eaten relative to piscivore size; (4) determine the magnitude of variation in potential availability of fish prey over time and with respect to piscivore size; and (5) understand the potential consequences of variable availability of prey fish for naturally occurring and stocked piscivores.

Study Site

Spirit Lake (43°28′N, 95°06′W) is located near the Iowa–Minnesota border in northwest Iowa (Figure 1). Iowa's largest natural lake, Spirit Lake has a surface area of 2,229 ha, a maximum depth of 7 m, and a mean depth of 5 m and is eutrophic (Bachmann et al. 1995). Ice cover occurs from early December to early April, and summer water temperatures peak in July and August at around 24–26°C with no thermal stratification.

We defined the littoral zone as extending from the shore to a depth of 3 m, which is the extent of submersed vegetation in most years. This zone occupies roughly 14% of the lake surface area. The bottom in the littoral zone is gently sloping, and the substrate consists of various mixtures of sand, gravel, and cobble, with clusters of boulders occurring sporadically. Submersed vegetation is essentially nonexistent in early spring; by early fall, it is dense in a few areas, sparse or nonexistent in others. Emergent vegetation is rare, occurring only in the few remaining undeveloped areas. Most of the shoreline is privately owned and has been developed with cottages and docks. Land use in the drainage basin is primarily agricultural.

Methods

Sampling.—We sampled in July and September 1995; May, July, and September 1996 and 1997; and monthly from June through September 1998. All sampling was done at night. Because of private cottages and docks along most of the shoreline, we used eight fixed sampling stations (Figure 1). We attempted to sample each station once during a 4–5-d period near the new moon phase of each sampling month; in some months, however, not all stations were sampled. During each sampling period the stations were sampled in haphazard order, the wind 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) for all samples. Seine dimensions were as follows: 133 × 4 m in September 1995 and all of 1996 and 1997 collections, 333 × 4 m in July 1995, and 152 × 4 m in all of 1998. Seines had weighted bottom lines and floats along the top lines; they were deployed from a boat in a semicircle extending out from the shoreline. Seines were pulled to shore from both ends simultaneously. Areas sampled were 0.28 ha (133-m seine), 1.76 ha (333-m seine), and 0.37 ha (152-m seine).

Estimating abundance.—Captured fish were processed quickly in the field and reasonable attempts were made to release all fish alive. Species were sorted into tubs and individual fish were counted, measured for total length (TL; to the nearest mm for specimens $\leq$150 mm or the nearest 2.5 mm for specimens $>$150 mm) and weighed wet (to the nearest 0.1 g for specimens $\leq$150 mm or the nearest 5 g for specimens $>$150 mm).

When large age-0 and age-1 catches were encountered, subsamples of roughly 100 specimens of each species and age-class were measured and weighed; the remaining unmeasured specimens were counted. Lengths were assigned to unmeasured specimens as random numbers drawn from normal distributions with means and standard deviations obtained from the measured subsamples. Lengths assigned in this way were constrained within the observed range of subsample lengths.

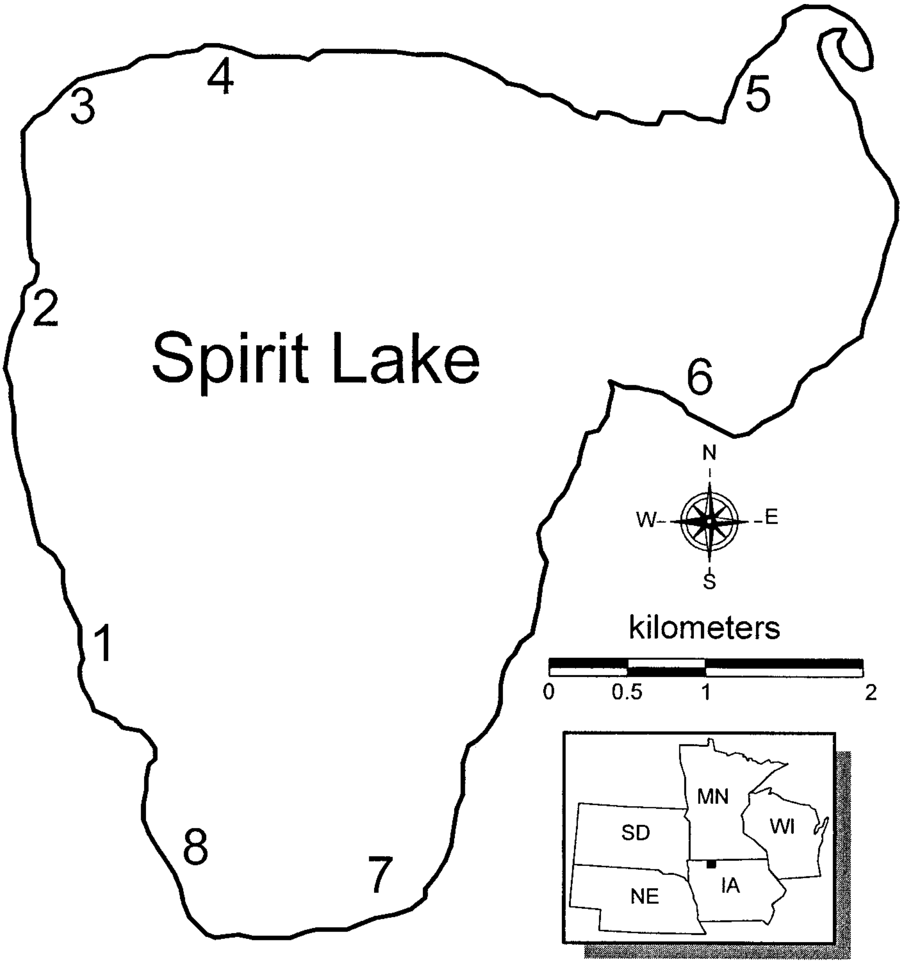

FIGURE 1.—Map of Spirit Lake, Iowa, showing locations of littoral zone sampling stations. Inset map shows location of Spirit Lake in relation to several states in the northcentral United States.

This approach to estimating lengths of unmeasured fish resulted in mean lengths of the entire cohort catches that very closely (within about 1–2 mm) approximated the mean lengths of measured subsamples and also generated realistic variation in individual fish lengths within subsampled cohorts. Weights of these fish were then estimated by using length–weight regressions derived from our measured and weighed specimens.

We estimated capture efficiency by recording the percentage of marked fish that were recaptured in seine samples. Fish were obtained for marking by deploying a small seine (30 × 2 m; 6-mm-bar mesh) inside the larger sampling seine after the latter was in place. Fish collected for marking were placed in tubs with lake water and processed quickly to minimize stress. We marked these fish with partial caudal fin clips and released them in various locations throughout the enclosed area roughly 15 min before pulling the seine to shore. Marked fish showing visible signs of stress were not released and were not included in capture efficiency calculations but were included in the final catch from the large seine. Coming directly from within the area enclosed by the large seine, the marked fish generally were members of the top two to four most abundant species present and roughly reflected the relative abundance of those species in the sampled assemblage. The proportion of marked fish recaptured in the large seine was considered an estimate of capture efficiency for that sample. Effects of number of marked fish, station, year, and month on capture efficiency were analyzed by split-plot analysis of variance (ANOVA) using SAS (SAS Institute Inc. 1988). The split-plot design was used because the same eight stations were sampled throughout the study (Maceina et al. 1994). Capture efficiency was arcsine-square root–transformed for the ANOVA.

Estimating potential prey availability for piscivores.—We examined stomach contents of the predominant piscivorous species in Spirit Lake to determine the size of prey fish eaten relative to predator size. The predominant piscivorous species were northern pike *Esox lucius*, walleye, largemouth bass *Micropterus salmoides*, smallmouth bass *M. dolomieu*, yellow perch *Perca flavescens*, and black crappie *Pomoxis nigromaculatus*. Piscivores longer than 100 mm (TL) were collected in the littoral zone from May through October 1995–1997, mostly at night, by using various gears, including electrofishing, beach seines, fyke nets, gillnets, and angling. Predator fish were measured to the nearest 2.5 mm (TL), stomach-flushed to remove stomach contents (Light et al. 1983), and released alive. Prey fish obtained from stomachs were immediately bagged, labeled, put on ice, and frozen within a few hours. In the laboratory, prey fish were identified and measured to the nearest 1 mm (TL). We used the approach of Knight et al. (1984) to identify and estimate lengths of partially digested prey fish.

We defined the size range of potentially available fish prey as encompassing most of the range of relative prey–predator sizes observed in Spirit Lake. To compare potential prey availability for piscivores of different sizes through time, we plotted mean biomass of potentially available prey against piscivore lengths ranging from 100 to 600 mm, which encompassed most piscivores age 1 and older in Spirit Lake.

Statistical analyses.—The littoral fish response variables we analyzed were density (fish/ha) and biomass (kg/ha) of major species and total fish. We used split-plot ANOVAs to test for effects of station, year, and month (SAS Institute, Inc. 1988; Maceina et al. 1994). Density and biomass data were transformed as $\log_{10}(x + 1)$ to stabilize variances.

Results

Abundance

We estimated capture efficiency in 62 out of 89 total samples. Because of difficulties in capturing large numbers of fish in the smaller seine, we were unable to standardize the numbers and species composition of marked fish used in efficiency estimates. We used only capture efficiency estimates that had been based on at least 10 marked fish. The average number of marked fish per estimate was 54 and ranged from 10 to 623. Most of the marked fish were yellow perch; smaller numbers of bluegill *Lepomis macrochirus*, walleye, spottail shiner *Notropis hudsonius*, black bullhead *Ameiurus melas*, and logperch *Percina caprodes* were used in most estimates. All stations were well represented in our efficiency estimates; the number of estimates per station ranged from five to nine. Capture efficiency averaged 48.1% ± 5.9% (95% C.L.) and did not vary significantly with number of marked fish used, station, year, or month (Table 1). These results suggested that sampling efficiency did not differ consistently among locations, among seines used (in different years), or at different vegetation densities (spring versus summer versus fall). The mean of the seven individual estimates generated with large numbers (≥100) of marked fish, 50.9%, was similar to the overall mean of 48.1%, which, together with the lack of significant effects in the ANOVA, suggested that 50% was a reasonable estimate of capture efficiency for all samples. We therefore multiplied all sample catches by 2 to yield efficiency-corrected estimates of density and biomass.

TABLE 1.—Analysis of variance (ANOVA) testing the effects of number of marked fish, station, year, and month on the capture efficiency of beach seines in the littoral zone of Spirit Lake, Iowa, 1995–1998. Mean squares (MS) are based on Type III sums of squares.

Source	df	MS	*F*	*P*
Number marked	1	0.0109	0.17	0.696
Station	7	0.0978	1.73	0.177
Year	3	0.0093	0.17	0.918
Station × year	15	0.0566	0.86	0.607
Month	4	0.0593	0.90	0.473

We found 26 species in the littoral zone of Spirit Lake (Table 2). Yellow perch and walleye were present in every sample and were among the three most abundant species. Total fish density averaged 10,024 fish/ha, and total fish biomass averaged 276.3 kg/ha. Annual averages for total fish density were 14,389 fish/ha in 1995, 13,381 fish/ha in 1996, 12,300 fish/ha in 1997, and 4,154 fish/ha in 1998. Annual averages for total fish biomass were 352.7 kg/ha in 1995, 331.8 kg/ha in 1996, 212.5 kg/ha in 1997, and 253.0 kg/ha in 1997.

Total fish densities peaked in different months during the 4 years of study, resulting in a significant year × month interaction (Table 3). In 1995 and 1998 the average total densities were greatest in September, whereas in 1996 and 1997 they were greatest in July (Figure 2). In all 3 years that in-

TABLE 2.—Composition, mean density, and mean biomass of fish species in the littoral zone of Spirit Lake, Iowa, 1995–1998. Species are listed in descending order of overall mean density. Means and percentages were calculated from sampling period means.

Species	% of samples in which present	Density (fish/ha)		Biomass (kg/ha)	
		Mean	% of total	Mean	% of total
Yellow perch	100	6,356	63	41.9	15
Bluegill	82	1,268	12	4.6	2
Walleye	100	834	8	38.2	14
Black crappie	85	556	5	6.8	2
Spottail shiner	91	525	5	3.2	1
Largemouth bass	72	181	2	7.9	3
Black bullhead	81	168	2	30.8	11
Logperch	88	108	1	0.4	<1
Smallmouth bass	84	55.8	1	5.7	2
Common carp	81	34.7	<1	83.4	30
Golden shiner *Notemigonus crysoleucas*	34	14.5	<1	0.5	<1
Freshwater drum	70	11.8	<1	19.1	7
Johnny darter *Etheostoma nigrum*	34	10.8	<1	<0.1	<1
Bigmouth buffalo	47	9.4	<1	25.4	9
Pumpkinseed *Lepomis gibbosus*	24	5.7	<1	0.7	<1
White bass *Morone chrysops*	22	5.6	<1	0.7	<1
Northern pike	45	4.7	<1	5.7	2
Shortnose gar *Lepisosteus platostomus*	9	1.2	<1	1.2	<1
Tadpole madtom Noturus gyrinus	7	0.8	<1	<0.1	<1
Green sunfish *Lepomis cyanellus*	7	0.7	<1	<0.1	<1
Muskellunge *Esox masquinongy*	9	0.6	<1	0.7	<1
Emerald shiner *Notropis atherinoides*	3	0.4	<1	<0.1	<1
Longnose gar *Lepisosteus osseus*	1	0.2	<1	0.1	<1
White sucker *Catostomus commersoni*	3	0.1	<1	0.2	<1
Bluntnose minnow *Pimephales notatus*	1	0.1	<1	<0.1	<1
Iowa darter *Etheostoma exile*	1	0.1	<1	<0.1	<1

cluded early sampling (1996–1998), May and June total densities were less than those in subsequent months (Figure 2). Greater densities in July–September correspond primarily to the appearance of the age-0 yellow perch and bluegill (Figure 3). Total fish biomass also peaked in different months over the course of the study, resulting in a significant year × month interaction (Table 4). In 1995, 1996, and 1998 the average total biomass was greatest in September, whereas in 1997 it was greatest in July (Figure 2). The timing of the lowest average total biomass did not show a consistent seasonal pattern; average biomass was lowest in early months (May or June) of 1997 and 1998, whereas average total biomass was lowest in July 1996.

Yellow perch was the predominant species in the littoral zone of Spirit Lake, ranking first in overall average density and second in overall average biomass over the 4-year study (Table 2). Mean annual density of yellow perch was fairly consistent during the first 3 years, but declined greatly in 1998, which resulted in a significant year effect (Table 3). Yellow perch density exhibited a similar seasonal trend in all 4 years of study (Figure 3), resulting in a significant month effect (Table 3). Yellow perch density was generally lowest in the spring and peaked in late summer or fall when age-0 perch were abundant and large enough to be sampled with our seines (Figure 3). Mean annual biomass of yellow perch varied more than threefold over the course of the study, which resulted in a significant year effect (Table 4). The seasonal trend was also significant (Table 4), with mean yellow perch biomass generally lowest in the spring (Figure 3).

Bluegill was the second most numerically predominant species over the 4-year study (Table 2). Bluegill densities varied significantly among years, months, and stations (Table 3). Bluegill densities increased dramatically from the early to later months in each year; their densities in September averaged two to three orders of magnitude higher than in early months (Figure 3), reflecting the appearance of age-0 fish in the littoral zone.

Walleye was the third most predominant species in the littoral zone of Spirit Lake, both numerically and by weight (Table 2). Mean annual density of walleye first increased then decreased over the 4 years of study, and the seasonal trend in walleye density differed among years (Figure 3). This inconsistent seasonal pattern of walleye density

TABLE 3.—ANOVAs testing the effects of station, year, and month on the density of predominant species and all fish in the littoral zone of Spirit Lake, Iowa, 1995–1998. Species are listed in descending order of overall mean density. Mean squares (MS) are based on Type III sums of squares. Asterisks indicate statistical significance at the Bonferroni-corrected *P*-value of 0.006.

Source	df	MS	*F*	*P*
Yellow perch				
Station	7	0.2690	1.37	0.27
Year	3	1.3303	6.79	0.003*
Station × year	20	0.1960	1.31	0.22
Month	4	8.7174	58.29	0.0001*
Year × month	4	0.5161	3.45	0.02
Bluegills				
Station	7	1.2415	9.22	0.0001*
Year	3	0.9803	7.28	0.002*
Station × year	20	0.1346	0.58	0.91
Month	4	30.1650	129.41	0.0001*
Year × month	4	0.1749	0.75	0.56
Walleye				
Station	7	0.3942	2.45	0.05
Year	3	1.6654	10.37	0.0003*
Station × year	20	0.1607	1.64	0.08
Month	4	2.0869	21.33	0.0001*
Year × month	4	0.5915	6.04	0.0005*
All Fish				
Station	7	0.2401	2.23	0.08
Year	3	0.7929	7.37	0.002*
Station × year	20	0.1076	1.63	0.08
Month	4	4.7108	71.41	0.0001*
Year × month	4	0.3670	5.56	0.0009*

among years resulted in a significant year × month interaction (Table 3). Mean annual biomass of walleye varied by roughly twofold over the course of the study, resulting in a significant year effect (Table 4). The seasonal trend was also significant (Table 4), with mean walleye biomass generally increasing over the course of a year (Figure 3).

Common carp was the predominant species by weight in the littoral zone of Spirit Lake (Table 2). The seasonal trend in common carp biomass differed among years, with the greatest biomass appearing in September 1995 and May 1996 (Figure 3), resulting in a significant year × month interaction (Table 4).

Potential Prey Availability for Piscivores

The majority of prey fish ($N = 4{,}396$) found in the stomachs of predator fish in Spirit Lake were roughly in the range of 10–30% of the length of the predator fish that ate them (Figure 4). In all six piscivorous species examined, we found at least one instance of a prey fish at least 50% as long as its predator, but the incidence of prey more than 40% of predator length was very limited in all species (Figure 4) and was less than 3% overall. Although the maximum lengths of prey fish eaten increased with predator size, minimum prey lengths remained relatively constant in all piscivorous species examined. Nineteen species were found as prey in piscivore stomachs, and although tendencies to prey more heavily on certain species were noted for each piscivore species, no evidence suggested that these preferences were due to mouth gape limitation (H. Liao, unpublished data). For example, the most deep-bodied of the major prey fish species, bluegill, was eaten most commonly by the piscivore species with the smallest mouth gape: yellow perch and black crappie (H. Liao, unpublished data). Therefore, we defined potentially available forage fish as consisting of individuals of any species with body length as much as 40% of the body length of piscivores of a given length. Several previous studies (Mauck and Coble 1971; Knight et al. 1984; Hoyle and Keast 1987; Einfalt and Wahl 1997; Porath and Peters 1997) support this definition.

Our graphical analysis of potentially available prey fish biomass illustrates how temporal changes in the fish assemblage produced dramatic changes in the potential availability of prey over time and with piscivore size (Figure 5). For a piscivore of any given size, the range of potentially available prey biomass spanned more than an order of magnitude over time. Likewise, at any given time, the biomass of potentially available prey often varied by an order of magnitude or more with piscivore size. In each sampling month, potentially available prey biomass increased with piscivore size because of the increasing size range of prey fish that the piscivore potentially was able to swallow. However, the rate of increase, as indicated by the variable slopes and inflections in Figure 5, varied considerably. This variation reflected the variation in abundance and size distribution of the littoral assemblage, which in turn were products of the dynamics of the component species. In the 3 years when we sampled in May and June, potentially available prey biomass was uniformly low for nearly all size classes of piscivores (Figure 5). Available prey biomass averaged less than 20 kg/ha for even the largest piscivores in May 1996 and 1997, and in June 1998 available prey biomass averaged less than 20 kg/ha for piscivores as long as 500 mm. The apparent scarcity of fish prey reflected low overall density (Figure 3), which, especially for smaller piscivores, was largely the result of a lack of age-0 fish at this time. July prey

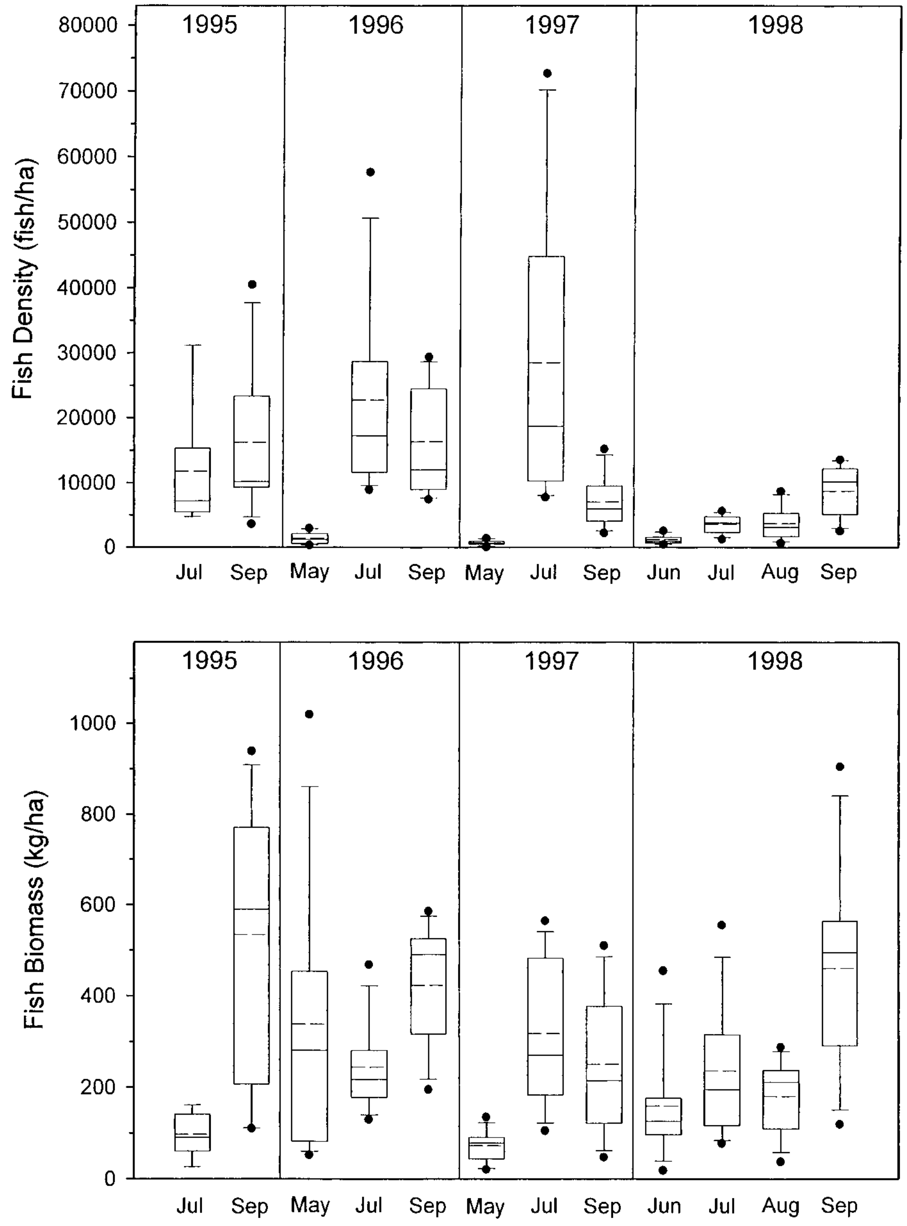

FIGURE 2.—Changes in total fish density (upper panel) and biomass (lower panel) in the littoral zone of Spirit Lake, Iowa, 1995–1998. Boxes encompass interquartile ranges; solid lines within boxes represent medians; dashed lines within boxes represent means; vertical lines above and below boxes extend to 90th and 10th percentiles, respectively, and dots indicate values beyond the 90th and 10th percentiles.

biomass was generally much greater than in earlier months (Figure 5), reflecting the appearance of age-0 fish, especially yellow perch. The steep increases in the July prey availability curves for piscivores between 100 and 150 mm long in 1995–1997 were directly attributable to these age-0 yellow perch cohorts, and the vertical extent of the steep portions of the curves were proportional to the strength of the cohorts at the time of sampling. Secondary steep increases were seen in the July 1996 and 1997 prey availability curves for piscivores between 300 and 350 mm long. These secondary increases correspond in part to the abundant age-1 yellow perch in the littoral zone but

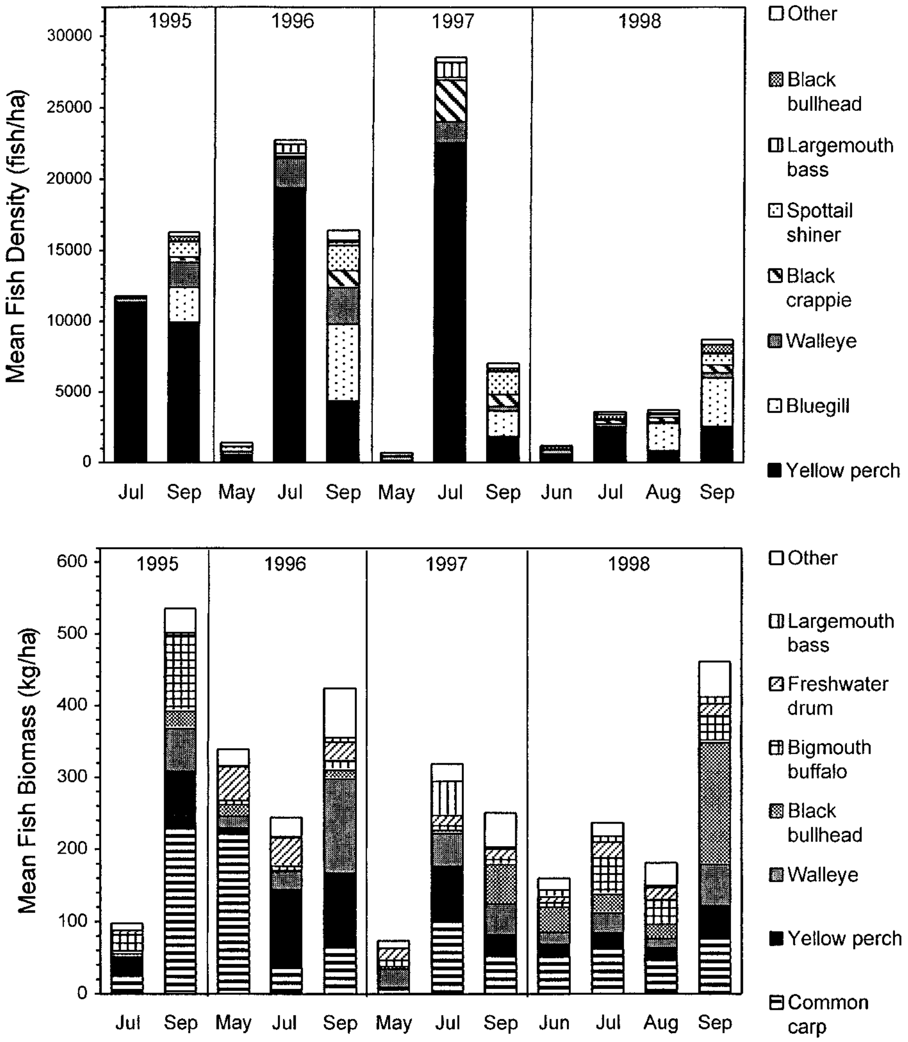

FIGURE 3.—Changes in mean density (upper panel) and biomass (lower panel) of fish species in the littoral zone of Spirit Lake, Iowa, 1995–1998. Species are indicated to the right of the panels.

also reflect vulnerability of several other species to larger piscivores. July average prey biomass potentially available to the largest piscivores varied widely among years, ranging from 17 kg/ha in 1995 to132 kg/ha in 1996 (Figure 5). September prey biomass was also much greater than in May and June, and the availability curves had stepped patterns qualitatively similar to but out of phase with July availability curves (Figure 5). The steeper portions of the September curves were displaced to the right from the corresponding July curves, reflecting growth of large cohorts of potential prey fish. However, September prey availability differed considerably from July availability in magnitude, being more in some years, less in other years, and alternating between more and less in some years, depending on piscivore size. September average prey biomass potentially available to the largest piscivores ranged from 74 kg/ha in 1997 to 180 kg/ha in 1996 (Figure 5).

Discussion

Our estimate of the average total fish biomass in the littoral zone of Spirit Lake, 276.3 kg/ha, was larger than comparable estimates from around the world. Whitfield (1993) reported littoral biomass of 124 kg/ha in an estuarine coastal lake; Pierce et al. (1994) reported littoral biomass ranging from 61 to 269 kg/ha (mean = 135 kg/ha) in 10 lakes in southern Quebec; and Fischer and Eckmann

TABLE 4.—ANOVAs testing the effects of station, year, and month on the biomass of predominant species and all fish in the littoral zone of Spirit Lake, Iowa, 1995–1998. Species are listed in descending order of overall mean biomass. Mean squares (MS) are based on Type III sums of squares. Asterisks indicate statistical significance at the Bonferroni-corrected *P*-value of 0.006.

Source	df	MS	*F*	*P*
Common carp				
Station	7	9.5853	5.42	0.001*
Year	3	6.1935	3.50	0.03
Station × year	20	1.7683	0.77	0.73
Month	4	7.9631	3.48	0.01
Year × month	4	11.1255	4.86	0.002
Yellow perch				
Station	7	0.4243	3.14	0.02
Year	3	0.8115	6.01	0.004*
Station × year	20	0.1350	1.48	0.131
Month	4	5.0750	55.69	0.0001*
Year × month	4	0.3366	3.69	0.01
Walleyes				
Station	7	0.6858	3.68	0.01
Year	3	1.8454	9.89	0.0003*
Station × year	20	0.1866	1.24	0.26
Month	4	2.5480	16.91	0.0001*
Year × month	4	0.5333	3.54	0.01
All Fish				
Station	7	0.3575	3.75	0.009
Year	3	0.4405	4.63	0.01
Station × year	20	0.0952	1.62	0.08
Month	4	0.8561	14.58	0.0001*
Year × month	4	0.4235	7.21	0.0001*

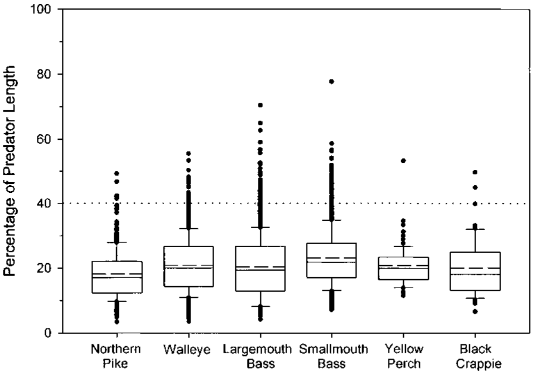

FIGURE 4.—Relative size of prey fish found in the stomachs of major piscivorous species in Spirit Lake, Iowa, 1995–1997. Data show the total lengths of prey fish, expressed as percentages of total lengths of their predator fish. The dotted horizontal line indicates 40% of predator length, which is the value used for estimating potentially available prey fish (i.e., fish no longer than 40% of the length of a predator are considered potential prey). See Figure 2 for an explanation of the boxes.

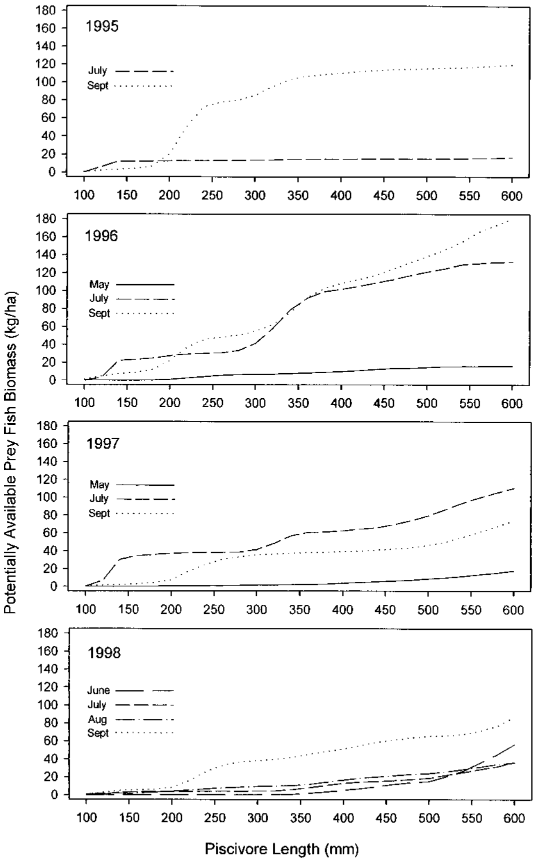

FIGURE 5.—Changes in the mean biomass of potentially available prey fish for piscivores of different lengths in the littoral zone of Spirit Lake, Iowa, 1995–1998.

(1997) reported littoral biomass of 90 kg/ha in Lake Constance, Germany. Our estimate was also near the top of the range of whole-lake biomasses compiled from numerous studies around the world (Randall et al. 1995). In contrast, our estimate of the average total fish density in the littoral zone of Spirit Lake, 10,024 fish/ha, was similar to the only (to our knowledge) comparable littoral zone estimate, 11,950 fish/ha reported for Lake Constance, Germany, by Fischer and Eckmann (1997). Average littoral density in Spirit Lake was nearly twice the average of whole-lake densities from the worldwide data set (Randall et al. 1995).

Although average abundance is useful for comparing systems, seasonal and annual changes in abundance of species in the littoral zone of Spirit Lake may greatly affect energy flow through the food web (Kitchell 1992), which in turn may affect water quality (Carpenter et al. 1985) and the fishery (Shroyer and McComish 1998). Temporal changes in Spirit Lake primarily reflect fluctuations in the predominant species, a phenomenon yellow perch and walleye are known to exhibit in other systems. Populations of yellow perch and the closely related European perch *Perca fluviatilis* are known to fluctuate on more or less regular cycles as a result of various combinations of biotic and abiotic factors (Alm 1952; Forney 1971; Wells 1977; Craig et al. 1979; Sanderson et al. 1999). Long-term angler harvest records for yellow perch in Spirit Lake show a similar cyclic pattern (J. Larscheid, unpublished data). Long-term population records of walleye abundance in Clear Lake, Iowa (Carlander and Payne 1977), and Red Lakes, Minnesota (Cyterski and Spangler 1996), showed large, cyclical fluctuations in abundance, but stocking density (Clear Lake) and commercial harvest (Red Lakes) were believed to account for some of this variation. Fluctuating walleye abundance in the Great Lakes has been shown to vary widely among lakes and regions within lakes because of a variety of biotic, abiotic, and cultural factors (Schneider and Leach 1977). A long-term data set for seven species in Clear Lake, Iowa, showed irregular, asynchronous fluctuation among species (Bulkley 1970). Littoral zone biomass of total fish and the predominant species varied significantly between early and late summer in 10 southern Quebec lakes, but which season had greatest biomass differed among lakes (Pierce et al. 1994). In contrast to our results and those of the other studies cited above, Hatzenbeler et al. (2000) found seasonal differences in only 3 of the 13 most abundant littoral species in five Wisconsin lakes, although yellow perch was one of the seasonally variable species. The yellow perch seasonal pattern they documented was similar to ours, with abundance peaking in midsummer.

The dramatic changes we saw in potentially available prey fish biomass over time in Spirit Lake suggest that feeding conditions for piscivores vary widely from month to month, from year to year, and with piscivore size. For example, the average prey fish biomass available to a 150-mm piscivore, a typical age-1 length of several piscivorous species in Spirit Lake, ranged from less than 1 to more than 30 kg/ha among years and months. A quality-length walleye (Gabelhouse 1984) of 380 mm would have had from 3 to more than 100 kg/ha of potentially available prey fish, depending on the year and month. Despite some broad similarities in seasonal and size-related patterns, potential availability of fish prey in Spirit Lake was highly variable. This variability was closely related to the dynamics of the most abundant species, yellow perch. In Lakes McConaughy and Ogallala, Nebraska, condition of walleye was positively correlated with abundance of appropriately sized prey fish (Porath and Peters 1997). Other studies have shown positive correlations of prey fish availability with growth of walleye (Knight et al. 1984; Hartman and Margraf 1992).

Our analysis of potentially available prey fish biomass also illustrates how differences in the timing of stocking and size of stocked piscivores could affect their ability to find prey and provides evidence in support of a proposed change in walleye stocking regime currently under consideration by the Iowa Department of Natural Resources. The walleye fishery in Spirit Lake is currently augmented by annual stocking of sac-fry in May, and additional stocking of 140-mm-long fingerlings in September in some years (Larscheid 1997). Studies in nearby East Okoboji Lake have documented low survival rates (Larscheid 1995) for 140-mm-long walleye fingerlings stocked in September, prompting development of special hatchery techniques for producing 200-mm fingerlings for stocking at approximately the same time as the 140-mm fingerlings (Larscheid 1997). Although previous work (Santucci and Wahl 1993) suggested that predation is a likely cause of poor survival of the smaller (140-mm) fingerlings, our results indicate that differential prey availability would also favor larger fingerlings. Biomass of potentially available prey would have been nearly 7 times greater for 200-mm fingerlings than 140-mm fingerlings in 1995, over 3 times greater in 1996, 4 times greater in 1997, but only about 1.5 times greater in 1998. In all 4 years, 140-mm fingerlings would have been too small to eat all but the smallest age-0 yellow perch, whereas 200-mm fingerlings would have been large enough to eat most of the size range of these age-0 cohorts. Furthermore, biomass of fish prey potentially available to stocked fingerlings also varied considerably from year to year, such that 140-mm fingerlings would have encountered 3, 7, 2, and 5 kg/ha of available prey, respectively, in the four Septembers of 1995–1998. Our results suggest that some of the annual variation in stocking success may be attributable to variation in prey availability, both in Spirit Lake and in other fisheries maintained or augmented by fingerling stocking. Furthermore, our results illustrate how annual variation in the resident fish assemblage may contribute to annual variation in the relative advantage of stocking different-sized fingerlings as a result of differential prey availability.

Much of the variation in abundance of fishes in Spirit Lake may be the result of variation in intensity of piscivorous consumption. In observational studies of large, natural systems, determining cause and effect is difficult, but several studies in other systems have strongly implicated piscivory as a likely factor contributing to fluctuations or declines in abundance of prey fish species (e.g., Jude and Tesar 1985; Lyons and Magnuson 1987; Knight and Vondracek 1993). The fact that two of the most abundant species in Spirit Lake, walleye and yellow perch, are prey when small but become important piscivores as they grow further complicates our understanding of their dynamics. Studies that examine the dietary and consumption patterns of these populations, combined with modeling studies that link population dynamics of major species in the food web, will be required to fully explore the mechanisms behind these dynamics and determine how they affect strategies for effective management.

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