ECOLOGY OF
FRESHWATER FISH

Diet dynamics of the juvenile piscivorous fish community in Spirit Lake, Iowa, USA, 1997–1998

Abstract – We assessed temporal dynamics and variation among species and age-classes in the diets of age 0 and age 1 piscivorous fish species in Spirit Lake, Iowa, USA during 1997 and 1998. Species included walleye *Stizostedion vitreum*, yellow perch *Perca flavescens*, smallmouth bass *Micropterus dolomieui*, largemouth bass *Micropterus salmoides*, black crappie *Pomoxis nigromaculatus* and white bass *Morone chrysops*. Thirty taxa were identified in diets, including 12 species of fish. We found dramatic differences in diets among species, among age-classes within species and over time. Walleye, largemouth bass, smallmouth bass and white bass were piscivorous at age 0. Black crappie began piscivory at age 1. Yellow perch also began piscivory at age 1, but fish were a very small fraction of age-1 diets. The primary temporal pattern, seen in several species and age-classes, was an increase in piscivory from spring to fall. This pattern was due to the lack of small, age-0 prey fish in spring. Although some patterns were evident, the taxonomic composition of the diets of all species was highly variable over time, making generalizations difficult. A surprising result was the absence of yellow perch in the diet of age-0 walleye, despite their abundance in Spirit Lake and prominence in diets of age-1 walleye and other age 1-piscivores. Age-0 yellow perch were consistently too large to be eaten by age-0 piscivores, which preyed primarily on invertebrates and smaller fish such as johnny darters *Etheostoma nigrum* and age 0 bluegill *Lepomis macrochirus*. This finding suggests that predator-prey interactions and resulting population dynamics may be quite different in Spirit Lake than in other systems dominated by walleye and yellow perch.

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Un resumen en español se incluye detrás del texto principal de este artículo.

Introduction

Piscivore diets are marked by seasonal, annual and ontogenetic variability (Ridenhour 1960; Keast 1977; Colby et al. 1979; Keast 1985; Keast & Eadie 1985; Olson 1996). Prey species composition, abundance and availability are dynamic factors reflected in the diets of their predators (Forney 1974; Knight et al. 1984; Hartman & Margraf 1992; Cobb & Watzin 1998), but piscivores may also exert strong controlling effects on the prey community (Lyons & Magnuson 1987; Northcote 1988; Carpenter & Kitchell 1993). Although the precise sequence of cause and effect may be elusive, piscivores and prey dynamics are clearly linked through piscivory.

Age 0 piscivores typically undergo profound changes in size and diet during their first growing season. Dietary changes are not uniform among species; some piscivores begin eating fish at age 0, whereas others begin at age 1 or later (Keast 1985; Mittelbach & Persson 1998). In addition, age or

size at the onset of piscivory may vary with environmental conditions within species, which in turn may affect growth, survival and recruitment of piscivorous fishes (Summerfelt 1975; Keast & Eadie 1985; Olson 1996).

Juvenile piscivores are often prey as well as predators, and they may be important in the diets of larger piscivores, particularly when other species are less available. As predators their individual consumption is small compared with older age-classes, but their abundance is typically much higher. Because of their great abundance, piscivory by juveniles may exert a large influence on prey species. However, because of the highly complex and dynamic nature of age-0 abundance, the resulting predatory impact of juvenile piscivores is likely to be equally complex and dynamic. A key step in understanding this linkage in lake food webs is documenting the dietary composition and dynamics of this potentially important group.

The purpose of this study was to examine diet dynamics among juvenile age classes of the piscivore community in Spirit Lake, Iowa, USA. Specifically, our objectives were (1) to characterize the diets of age-0 and age-1 members of the dominant piscivorous species in Spirit Lake and (2) to examine seasonal, annual and age-class patterns of dietary similarity among study species.

Study area

Spirit Lake (43°28'N, 95°06'W) is the largest natural lake in Iowa (2229 ha), located near the Iowa-Minnesota border in northwest Iowa, USA. It is eutrophic, has a relatively uniform basin, a mean depth of 5 m and a maximum depth of 7 m. Spirit Lake supports a diverse recreational fishery, including walleye *Stizostedion vitreum* (Mitchell*)*, yellow perch *Perca flavescens* (Mitchell), black bullhead *Ictaluras melas* (Rafinesque), smallmouth bass *Micropterus dolomieui* Lacepede, largemouth bass *M. salmoides* (Lacepede), black crappie *Pomoxis nigromaculatus* (Lesueur), northern pike *Esox lucius* L., muskellunge *Esox masquinongy* Mitchell and white bass *Morone chrysops* (Rafinesque). Yellow perch and walleye are abundant, both in the lake and in the angler's harvest, and are highly sought after by anglers (Pierce et al. in press). Northern pike, muskellunge and white bass are present in low abundance. The fishery has been actively managed by the Iowa Department of Natural Resources for many years and, because natural walleye reproduction in Spirit Lake is limited (McWilliams 1990), the walleye population is augmented through annual fry stocking.

Material and methods

Data collection

We sampled juvenile piscivores for stomach analysis from both the littoral and offshore zones. The littoral zone (<3 m depth) was sampled in both 1997 and 1998; the offshore zone (>3 m depth) was sampled only in 1998. Littoral sampling was done only at night, whereas offshore sampling was done both day and night.

We sampled the littoral zone using large, lampara-style beach seines (Hayes et al. 1996). Sampling was done on 3–4 successive nights in July and September of 1997 and monthly from June to September in 1998. The seine dimensions were 133×4 m in 1997 and 152×4 m in 1998, and the mesh size was 6 mm (bar). Seines had weighted bottom lines and floats along the top lines, were deployed from a boat in a semi-circle extending out from the shoreline and were pulled to shore from both ends simultaneously. The areas sampled were 0.28 ha (133 m seine) and 0.37 ha (152 m seine). The first seine haul began at dark and two or three hauls were made per night. We used eight fixed sampling stations due to the heavily developed shoreline and limited locations for deploying large seines.

We sampled the offshore zone using a semi-balloon otter trawl (Hayes et al. 1996) with a 7.9 m head rope, 38-mm stretch mesh body and 6-mm (bar) mesh cod end. Using an underwater video camera, we determined that the trawl sampled from the bottom to roughly 1 m above the bottom. Trawling was done monthly from May through September in 1998 and was generally completed within a few days of littoral sampling. Day sampling was generally conducted between 0900 and 1400; night sampling between 2200 and 0200. The duration of trawl runs was between 5 and 10 minutes. Locations of trawl runs were haphazardly chosen at depths greater than 3 m throughout the offshore portion of the lake.

We examined diets of age-0 and age-1 individuals of six piscivorous species: black crappie, largemouth bass, smallmouth bass, walleye, white bass and yellow perch. These species account for over 99% of all the juvenile fish that could be considered piscivorous in Spirit Lake (unpublished data). Thus, our study largely encompassed the entire juvenile piscivore community.

In the field, all captured fish were identified to species, counted and measured (TL) to the nearest 1 mm. Samples of age-0 and age-1 specimens of the six piscivorous species were selected randomly from the total seine and trawl catches for stomach analysis. These samples of fish were first anesthetized in tricaine methanesulfonate (Finquel) to prevent regurgitation (Sigler & Sigler 1990) and then

preserved whole in buffered, 10% formalin (Kelsch & Shields 1996). Fish ≥75 mm received a ventral incision to allow formalin into the body cavity (Emmett et al. 1982). For each seine and trawl sample, all fish were identified to species and counted. Subsamples of abundant species and all individuals of the remaining species were weighed (nearest 0.1 g) and measured (TL, nearest 1 mm) in the field.

In the laboratory, all preserved fish were measured (TL, nearest 1 mm) and weighed (nearest 0.1 g). Lengths and weights were corrected for the effects of storage in formalin by assuming 2% shrinkage and weight gains of 10% (stored 14 days or less) or 7% (>14 days) (Parker 1963). Scale samples were taken from a subset of each species and age combination to verify ages. Stomachs were removed and contents identified to order for invertebrates and to species for fish. Only stomachs containing food were counted as samples. Unidentifiable items were noted, but excluded from analysis. Prey items were counted and measured (TL, nearest 0.01 mm) using a dissecting microscope and computerized video image analysis system. We estimated total lengths of partially digested prey fish following Knight et al. (1984). Prey fish lengths were converted to wet weight using regression equations developed from Spirit Lake fish (H. Liao, Iowa State University, personal communication). Invertebrate prey lengths were converted to dry weight using published equations (Bottrell et al. 1976; Smock 1980; Lawrence et al. 1987; Meyer 1989). Invertebrate wet weight was assumed to be five times dry weight (Morin & Dumont 1994) and zooplankton dry weight was assumed to be 7% of wet weight (Lawrence et al. 1987). The diets are presented as percentage by wet weight.

Data analysis

We ran preliminary analyses to examine potential diel differences in the 1998 offshore samples and potential inter-zone differences in the 1998 night samples. Very few diel or inter-zone differences were evident, so data were pooled over diel periods (offshore samples) and zones (1998 samples) in all subsequent analyses.

Because diets of predators typically include several prey taxa, we used a multivariate approach to explore diet similarities among and within the six piscivorous species. The units of comparison in these analyses were the "average" diets of each combination of piscivore species, age class, year and month, which hereafter are referred to as piscivore units. We used mean %W of each prey taxon in the diet of each piscivore unit as input data. %W

data were transformed as ($\log_{10}[x+1]$) prior to analysis. The following analyses were run with all piscivore species together and separately for each species. First, we calculated pair-wise similarities between piscivore units using the Bray-Curtis similarity coefficient (Clarke & Warwick 1994). The resulting similarity matrices were then used as input for non-metric multi-dimensional scaling (MDS) ordinations. Finally, we calculated Pearson correlations of MDS dimension scores with the transformed %W data for each prey taxon to assist interpretation of ordinations. Prey taxa with correlations explaining at least 50% of the variation with dimension scores and significant at the 5% level (i.e., $r \geq 0.7$ and $P < 0.05$) were considered of major importance in defining dimensions and are shown on ordination axes. It is important to understand that the taxa shown on axes are not necessarily the most important taxa in the diets, but are the most important in defining differences in diets among the units being compared. Similarity matrices and MDS ordinations were performed using PRIMER (Carr 1997; Clarke & Warwick 1994), and correlations were run using the CORR procedure of SAS (SAS Institute Inc. 1988). See Clarke & Warwick (1994) for a detailed discussion of this approach and procedures.

We tested for differences in diets among piscivore species and age classes using a multivariate analysis of similarities (ANOSIM), which is roughly analogous to a univariate 2-way ANOVA, but uses a nonparametric, randomization approach (Clarke & Warwick 1994). ANOSIM uses a similarity matrix as input, in this case Bray-Curtis similarities among all piscivore units and is based on random permutations of similarities among and within main effect groupings. The species main effect had five levels (white bass omitted from this test because only one age class was sampled), and ANOSIM calculated pair-wise tests among species in addition to the overall test of differences across all species. The ANOSIM was performed using PRIMER (Carr 1997; Clarke & Warwick 1994). See Clarke & Warwick (1994) for a detailed discussion of this approach to testing for differences in multivariate responses.

A drawback of the ANOSIM approach compared with conventional ANOVA is limitation of the number of main effects tested. To include temporal effects along with the species and age effects tested with ANOSIM, we ran a multi-way ANOVA on the proportion of fish in the diets, with species, age, year and month as main effects. We used the mean proportion of fish in the diet of each piscivore unit as input data, and proportion of fish was arcsine-square root transformed. The ANOVA was run using the GLM procedure of SAS (SAS Insti-

tute Inc. 1988), and Tukey tests were used to test for pair-wise differences between species.

Finally, to complement our MDS ordinations of diet similarity, we calculated conventional diet overlap indices between all species pairs within each age class. We used the percentage overlap index of diet overlap (Krebs 1999), which was calculated as:

$$\alpha = 1 - 0.5 \left(\sum_{x=i}^{n} |p_{xi} - p_{yi}| \right),$$

where n=number of prey categories, p_{xi}=proportion by weight of prey category i in the diet of species x, and p_{yi}=proportion by weight of prey category i in the diet of species y. Possible values range from 0 to 1; a value of 0 indicates no overlap, whereas a value of 1 indicates complete overlap. Mean proportions of each prey category in each sampling period were used in calculations.

Results

Diet composition

Juvenile fish diets in Spirit Lake included 30 recognizable taxa, including 12 species of fish and 18 invertebrate taxa (Table 1). We identified 19 taxa in the diets of juvenile walleye (Table 1). Age-0 walleye were strongly piscivorous, with darter species (primarily johnny darter *Etheostoma nigrum* Rafinesque, but also Iowa darter *Etheostoma exile* [Girard]) contributing 49% of the total diet by weight (Table 1) and monthly proportions ranging from 0 to 65% (Fig. 1). In both years, zooplankton (cladocerans) was a major part of the diet in July, whereas bluegill *Lepomis macrochirus* Rafinesque and logperch *Percina caprodes* (Rafinesque) were significant components later in the summer. No age-0 walleye were captured in May. Surprisingly, although

Table 1. Diet proportions by weight for age 0 and age 1 piscivorous fish species in Spirit Lake, Iowa, 1997–1998. Sampling period means were averaged to give an overall mean for each species and age. Piscivore species are abbreviated as: BLC=black crappie, LMB=largemouth bass, SMB=smallmouth bass, WAE=walleye, WB=white bass, YP=yellow perch. N=number of non-empty stomachs.

Piscivore species:		BLC	LMB	SMB	WAE	WB	YP
					Age 0		
Prey taxon		N=65	54	58	107	29	102
black bullhead	*Ictalurus melas*	0	0	0	0	0	0
black crappie	*Pomoxis nigromaculatus*	0	0	0.1651	0	0	0
bluegill	*Lepomis macrochirus*	0	0.0599	0.0088	0.1354	0	0
bluntnose minnow	*Pimephales notatus* (Rafinesque)	0	0	0	0	0	0
freshwater drum	*Aplodinotus grunniens*	0	0	0	0.0287	0.5037	0
Iowa darter	*Etheostoma exile*	0	0	0	0.0822	0	0
johnny darter	*Etheostoma nigrum*	0	0.7735	0.5868	0.4851	0	0
bass	*Micropterus spp.*	0	0	0.0027	0	0	0
logperch	*Percina caprodes*	0	0.0297	0.0020	0.1253	0	0
spottail shiner	*Notropis hudsonius* (Clinton)	0	0	0	0.0002	0	0
walleye	*Stizostedion vitreum*	0	0	0	0.0041	0	0
yellow perch	*Perca flavescens*	0	0	0	0	0	0
Amphipoda		0.1004	0.0159	0.0429	0.0068	0.0173	0.0128
Branchiopoda		0.0016	0	0	0	0	0
Cladocera		0.3864	0.0515	0.0261	0.1101	0.2042	0.6397
Coleoptera		0.0013	0	0.0021	0	0	0
Copepoda		0.4744	0.0173	0.0061	0.0046	0.2584	0.3023
Decapoda		0	0	0	0	0	0
Diptera		0.0272	0.0055	0.0723	0.0163	0.0087	0.0446
Ephemeroptera		0.0003	0.0040	0.0177	0	0	0
Gastropoda		0	0	0	0.0009	0	0
Hemiptera		0	0.0025	0.0057	0	0	0
Hirudinea		0	0	0.0016	0	0	0
Hydracarina		0	0	0	0.0002	0	0
Hymenoptera		0	0.0058	0.0051	0	0	0
Lepidoptera		0	0	0	0	0	0
Megaloptera		0	0	0	0	0	0
Odonata		0	0.0338	0.0472	0	0	0
Plecoptera		0	0	0	0	0	0
Trichoptera		0.0083	0.0004	0.0079	0	0.0077	0.0007

age-0 yellow perch were abundant in diets of age-1 piscivores of several species, none were found in age-0 walleye stomachs.

Age-1 walleyes fed primarily on yellow perch (56% of total diet by weight) and ate nearly 100% fish, except for May 1998, when their diet was entirely invertebrate and 96% insect (dipteran) (Fig. 2, Table 1). Monthly means for yellow perch in age-1 walleye diet ranged from 0% to 84%. The proportion of yellow perch declined through the 1998 season and freshwater drum *Aplodinotus grunniens* (Rafinesque) and darters were important in the diet in September 1998. No age-1 walleyes were examined in 1997.

We identified 19 taxa in the diets of juvenile smallmouth bass (Table 1). Age-0 smallmouth bass were piscivorous; several fish species were eaten and johnny darters were 59% of the total diet, primarily in August and September 1998 (Fig. 1, Table 1). However, the percentage of fish in the diet varied widely between years; e.g. 0% fish in September 1997, but 100% fish in September 1998. Their diet was also diverse; several invertebrate taxa were eaten and diets in September 1997 and July 1998 were composed of invertebrates exclusively.

Age-1 smallmouth bass were mainly piscivorous, consuming primarily bluegill, logperch, walleye, and yellow perch (Fig. 2). However, decapods were 37% of the total diet and 82% in July 1998. It should be noted, however, that smallmouth bass sample sizes are small and no age-1 smallmouth bass were examined in 1997.

We identified 19 taxa in the diets of juvenile black crappie (Table 1). Age-0 black crappie stomach samples contained no fish; their diet was almost entirely zooplankton and amphipods (Fig. 1). Copepods were 47% of their total diet and monthly means ranged from 26% to 56% (Table 1). Proportions varied and no seasonal trend was evident. No age-0 crappie were collected in May.

Age-1 black crappie diets included a total of 17 taxa (Table 1). They consumed both fish and invertebrates and were increasingly piscivorous from July through September 1998 (Fig. 2). Amphipods were the dominant invertebrate prey; however, insects (trichopterans) were 82% of the diet in July 1997. Bluegill were the primary prey fish, but

Table 1. Continued.

| Prey taxon		Piscivore species: BLC	LMB	SMB	WAE	WB	YP
				Age 1			
		N=65	49	16	103	0	114
black bullhead	*Ictaluras melas*	0.0037	0	0	0	—	0
black crappie	*Pomoxis nigromaculatus*	0	0.0656	0.0600	0.0309	—	0
bluegill	*Lepomis macrochirus*	0.0830	0.0835	0.2401	0.0298	—	0
bluntnose minnow	*Pimephales notatus*	0.0617	0	0	0	—	0
freshwater drum	*Aplodinotus grunniens*	0.0046	0.0198	0	0.2251	—	0
Iowa darter	*Etheostoma exile*	0	0	0	0.0222	—	0
johnny darter	*Etheostoma nigrum*	0	0.1359	0.0398	0.0554	—	0
bass	*Micropterus spp.*	0	0.0069	0.0104	0.0005	—	0
logperch	*Percina caprodes*	0.0132	0.0570	0.2127	0.0009	—	0
spottail shiner	*Notropis hudsonius*	0	0	0	0.0253	—	0
walleye	*Stizostedion vitreum*	0	0.0115	0.0183	0.0023	—	0
yellow perch	*Perca flavescens*	0.0372	0.5810	0.0164	0.5635	—	0.0013
Amphipoda		0.3364	0.0018	0.0012	0.0002	—	0.0547
Branchiopoda		0	0	0	0	—	0
Cladocera		0.1319	0.0001	0.0005	0.0014	—	0.3601
Coleoptera		0	0	0	0	—	0.0007
Copepoda		0.0011	0	0	0	—	0.0019
Decapoda		0	0.0002	0.3726	0	—	0.2719
Diptera		0.0731	0.0089	0.0007	0.0400	—	0.2556
Ephemeroptera		0.1229	0.0030	0	0.0019	—	0.0348
Gastropoda		0	0	0	0	—	0.0064
Hemiptera		0.0286	0.0167	0.0264	0	—	0.0007
Hirudinea		0.0081	0.0039	0.0008	0.0003	—	0.0006
Hydracarina		0	0	0	0	—	0
Hymenoptera		0	0.0001	0	0	—	0
Lepidoptera		0	0.0035	0	0	—	0.0004
Megaloptera		0.0017	0	0	0	—	0
Odonata		0.0585	0	0	0	—	0
Plecoptera		0.0002	0	0	0	—	0.0001
Trichoptera		0.0342	0.0004	0	0.0001	—	0.0109
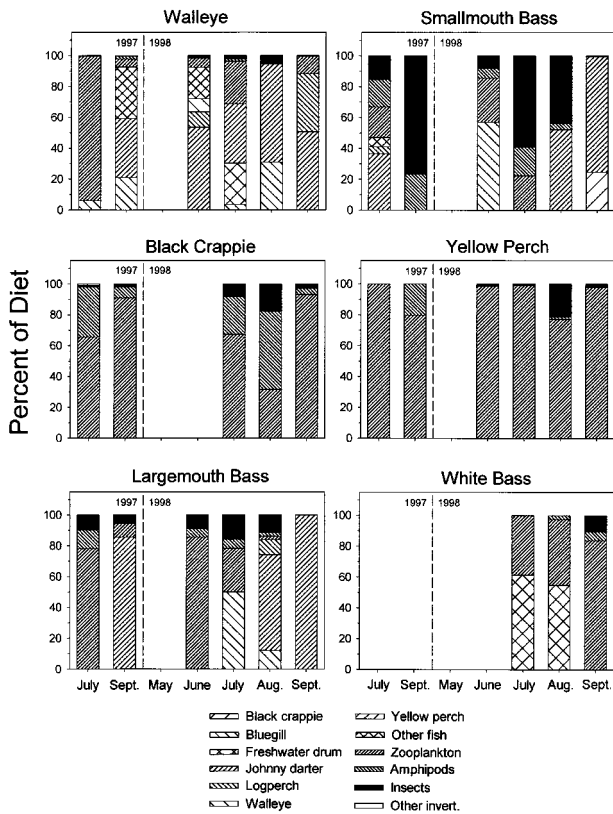
Fig. 1. Diet composition (by weight) of age 0 piscivorous fish species in Spirit Lake, Iowa, USA, 1997–1998. Prey taxa are indicated by shading and cross-hatching at the bottom of the figure.

found almost entirely in September 1998. No results are given for September 1997 or May 1998 due to low sample sizes.

We identified 14 taxa in the diets of juvenile yellow perch (Table 1). Age-0 yellow perch consumed only five taxa and zooplankton were 94% of the total diet (Table 1, Fig. 1). No fish were found in the diet. Cladocerans were 23% to 100% of age-0 perch diet and their proportion was highest in July of both years, but no other trend is apparent.

Age-1 yellow perch ate a diverse diet of invertebrates, but only a single fish (yellow perch) was found in all the stomachs examined. Dipterans were the major prey early in the season, followed by cladocerans later (Fig. 2). Cladocerans were 36% of the total diet (Table 1).

We identified 20 taxa in the diets of juvenile largemouth bass (Table 1). Age-0 largemouth bass were increasingly piscivorous through the season in both years (Fig. 1). Zooplankton dominated the diet early, while darters were the dominant prey later and comprised 77% of the overall diet (Table 1). A seasonal progression of zooplankton, then darters was evident (Fig. 1).

Age-1 largemouth bass were strongly piscivorous

(Fig. 2). Yellow perch accounted for 58% of the overall diet, but darters and bluegill were important prey in September of both years (Table 1, Fig. 2). However, invertebrates (primarily hemipterans) dominated the diet in May 1998 before age-0 fish became available. Sample size for August 1998 was insufficient, and it should be noted that sample sizes are relatively small for most periods.

We identified six taxa in the diets of juvenile white bass (Table 1). Age-0 white bass were piscivorous; however, age-0 freshwater drum were the only fish consumed and represented 50% of the total diet (Table 1). No fish prey were found in September, when zooplankton were 82% of the diet (Fig. 1). Age-0 freshwater drum grew rapidly and were too large to be consumed in September (personal observation). Zooplankton were the major invertebrate prey in all months. No white bass were captured in 1997.

Walleye, both age 0 and age 1, was the most strongly piscivorous species; fish were 86% and 96% of their total diets, respectively (Table 1). Walleye, smallmouth bass and largemouth bass of both age classes and age-1 black crappie showed a trend of increasing piscivory during the season, with invertebrate prey important early and fish dominating the diet later (Figs. 1, 2). Age-0 white bass were an exception to this trend, relying solely on invertebrates in September (Fig. 1).
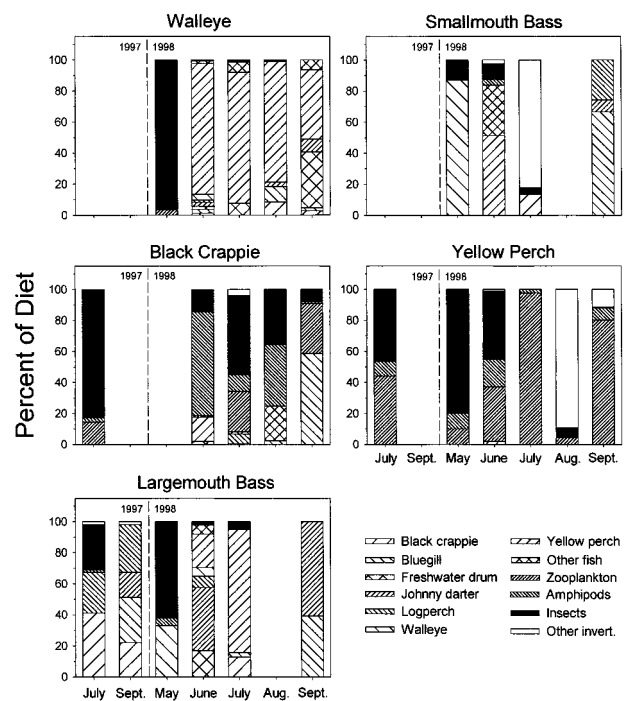

Fig. 2. Diet composition (by weight) of age 1 piscivorous fish species in Spirit Lake, Iowa, USA, 1997–1998. Prey taxa are indicated by shading and cross-hatching at the lower right corner of the figure.
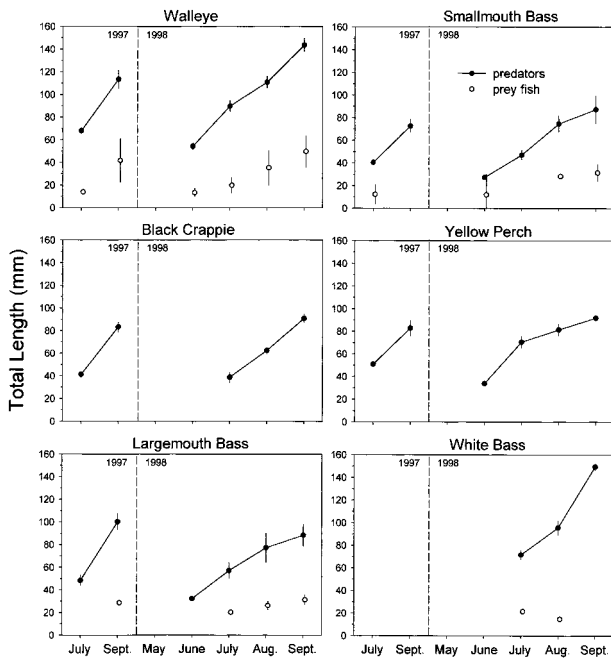
Fig. 3. Mean total lengths of age 0 piscivorous fish species and prey fish eaten in Spirit Lake, Iowa, USA 1997–1998. Error bars are 95% confidence intervals. Symbols indicating predators and prey are shown in the upper right panel.
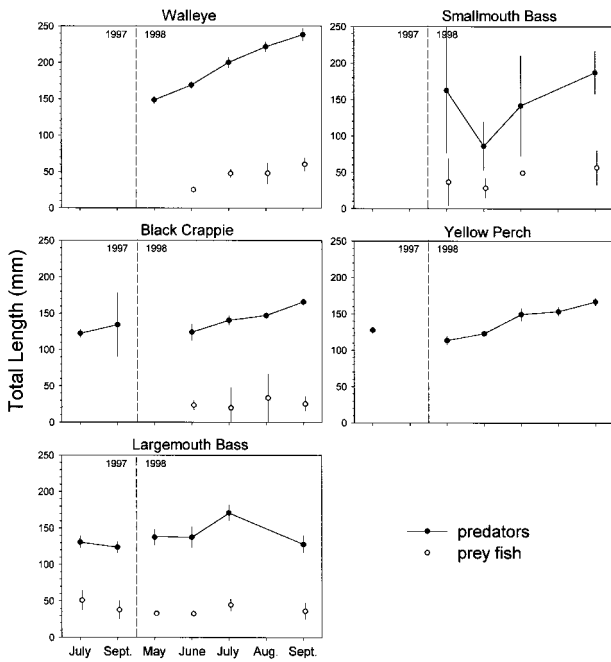

Fig. 4. Mean total lengths of age 1 piscivorous fish species and prey fish eaten in Spirit Lake, Iowa, USA 1997–1998. Error bars are 95% confidence intervals. Symbols indicating predators and prey are shown at the lower right corner of the figure.

Size of prey fish in diets

The mean lengths of prey fish in the diets of juvenile piscivores ranged from 12 mm in age-0

smallmouth bass in July 1997 to 60 mm in age-1 walleye in September 1998 (Fig. 3, 4). Over the course of the study, prey fish in the diets of age-0 piscivores ranged from 5 to 70 mm, averaging 25 mm, and prey fish in the diets of age-1 piscivores ranged from 10 to 89 mm, averaging 33 mm. Lengths of prey fish ranged from 7 to 65% of the lengths of their predators, but very few were greater than 40%. The mean length of prey fish eaten generally increased with predator size in both age-0 and age-1 piscivores (Fig. 3, 4). Sizes of prey fish eaten were fairly similar among piscivore species at any given time, despite substantial differences in predator size (Fig. 3, 4).

Diet similarities

MDS ordination of the Bray-Curtis similarity matrix for all piscivore units provided a graphical representation of the similarities in the composition and relative importance of prey taxa in the diets of age 0 and age 1 piscivore species over the course of the study (Fig. 5). The stress value of the ordination was 0.15, which indicates a reasonably good
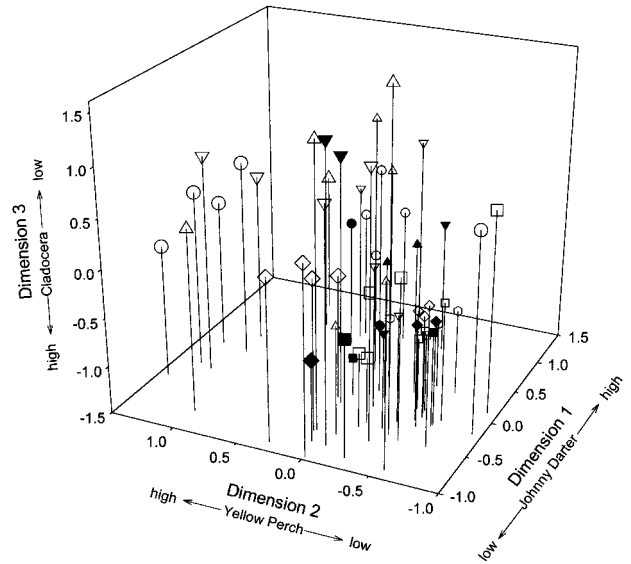

Fig. 5. Overall MDS ordination of diet similarities among age 0 and age 1 piscivorous fish species in Spirit Lake, Iowa, USA, 1997–1998. Ordination was based on a matrix of pair-wise Bray-Curtis similarity coefficients constructed from transformed ($\log_{10}[x+1]$) mean %W values of all prey taxa for each piscivore unit. Prey taxa listed along ordination axes were significantly ($P<0.05$) correlated with dimension scores, accounted for at least 50% of the variation ($r \geq 0.7$), and are included to facilitate interpretation. Small symbols indicate age 0; large symbols indicate age 1; filled symbols indicate 1997; open symbols indicate 1998. Piscivore species are indicated by symbol type as follows: walleye=circles, yellow perch=squares, smallmouth bass=upright triangles, largemouth bass=upside-down triangles, black crappie=diamonds, white bass=hexagons.
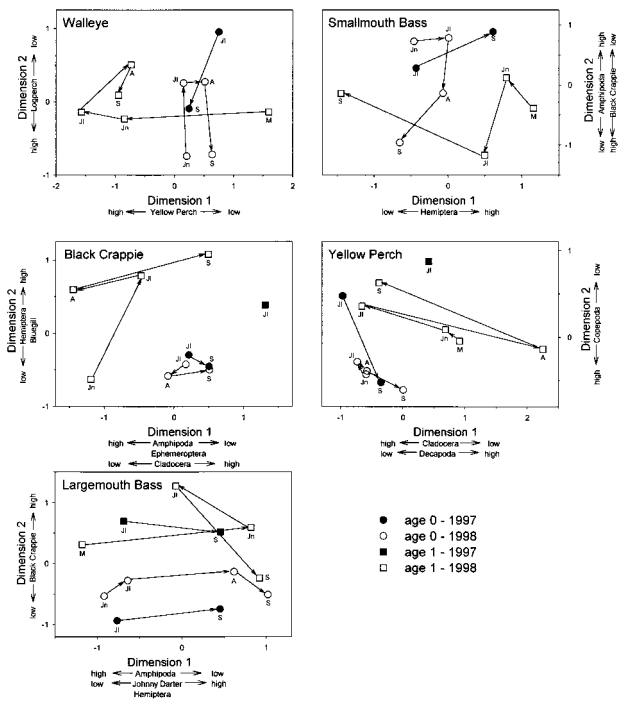
Fig. 6. Within-species MDS ordinations of diet similarities among age 0 and age 1 piscivorous fish species in Spirit Lake, Iowa, USA, 1997–1998. Ordinations were based on a matrix of pairwise Bray-Curtis similarity coefficients constructed from transformed ($\log_{10}[x+1]$) mean %W values of all prey taxa for each piscivore unit. Prey taxa listed along ordination axes were significantly ($P < 0.05$) correlated with dimension scores, accounted for at least 50% of the variation ($r > 0.7$), and are included to facilitate interpretation. Key to symbols is located in lower right corner of figure. Letters near symbols indicate month: M=May, Jn=June, Jl=July, A=August, S=September.

representation of the diet similarities among units in three-dimensional space (Clarke & Warwick 1994). Although few clear separations of piscivore species or age classes are evident, Fig. 5 illustrates a broad continuum in diet composition within the juvenile piscivore community. A large aggregation of units at the lowest values of all three dimensions (lower front corner of Fig. 5), consisting primarily of both age classes of yellow perch, age-0 black crappie, and a few age-0 units of the other species, had similar diets. These diets generally included high percentages of invertebrates, especially cladocerans and little or no fish prey. Units appearing elsewhere in Fig. 5, consisting primarily of both walleye age classes and age-1 units of largemouth and smallmouth bass, had diets that generally included greater percentages of fish prey such as yellow perch and johnny darter.

These patterns in the three-dimensional ordination (Fig. 5) of diet similarities within the juvenile piscivore community were supported by our ANOSIM results. The overall test of differences across all piscivore species was significant at the

0.0% level, and pairwise tests indicated significantly different diets between walleye and yellow perch, walleye and black crappie, yellow perch and smallmouth bass, and yellow perch and largemouth bass. The overall test of diet differences between age classes was also significant at the 0.0% level.

Although significant patterns of species and age class difference are evident in Fig. 5, there is also ample evidence of within-species variability and among-species overlap in diets. Numerous examples can be found in Fig. 5 where diets from different species and age classes were more similar than those of the same species and age class from a different month or year. For example, diets of age-1 walleye in four of the 5 months sampled in 1998 were similar, appearing to the far left of Fig. 5, primarily as a result of high percentages of yellow perch in their diets. In the remaining month, May, age-1 walleye diet was very different from age-1 walleye diets in the other months, but very similar to May 1998 age-1 yellow perch diets, both appearing to the far right of Fig. 5. This similarity was due to high percentages of dipterans in age-1 diets of both species in May, when the small age-0 fishes that otherwise make up the majority of age-1 walleye diets were not yet available.

Within-species MDS ordinations of Bray-Curtis diet similarities illustrated how diets differed between age classes and how the diets of each age class changed over time (Fig. 6). (No ordination of white bass diets was attempted, because data were limited to age-0 diets during 3 months in 1998). The stress values of these ordinations ranged from 0.12 to 0.07, indicating good representation of the diet similarities among units in two-dimensional space (Clarke & Warwick 1994). In all five piscivorous species shown in Fig. 6, there was reasonably
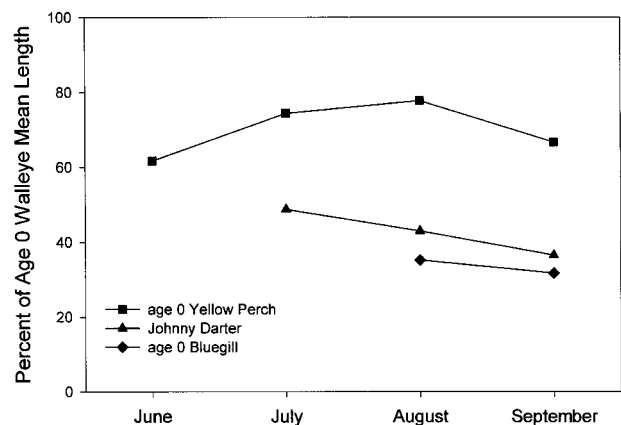

Fig. 7. Length of potential prey fish species as a percentage of age 0 walleye length in Spirit Lake, Iowa, USA, 1997–1998. All values were calculated using mean total lengths.

Table 2. Percentage Overlap index of diet overlap (proportion by wet weight) for age 0 and age 1 piscivorous fish species in Spirit Lake, Iowa, 1997–1998. A value of 1 indicates complete overlap; a value of 0 indicates no overlap. Species codes as in Table 1. Number following code is age.

Diet comparison	Sample period						
	Jul-97	Sep-97	May-98	Jun-98	Jul-98	Aug-98	Sep-98
blc0-lmb0	0.49	0.09	–	–	0.42	0.05	0
blc0-smb0	0.16	0.09	–	–	0.41	0.10	0.003
blc0-wae0	0.37	0.07	–	–	0.31	0.06	0.12
blc0-yp0	0.32	0.82	–	–	0.60	0.39	0.80
lmb0-smb0	0.17	0.001	–	0.37	0.30	0.55	0.75
lmb0-wae0	0.78	0.44	–	0.07	0.35	0.75	0.51
lmb0-yp0	0.73	0.09	–	0.87	0.29	0.04	0
smb0-wae0	0.10	0.02	–	0.07	0.24	0.57	0.51
smb0-yp0	0.07	0.20	–	0.30	0.23	0.23	0.004
wae0-yp0	0.89	0.07	–	0.07	0.29	0.06	0.12
wb0-blc0	–	–	–	–	0.39	0.34	0.46
wb0-lmb0	–	–	–	–	0.15	0.05	0
wb0-smb0	–	–	–	–	0.15	0.03	0.004
wb0-wae0	–	–	–	–	0.42	0.01	0.12
wb0-yp0	–	–	–	–	0.31	0.44	0.61
Age 0 mean	0.41	0.19		0.29	0.33	0.24	0.27
blc1-lmb1	0.03	–	–	0.18	0.03	–	0.39
blc1-smb1	–	–	–	0.20	0.04	–	0.59
blc1-wae1	–	–	–	0.18	0.02	0.04	0.02
blc1-yp1	0.36	–	–	0.29	0.28	0.07	0.33
lmb1-smb1	–	–	0.46	0.29	0.16	–	0.47
lmb1-wae1	–	–	0.07	0.31	0.79	–	0.10
lmb1-yp1	0.09	–	0.12	0.03	0.001	–	0
smb1-wae1	–	–	0.03	0.52	0	–	0.10
smb1-yp1	–	–	0.03	0.07	0	–	0
wae1-yp1	–	–	0.78	0.03	0	0.01	0
Age 1 mean	0.16		0.25	0.21	0.13	0.04	0.20

clear separation between age-0 and age-1 diets. This observation is in general agreement with the significant age-class effect in the ANOSIM. Monthly changes in age-0 diets tended to be similar between years, although this varied from black crappie, which showed very similar monthly changes to smallmouth bass, which showed fairly divergent monthly changes in the 2 years. Age-1 diets tended to vary more over the course of the study than did age-0 diets, as indicated by a greater spread of age-1 points on ordinations (Fig. 6). Age-1 diets also tended to change more dramatically from month to month than did age-0 diets, as indicated by longer lines separating points. Few yearly comparisons of age-1 diets are possible because age-1 data from 1997 are absent for walleye and smallmouth bass and limited for the other species. However, a roughly similar diet change from July to September was seen in both years in age-1 largemouth bass. As did the ordination of all piscivore units together (Fig. 5), ordinations of single species (Fig. 6) reflected large variation in diets among age classes and over time.

Our ANOVA testing the effects of species, age, year and month on proportion of fish in the diet suggested differences that corresponded well with both our MDS and ANOSIM results. The ANOVA results for species ($P<0.0001$) and age ($P=0.003$) were similar to the ANOSIM results, as were the Tukey tests which grouped walleye, largemouth bass and smallmouth bass together with higher proportions of fish in the diets, and yellow perch and black crappie together with lower proportions of fish. The first group was strongly piscivorous at age 0, whereas the second group was not piscivorous at age 0. White bass were not significantly different from any other species, but the small number (3) of white bass units in our data set limit comparisons with the other species. The month effect was significant ($P=0.01$), which was evident in the clear seasonal changes in diets we observed in all species (Figs. 1, 2, 6). The year effect was not significant ($P=0.15$).

Diet overlap

Diet overlap values were in broad agreement with our MDS ordinations (Table 2, Figs. 5, 6). Diet overlaps among age-0 piscivore units were generally higher than among age-1 piscivore units; for

every month, age-0 mean overlap was higher than age-1 means. Overlap among the more piscivorous species, walleye, largemouth bass and smallmouth bass, tended to be higher than between these species and the less piscivorous species, black crappie and yellow perch. Overlap among black crappie and yellow perch tended to be higher than with the other species. Seasonal changes in diet overlap reflected seasonal divergences in diet proportions; this was especially pronounced in species-age class pairs where one became increasingly piscivorous and the other remained invertivorous. For example, walleye, largemouth and smallmouth bass began eating fish at age 0, and overlap values among them increased during the season. However, overlap values decreased between these three species and age-0 black crappie and yellow perch, which were not piscivorous. Overlap values between age-0 black crappie and yellow perch were relatively high, reflecting diets including only invertebrates and in roughly comparable proportions. Diet overlap among age-1 walleye, largemouth bass and smallmouth bass was variable, however, reflecting variable levels of piscivory and differences in fish species eaten.

Discussion

Our results demonstrated a broad continuum in the onset and level of piscivory among species that eventually become piscivorous in Spirit Lake. Walleye, largemouth bass, smallmouth bass and white bass were piscivorous at age 0, whereas black crappie began piscivory at age 1 and yellow perch were not piscivorous at either age. Our results indicated similarities and differences among these species and age classes that suggest some important potential implications for food-web interactions and resulting growth and population dynamics of piscivorous species in Spirit Lake.

The onset of piscivory is a crucial point in the life history of piscivores. Species that begin piscivory at age 0 may maximize growth and increase survival by switching to a fish diet as soon as possible; if piscivory is delayed they may incur large costs in terms of growth and survival (Keast & Eadie 1985; Olson 1996; Mittelbach & Persson 1998). Species with a later onset of piscivory may be limited in their growth potential and exhibit lower growth, but not necessarily survival (Buijse 1992; Mittelbach & Persson 1998).

Availability of suitable sizes of prey fish is an important factor in the establishment of year-class strength for piscivores that become piscivorous during their first year of life (Wicker & Johnson 1987; Buijse & Houthuijzen 1992; van Densen et al. 1996). Gape size is an important factor limiting

piscivore prey selection (Hoyle & Keast 1987, 1988); gape size increases as a fish grows and widens the range of available prey. If age-0 growth is dependent on piscivory, fish of a vulnerable size need to be present throughout the growing season to maximize growth. If vulnerable prey fish are not available, a "bottleneck" may occur where growth is slowed or stopped, and piscivores must rely on alternate prey or starve.

Alternatively, insufficient prey fish may result in cannibalism within a cohort or by older conspecifics. In Oneida Lake, New York, when age-0 yellow perch were not abundant, cannibalism among walleye was a significant source of mortality and may have determined year class strength (Forney 1974, 1976; Chevalier 1973). We observed walleye cannibalism only in June 1998, when walleye were 9% of age-0 total diet by weight and 4% of age-1 diet. This may indicate a shortage of vulnerable prey fish in early summer and may also reflect growth depensation among age 0, where some members of a cohort have a size advantage that allows them to consume smaller conspecifics.

Piscivores follow a dietary progression after hatching from eating zooplankton, to larger invertebrates, to fish (Mittelbach & Persson 1998). Growth rates typically increase after fish begin piscivory (Summerfelt 1975; Timmons & Shelton 1980; Keast & Eadie 1985; Olson 1996; van Denson et al. 1996) and species that switch to piscivory at smaller sizes show better first-year growth and eventually become larger (Mittelbach & Persson 1998).

In species that begin piscivory during their first growing season, there is a significant growth advantage for individuals that are able to make this shift early in the season. Largemouth bass begin piscivory at age 0, and individuals that begin feeding on fish early exhibit higher growth than those beginning piscivory later (Keast & Eadie 1985; Olson 1996). Olson (1996) found that largemouth bass that began eating fish later than others in the same cohort could not maintain a sufficient size advantage over age-0 bluegill, their primary prey. These individuals reverted to eating invertebrates and grew more slowly than individuals who switched early and were able to continue eating fish.

We observed age-0 piscivory in walleye, largemouth bass, smallmouth bass and white bass, but there was considerable variation in the proportion of fish consumed through the season. Age-0 largemouth bass grew rapidly, and the seasonal increase in piscivory seemed to be a response to increasing prey availability as largemouth bass size increased. However, declines in piscivory among other species are more difficult to explain. Declines

in piscivory for smallmouth bass may be due to temporarily high abundance of alternate prey. Invertebrates dominated age-0 smallmouth bass diet in September 1997 and July 1998 and age-1 smallmouth bass showed a temporary decline in fish consumption in July 1998, when decapods were the major prey. Alternatively, observed declines in piscivory could also be in response to lowered availability of prey fish.

The decline in piscivory by age-0 white bass during 1998 appeared to be due to the rapid growth (personal observation) of its primary fish prey, age-0 freshwater drum. Bailey & Harrison (1945) observed a similar switch from fish to invertebrates by white bass in Clear Lake, Iowa, in response to decreased prey fish abundance in fall. However, we captured age-0 white bass along with small darters offshore and in the littoral zone, as well as small age-0 bluegill, and it is unclear why these were not found in white bass stomachs. Freshwater drum were consumed by several species and ages in 1998 but grew rapidly in late summer (personal observation) and, in September, were found only in age-1 walleye diet.

The diets of the juvenile predators in our study consisted of a mix of numerous prey taxa, suggesting that multivariate analyses were appropriate to explore similarities and differences among species, age-classes and over time. Our MDS and ANOSIM analyses separated the six study species into two broad juvenile feeding groups. The first group was characterized by high percentages of fish in diets and included walleye, largemouth bass and smallmouth bass. These species all began piscivory in age 0 and consistently fed on high percentages of fish thereafter. The second group consisted of yellow perch and black crappie, which were not piscivorous at age 0 and were either not piscivorous at age 1 (yellow perch) or included lower percentages of fish in their age-1 diets (black crappie) than the more strongly piscivorous species. White bass were difficult to categorize due to limited data.

Comparisons between age classes within species showed clear differences between age-0 and age-1 diets. Age-0 piscivores generally had higher overlap values and greater similarities compared to age-1 piscivores. Our MDS ordinations also showed consistent separation between age-0 and age-1 diets for most species. Gape size limits the availability of prey and gape increases as fish grow. Larger fish, then, have more potential prey types and sizes to choose from, whereas smaller fish have fewer options. The effect of age was highly significant in the ANOVA of proportion of fish prey in diets, indicating that as piscivores age, they show an increasing preference for fish prey, yet still utilize a wide spectrum of prey taxa.

Largemouth bass, smallmouth bass and walleye began eating fish in their first summer and, in general, as fish increased in the diet of these species, diet overlap decreased with age-0 perch and age-0 crappie, which ate only invertebrate prey. White bass were an exception; they switched from eating age-0 freshwater drum as their major prey in July and August 1998 to mainly cladocerans in September 1998.

In Oneida Lake, New York, Mills & Forney (1981) found that age-0 yellow perch growth was higher when they fed on *Daphnia* than when they switched to eating other invertebrates. Although zooplankton provide the lowest energy density among invertebrates (Cummins & Wuycheck 1971) and *Daphnia* are smaller than other invertebrate prey, *Daphnia* apparently provided a higher energy return, presumably due to lower search or capture costs. However, Cobb & Watzin (1998) found that fast yellow perch growth depended on availability of benthic invertebrates.

In Spirit Lake, zooplankton dominated age-0 yellow perch diets and were a major part of age-1 diets, although larger invertebrate taxa were found concurrently in other species' stomachs and seemingly should have been equally available to yellow perch. Larger prey have been shown to confer energetic advantages (Werner 1979), and larger invertebrates were important in age-1 perch diet, but if zooplankton are highly abundant, it may be advantageous for yellow perch of both ages to prey on them.

Although age-0 yellow perch were abundant in Spirit Lake during our study, none appeared in the diets of age-0 walleye. Age-0 walleyes in Spirit Lake preyed heavily on johnny darters, which accounted for about half of their diet overall. This was surprising, given that several previous studies found age-0 walleyes preying primarily on age-0 yellow perch when they were present, and age-0 walleye growth positively correlated with age-0 yellow perch abundance (Maloney & Johnson 1955; Forney 1974; Carlander & Payne 1977; Kempinger & Carline 1977). In Sparking Lake, Wisconsin, age-0 walleye fed primarily on age-0 yellow perch in years when they were abundant; when perch were not abundant, darters and small cyprinids were important in walleye diets (Lyons & Magnuson 1987). In a laboratory study, Campbell (1998) found that small walleyes often selected relatively small prey from a range of available sizes, and generally preferred prey that were <=40% of their own length. Both age-0 and age-1 walleyes in Spirit Lake showed a similar preference for prey fish <= 40% of their own length.

In Spirit Lake, the lack of yellow perch in age-0 walleye diets appeared to be due to the large size

of yellow perch relative to alternate prey species. The mean length of age-0 yellow perch ranged from 62 to 78% of age-0 walleye mean length, compared with 37 to 49% for johnny darters and 32 to 35% for age-0 bluegill (Fig. 7). Since the overwhelming majority of fish found in stomachs of age-0 walleyes and other juvenile piscivores in Spirit Lake were <40% of predator length, it appears that age-0 yellow perch avoid predation by age-0 walleye in Spirit Lake by maintaining a size advantage.

Age-0 yellow perch growth is rapid in Spirit Lake, as mean lengths throughout the summer months are greater than reported in other lakes (Keast 1977; Carlander 1997). September mean lengths of age-0 yellow perch in 1995 and 1996 ranged from 82–91 mm in Spirit Lake (unpublished data), which correspond closely to the mean lengths we documented in 1997 and 1998. This suggests that the size advantage of age-0 yellow perch and resulting freedom from predation by age-0 walleye may be a regular phenomenon in Spirit Lake. Consequently, the major interaction driving population and fishery dynamics of yellow perch and walleye in most systems may be fundamentally different in Spirit Lake.

Age-0 walleye growth in Spirit Lake is near the mean of other lakes in the northern and central part of its range (Colby et al. 1979; Carlander 1997). September mean lengths during the period from 1995 to 1998 in Spirit Lake ranged from 118–142 mm (unpublished data). Despite the size-related unavailability of age-0 yellow perch, the primary prey in many other systems, reliance on alternate prey appears sufficient to allow roughly normal growth of age-0 walleye in Spirit Lake.

The proportion of fish in age-0 walleye diets was lowest in July of both years, when cladocerans, and to a lesser extent other invertebrates, increased in the diet. Yellow perch diets in July of both years were also dominated by cladocerans, and cladocerans were prominent in the July diets of other species as well. We collected no data on zooplankton abundance, but the convergent diet patterns among several piscivore species suggests either very high cladoceran abundances in July, low abundances of other prey taxa, or a combination of both. Although some potential prey fish taxa were present in July, they may have been largely invulnerable to age-0 walleye. Age-0 perch and johnny darter mean lengths in July 1998 were 74% and 49% of age-0 walleye mean length, respectively. Thus, virtually all the age-0 yellow perch and many of the johnny darters would have been too large for walleye to prey on.

Age-0 bluegill were abundant from August to September (Pierce et al. in press), and age-0 walleye diet was composed of 31% bluegill in August 1998. However, no small potential prey fishes other than johnny darters and age-0 yellow perch were abundant in June or July. Since age-0 yellow perch are too large to be eaten by age-0 walleye, johnny darters appear to be the only abundant, alternative prey fish in early to midsummer in Spirit Lake. In Sparkling Lake, Wisconsin, alternate prey fishes such as darters and small cyprinids are important food for age-0 walleye, when yellow perch abundance declines (Lyons & Magnuson 1987). In Spirit Lake, age-0 perch were abundant, but due to their rapid growth are essentially unavailable to age-0 walleyes. Thus, johnny darters may constitute a crucial link in the dietary progression of age-0 walleyes, preventing a growth "bottleneck" early in the summer. Without an abundance of small johnny darters, age-0 walleye would presumably have to prey largely on invertebrates, potentially reducing growth. In turn, reduced growth may increase predatory mortality, including cannibalism, and reduce over-winter survival (Chevalier 1973; Forney 1974, 1976). It is not unreasonable to speculate that year-to-year variation in johnny darter abundance in Spirit Lake could, in part, determine year class strength of walleye, much like age-0 perch do in other systems. We are not aware of studies of annual variation in abundance of johnny darters, but such studies may prove valuable in Spirit Lake and other systems where johnny darters are important as prey.

Resumen

Evaluamos las dinámicas y la variación entre especies y clases de edad en las dietas de edad 0 y edad 1 entre los especies piscívoros en Spirit Lake, Iowa, Estados Unidos durante 1997 y 1998. Los especies incluyen leucoma *Stizostedion vitreum*, perca amarilla *Perca flavescens*, róbalo de boca pequeña *Micropterus dolomieui*, róbalo de boca grande *Micropterus salmoides*, pomosio negro *Pomoxis nigromaculatus*, y róbalo blanco *Morone chrysops*. 30 grupos taxonómicos se identificaron en dietas, incluyendo 12 especies de pez. Encontramos diferencias dramáticas de las dietas entre especies, entre clases de edad dentro de la misma especie y en un cierto plazo. Los leucomas, el róbalo de boca grande, el róbalo de boca pequeña y róbalo blanco eran piscívoros de la edad 0. Los pomosios negros empezaron a ser piscívoro a la edad 1. Ningún piscívoro se documentó por clase de edad para la perca amarilla. El patrón temporal primario, considerado entre varios especies y clases de edad, era un incremento de piscívoros desde la primavera hasta el otoño. Este patrón era debido a la falta de peces de rapiña pequeños de edad 0 en la primavera. Aunque algunos patrones fueron evidentes, la composición taxonómica de las dietas de todas las especies variaba altamente en un cierto plazo, haciendo las generalizaciones difíciles. Un resultado sorprendente fue la ausencia de perca amarilla en la dieta de los leucomas de la edad 1, a pesar de su abundancia en Spirit Lake y la prominencia en las dietas de los leucomas de la edad 1 y otros piscívoros de la edad 1. Las percas amarillas de la edad 0 fueron consecuentemente demasiados grandes para que los coman los piscívoros de la edad 0, que rapiñaron fundamentalmente en los

invertebrados y peces pequeños así como los eteostomas johnny *Etheostoma nigrum* y los bluegill *Lepomis macrochirus* de la edad 0. Este descubrimiento sugiere que las interacciones entre los peces de rapiña y su rapiña y las dinámicas de la población resultante puede ser bastante diferente en Spirit Lake que en otros sistemas dominados por los leucomas y las percas amarillas.

Acknowledgments

References

Bailey, R.M. & Harrison, H.M. Jr. 1945. The fishes of Clear Lake, Iowa. Iowa State College Journal of Science 20: 57–77.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. & Weglenska, T. 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24: 419–456.

Buijse, A.D. 1992. Dynamics and exploitation of unstable percid populations. Ph.D. thesis, Agricultural University, Wageningen, the Netherlands.

Buijse, A.D. & Houthuijzen, R.P. 1992. Piscivory, growth, and size-selective mortality of age 0 pikeperch (*Stizostedion lucioperca*). Canadian Journal of Fisheries and Aquatic Sciences 49: 894–902.

Campbell, E.A. 1998. Predation by small walleyes on yellow perch: effects of prey size distribution. Transactions of the American Fisheries Society 127: 588–597.

Carlander, K.D. 1997. Handbook of freshwater fishery biology, volume 3. Ames, Iowa: Iowa State University Press.

Carlander, K.D. & Payne, P.M. 1977. Year-class abundance, population, and production of walleye (Stizostedion vitreum vitreum) in Clear Lake, Iowa, 1948–74, with varied fry stocking rates. Journal of the Fisheries Research Board of Canada 34: 1792–1799.

Carpenter, S.R. & Kitchell, J.F., eds. 1993. The trophic cascade in lakes. Cambridge, UK: Cambridge University Press.

Carr, M.R. 1997. PRIMER user manual. London: Natural Environment Research Council.

Chevalier, J.R. 1973. Cannibalism as a factor in first year survival of walleye in Oneida Lake. Transactions of the American Fisheries Society 4: 739–744.

Clarke, K.R. & Warwick, R.M. 1994. Change in marine communities: an approach to statistical analysis and interpretation. London: Natural Environment Research Council. 144 pages.

Cobb, S.E. & Watzin, M. C. 1998. Trophic interactions between yellow perch (*Perca flavescens*) and their benthic prey in a littoral zone community. Canadian Journal of Fisheries and Aquatic Sciences 55: 28–36.

Colby, P.J., McNicol, R.E. & Ryder, R.A. 1979. Synopsis of biological data on the walleye (*Stizostedion vitreum vitreum*). FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis.

Cummins, K.W. & Wuycheck, J.C. 1971. Caloric equivalents for investigations in ecological energetics. International Association of Theoretical and Applied Limnology Proceedings 18: 1–158.

Emmett, R.T., Muir, W.D. & Pettit, R. D. 1982. A device for injecting preservative into the stomach of fish. Progressive Fish-Culturist 44: 107–108.

Forney, J.L. 1974. Interactions between yellow perch abundance, walleye predation, and survival of alternate prey in Oneida Lake, New York. Transactions of the American Fisheries Society 103: 15–24.

Forney, J.L. 1976. Year-class formation in the walleye (*Stizostedion vitreum vitreum*) population of Oneida Lake, New York, 1966–73. Journal of the Fisheries Research Board of Canada 33: 783–792.

Hartman, K.J. & Margraf, F.J. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. Transactions of the American Fisheries Society 121: 245–260.

Hayes, D.B., Ferreri, C.P. & Taylor, W.W. 1996. Active fish capture methods. In: Murphy, B.R. & Willis, D.W., eds. Fisheries techniques. Bethesa, MD: American Fisheries Society,, pp. 193–220.

Hoyle, J.A. & Keast, A. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Canadian Journal of Zoology 65: 1972–1977.

Hoyle, J.A. & Keast, A. 1988. Prey handling time in two piscivores, *Esox americanus vermiculatus* and *Micropterus salmoides*, with contrasting mouth morphologies. Canadian Journal of Fisheries and Aquatic Sciences 66: 540–542.

Keast, A. 1977. Diet overlaps and feeding relationships between the year classes in the yellow perch (*Perca flavescens*). Environmental Biology of Fishes 2: 53–70.

Keast, A. 1985. The piscivore feeding guild of fishes in small freshwater ecosystems. Environmental Biology of Fishes 12: 119–129.

Keast, A. & Eadie, J.M. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Transactions of the American Fisheries Society 114: 204–213.

Kelsch, S.W., & Shields, B. 1996. Care and Handling of Sampled Organisms. Pages 121–55 *in* Murphy, B. R. & Willis, D. W. editors. Fisheries Techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Kempinger, J.J. & Carline, R.F. 1977. Dynamics of the walleye (*Stizostedion vitreum vitreum*) population in Escanaba Lake, Wisconsin, 1955–72. Journal of the Fisheries Research Board of Canada 34: 1800–1811.

Knight, R.L., Margraf, F.J. & Carline, R.F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Transactions of the American Fisheries Society 113: 677–693.

Krebs, C.J. 1999. Ecological methodology, 2nd edn. Menlo Park, CA: Benjamin Cummungs. California.

Lawrence, S.G., Malley, D.F., Findlay, W.J., MacIver, M.A. & Delbaere, I.L. 1987. Method for estimating dry weight of freshwater planktonic crustaceans from measures of length and shape. Canadian Journal of Fisheries and Aquatic Sciences 44: 264–274.

Lyons, J. & Magnuson, J.J. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Transactions of the American Fisheries Society 116: 29–39.

Maloney, J.E. & Johnson, F.H. 1955. Life histories and interrelationships of walleye and yellow perch, especially during their first summer, in two Minnesota lakes. Transactions of the American Fisheries Society 85: 191–202.

McWilliams, R.H. 1990. Large natural lakes. Federal Aid to Fish Restoration Completion Report F-95-R. Des Moines, Iowa: Iowa Department of Natural Resources.

Meyer, E. 1989. The relationship between body length parameters and dry mass in running water invertebrates. Archiv für Hydrobiologie 117: 191–203.

Mills, E.L. & Forney, J.L. 1981. Energetics, food consumption,

and growth of young yellow perch in Oneida Lake, New York. Transactions of the American Fisheries Society 110: 479–488.

Mittelbach, G.G. & Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. Canadian Journal of Fisheries and Aquatic Sciences 55: 1454–1465.

Morin, A. & Dumont, P. 1994. A simple model to estimate growth rate of lotic insect larvae and its value for estimating population and community production. Journal of the North American Benthological Society 13(3): 357–367.

Northcote, T.G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. Canadian Journal of Fisheries and Aquatic Sciences 45: 361–379.

Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77: 179–190.

Parker, R.R. 1963. Effects of formalin on length and weight of fishes. Journal of the Fisheries Research Board of Canada 20: 1441–1455.

Pierce, C.L., Sexton, M.D., Pelham, M.E., Liao, H. & Larscheid, J.G. In press. Dynamics of the littoral fish assemblage in Spirit Lake, Iowa and implications for prey availability for piscivores. North American Journal of Fisheries Management 21: in press.

Ridenhour, R.L. 1960. Abundance, growth and food of young game fish in Clear Lake, Iowa, 1949 to 1957. Iowa State College Journal of Science 35: 1–23.

SAS Institute, Inc. 1996. SAS user's guide, ver. 6.12. Cary, North Carolina: SAS Institute.

Sigler, W.F. & Sigler, J.W. 1990. Recreational Fisheries. Reno, Nevada: University of Nevada Press.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Journal of Freshwater Biology 10: 375–381.

Summerfelt, R.C. 1975. Relationship between weather and year-class strength of largemouth bass.In: Stroud, R. H. & Clepper, H., eds. Black bass biology and management. Washington, DC: Sport Fishing Institute pp. 166–174.

Timmons, T.J. & Shelton, W.L. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama-Georgia. Transactions of the American Fisheries Society 109: 176–186.

van Densen, W.L.T., Ligvoet, W. & Roozen, R.W.M. 1996. Intra-cohort variation in the individual size of juvenile pike-perch, *Stizostedion lucioperca*, and perch, *Perca fluviatilis*, in relation to the size spectrum of their food items. Annales Zoologici Fennici 33: 495–506.

Werner, E.E. 1979. Niche partitioning by food size in fish communities. In: Clepper, H., ed. Predator-prey systems in fisheries management. Washington, DC: Sport Fishing Institute, pp. 311–322.

Wicker, A. M. & Johnson, W.E. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. Transactions of the American Fisheries Society 116: 264–271.