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Ontogenetic and habitat-related changes in diet of late larval and juvenile suckers (Catostomidae) in Upper Klamath Lake, Oregon

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ONTOGENETIC AND HABITAT-RELATED CHANGES IN DIET OF LATE LARVAL AND JUVENILE SUCKERS (CATOSTOMIDAE) IN UPPER KLAMATH LAKE, OREGON

Douglas F. Markle[1] and Kale Clauson[2]

ABSTRACT.—We describe ontogenetic patterns in the diets of shortnose and Lost River suckers (15.8–92.8 mm standard length) from Upper Klamath Lake in summer 1999. Both species made a transition from surface and planktonic prey to benthic prey at about 20–30 mm standard length, corresponding to the approximate size of the juvenile morphological transition. Surface prey was dominated by adult chironomids and undigestable pollen, while benthic prey was dominated by larval chironomids, chydorids, and ostracods. In the 15–20-mm size class, pollen made up >75% of food particles in 68% of specimens, and only 2 specimens in this size class lacked any pollen grains. A better understanding of the prey selection process in larval suckers is needed to determine the importance of this potential source of starvation. The planktonic prey eaten during the surface-to-benthic feeding transition were widely distributed in the lake, suggesting that larvae use emergent vegetation primarily as a refuge from predators. On a numerical basis, crustaceans and larval chironomids contributed most to the diets of larger juveniles. In specimens >40 mm, shortnose suckers ate more Tanytarsini and Lost River suckers ate more chironomid pupae and chydorids. In specimens >40 mm there was a strong habitat-related difference in diet: specimens collected in offshore samples ate more chironomid larvae and pupae, harpacticoid copepods, and chydorids, whereas onshore specimens ate more cyclopoid copepods and invertebrate eggs. The transition from onshore to offshore habitat appears to occur over a broad size range of about 40–90 mm.

Key words: Chasmistes brevirostris, Deltistes luxatus, *feeding, larvae, juveniles, pollen, chironomids, ontogeny.*

Upper Klamath Lake, Oregon, is a highly eutrophic system (Kann and Smith 1999, Bradbury et al. 2004) with a near monoculture of the cyanobacterium *Aphanizomenon flos-aquae* in summer. The lake also harbors 2 endangered fishes, *Chasmistes brevirostris* (shortnose sucker) and *Deltistes luxatus* (Lost River sucker), whose variable and apparently low recruitment success contributed to their original listing (USFWS 1988, 2002, Markle and Cooperman 2002). Both species are long lived and fecund (Scoppettone and Vinyard 1991). Although most spawning occurs in inlet tributaries, the Williamson and Sprague Rivers, larvae drift downstream to the lake (Cooperman and Markle 2003) and utilize nearshore lake habitats in summer (Cooperman and Markle 2004). As they grow, juveniles tend to be more broadly dispersed in nearshore rocky and open lake, mud-bottom habitats.

Ontogenetic changes in feeding are an expected consequence of larval fish growth and habitat changes (Gerking 1994, Osenberg et al. 1994, Fuiman 2002). Feeding is a difficult task for larval fish because most are visual planktivores, limited to a field of detection of 1–2 body lengths, and their planktonic prey are somewhat transparent (Britt et al. 2001). Cobcraft et al. (2001) demonstrated that feeding decreased over 30% when fish larvae were subjected to a change from clear water to water with algae-induced turbidity. Feeding changes that increase diet breadth may also be critical to survival (Fuiman 2002). For instance, growth of larval suckers makes larger prey available to them while their ability to feed on smaller prey is retained. Little is known about food habits of larval and juvenile suckers in Upper Klamath Lake. Cooperman and Markle (2004) found that larger larvae with full stomachs were associated with emergent macrophytes (*Scirpus, Sparganium,* and *Polygonum*) rather than submergent macrophytes, woody vegetation, or open water. They did not describe food habits but suggested that larval suckers may accumulate in emergent macrophytes because their food is more abundant and accessible there or because the habitat provides better physical cover from predators and wind-generated waves. Maximizing growth rate

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and minimizing predation risk are both necessary components of habitat selection by larval and juvenile fish (Werner 2002); however, partitioning the relative importance of these components can be difficult.

In this study we describe ontogenetic and habitat-related changes in diet for late larval and juvenile shortnose and Lost River suckers. Our purpose is to describe the dietary component of each species' niche to determine if ontogenetic changes in diet differ between species or areas of the lake.

METHODS

Fish Collections

All fish were collected in 1999 as part of long-term monitoring of sucker year-classes in Upper Klamath Lake. Four sampling techniques were used: fixed-site larval trawls, fixed-site beach seines, stratified random nearshore cast-nets, and stratified random offshore otter trawls. We conducted 6 surveys every 3rd week from April to July with a 0.8 m × 1.5-m larval trawl with 1.0-mm bar mesh (LaBolle et al. 1985). Two samples were collected from each of 10 fixed sites in Upper Klamath Lake and 6 of those sites were used for this study (Fig. 1). Larval samples were preserved in 10% formalin for a maximum of 48 hours, and switched to 50% isopropanol for long-term storage. Four beach seine (6.1 m long with a 2 m × 2 m × 2-m bag and 4.8-mm bar mesh) surveys were conducted every 3rd week from June to August. Age-0 suckers were preserved in 95% ethanol and transferred to fresh ethanol within 24 hours. The last 3 larval trawl surveys were concurrent with the first 3 beach seine surveys. Concurrent cast-net (5-m-diameter multifilament net with 6.3-mm bar mesh) and otter trawl (5-m semi-balloon otter trawl with 16-mm bar mesh and 6-mm bar mesh liner with attached tickler chain) surveys were conducted at 3-week intervals in August, September, and October. Cast-net and otter trawl surveys were based on random sampling with the cast-net surveys stratified on 8 shoreline substrate categories.

Size-based subsamples were selected for each species over the range 15.8–92.8 mm standard length (SL). For each species we examined up to 10 individuals in each 5-mm size class from 15 mm to 40 mm SL (n = 99, $\bar{x}$ = 27.7) and up to 17 individuals in each 5-
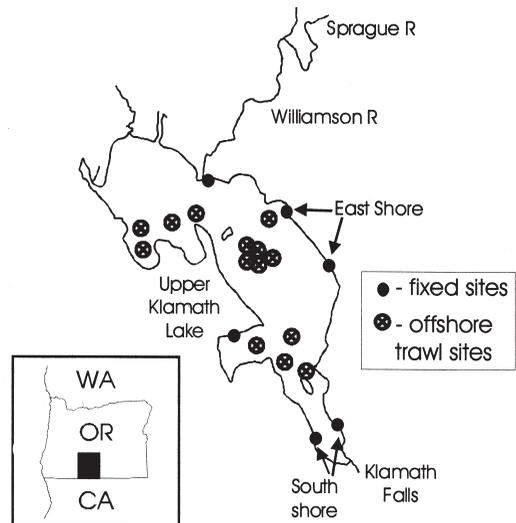

Fig. 1. Map of Upper Klamath Lake showing distribution of sample sites where larval and juvenile suckers were collected for food habits study in 1999. Most shoreline specimens were collected in the east shore and south shore areas. Inset shows location relative to states of Oregon and California.

mm size class from 41 mm to 70+ mm SL (n = 180, $\bar{x}$ = 57.0). When possible, specimens in a size class came from different samples and different areas (Table 1). For size classes >40 mm we also attempted to examine up to 7 individuals from each of 3 areas in the lake: south shore (south and east of Caledonia Marsh, including Buck Island; n = 70, $\bar{x}$ = 58.5 mm), east shore (between Hagelstein Park and Modoc Point; n = 50, $\bar{x}$ = 54.3 mm) and offshore (n = 60, $\bar{x}$ = 57.5 mm; Fig. 1). Although we primarily refer to size groups, we use the terms larva and juvenile broadly to distinguish individuals with (juvenile) and without (larva) the adult complement of fin rays. For both species the morphological transition occurs at about 20–25 mm SL (unpublished data).

Food Habits Analysis

In the laboratory, specimens were weighed to the nearest 0.1 g and dissected to remove the gut (esophagus to beginning of the intestine). Total stomach volume was approximated by measuring the length, width, and depth of the intact gut to the nearest millimeter. Gut contents were removed, rinsed with 70% ethanol, identified to the lowest possible taxon

TABLE 1. Distribution of specimens of shortnose (SNS) and Lost River (LRS) suckers used for food habits study by area and size group (in millimeters).

Size group	East		South		Other		Offshore		Total
	SNS	LRS	SNS	LRS	SNS	LRS	SNS	LRS	
15	9	9	1	0	0	0	0	0	19
20	6	8	4	1	0	1	0	0	20
25	7	10	3	0	0	0	0	0	20
30	5	6	3	4	2	0	0	0	20
35	7	7	1	3	2	0	0	0	20
40	5	2	5	4	0	0	1	5	22
45	6	6	5	4	0	0	6	6	33
50	6	3	5	7	0	0	6	5	32
55	5	4	5	4	0	0	2	4	24
60	5	2	5	7	0	0	6	5	30
65	2	3	5	5	0	0	2	5	22
70	0	1	5	4	0	0	2	5	17
TOTAL	63	61	47	43	4	1	25	35	279

using standard references (Merrett and Cummins 1996, Pennak 1953), and counted under a dissecting scope. Composites of sand particles, filamentous algae, and other digested material were categorized as goop. Percent total volumes were estimated for major food categories (Chironomidae, Crustacea, eggs, goop, and other) by estimating their surface area on a 5 mm × 5-mm, grid-marked petri dish. Major prey taxa were also assigned to nominal water column categories called surface, planktonic, and benthic (based on Williams and Feltmate [1992], Pennak [1953], and Pinder [1995]), and the percentage of food items in each category were calculated for each fish specimen. Within the benthic category, taxa were assigned to either vegetated habitat or rocky habitat (based on Williams and Feltmate [1992], Pennak [1953], and Hazel [1969]). Identified samples were archived in 70% ethanol.

Statistical Analyses

Data were analyzed using STATGRAPHICS Plus 5.0 (Manugistics 2001). Because we were interested in sources of variation in diet, our primary approach was a multiway factorial ANOVA using species, size class, and location as predictor variables for stomach contents. Data were grouped and values for degrees of freedom for error were large (usually >250), so our analyses should not have violated multivariate normality and should have been robust to any violations of normality (Tabachnick and Fidell 2001). In addition, we examined the distribution of residuals after analyses and found little or no deviations from normality. Because multiple comparisons inflate Type I error, we used a Bonferroni adjustment (Tabachnick and Fidell 2001) to display confidence intervals in graphical summaries.

RESULTS

Combined stomach contents were dominated by chironomids, cyclopoid copepods, chydorids, pollen, and invertebrate eggs (Table 2). Mean number of prey taxa per stomach was lowest in the 15-mm size group (3.7 taxa) and highest in the 55-mm size group (5.5 taxa). In both species the greatest change was the ontogenetic change in relative contribution of surface to benthic prey (Fig. 2). In the multiway factorial ANOVA, species had no effect ($P > 0.74$) on the proportion of surface or benthic prey consumed, whereas size group did ($P < 0.001$). A transition from surface to benthic food items occurred in the 20–30-mm size groups (Fig. 2).

The surface prey eaten by larvae was adult chironomids (Table 2). In addition, many larvae and some juveniles consumed undigestable pollen, which declined from 74.6% of all food particles in the 15–20-mm size class to <13% in the 25–40-mm size classes (Fig. 3A). In the 15–20-mm size class, pollen made up >75% of food particles in 13 of 19 specimens, and only 2 specimens in this size class lacked any pollen grains. Twenty pollen grains, a subsample, had diameters of 39–98 µ with paired bladders suggesting they were a mixture of pine, spruce, and fir (Woodhouse 1935). Only

TABLE 2. Combined summary of prey taxa, percent of total stomach volume, and total counts in stomachs of shortnose and Lost River sucker larvae and juveniles from Upper Klamath Lake, 1999. Assignment of prey taxa to water column category and benthic habitat is as described in text; parenthetical descriptions are from Hazel's (1969) Upper Klamath Lake study; n/a = not assigned.

Prey taxa	Water column	Benthic habitat	Total volume (%)	Total counts
CHIRONOMIDAE			31.2	6212
Adult	surface			447
Pupae	benthic	rocky		144
Larvae	benthic			5621
Chironominae	benthic			3964
Chironomini	benthic	vegetated (sand–gravel)		2551
Tanytarsini	benthic	rocky		1413
Orthocladinae	benthic	rocky (sand–gravel)		1429
Tanypodinae	benthic	rocky (sand–mud)		158
unidentifiable	benthic	rocky		70
CRUSTACEA			17.4	7457
Amphipoda	benthic	vegetated		162
Copepoda				2578
Cyclopoida	planktonic			2561
Harpacticoida	benthic	rocky		17
Cladocera				3403
Daphniidae	planktonic			595
Chydoridae	benthic	rocky		2799
unidentifiable	n/a			9
Ostracoda	benthic	rocky		1314
OTHER			3.1	7065
Trichoptera (Leptoceridae)	benthic	vegetated?		3
Arrenuridae (*Arrenurus*)	benthic	vegetated		218
Pollen	surface			6844
EGGS	benthic	rocky	3.7	2179
GOOP	benthic		44.2	

5 individuals >30 mm SL had consumed pollen, but 3 (30.8–39.5 mm SL), all from the eastern shoreline, had consumed >500 pollen grains each. The greatest consumption of pollen (~965 grains each) was by 2 juveniles, 27.4 mm and 39.5 mm SL, also from the eastern shoreline.

The 2 nominal planktonic prey, adult *Daphnia* and cyclopoid copepods, increased steadily from 8% to 53% in the 15–35 mm size groups, then declined to <30% in larger size classes. Invertebrate eggs showed a similar trend, making up about 5% of food items except in the transitional 20–35-mm size groups where they were 10%–20% of all food items (Fig. 3B). Chironomids made up >34% of the volume of stomach contents in specimens <35 mm SL (Fig. 4A). Crustaceans constituted 19%–29% of the volume of stomach contents in specimens 20–40 mm (Fig. 4B). Stomach contents of larger specimens were the most difficult to identify; 60%–76% of the volume from specimens >40 mm SL was unidentified goop (Fig. 4C). We detected no differences in stomach contents between the 2 species ($P = 0.68$), but the location effect was significant ($P < 0.0001$), with eastern and southern shoreline specimens having about double (43%–50%) the volume of goop as offshore specimens (23%). Numerically, crustaceans, such as chydorids, and larval chironomids contributed most to the diet of larger juveniles (Fig. 5).

For identifiable and countable stomach contents in specimens 40–70 mm SL, the percent composition of benthic prey items was partly related to sucker species but most strongly affected by location (Table 3). Shortnose suckers had a greater percentage of larval Tanytarsini, while Lost River suckers had a greater percentage of chironomid pupae and chydorids. In 8 cases consumption of prey species was most strongly related to location, and in 6 cases juvenile suckers consumed more prey when caught offshore than onshore (Table 3). Total stomach content volume with the effects of size and species removed was also greater in fish collected offshore ($P = 0.04$). Only cyclopoid copepods and eggs were eaten in greater numbers in onshore-collected suckers.
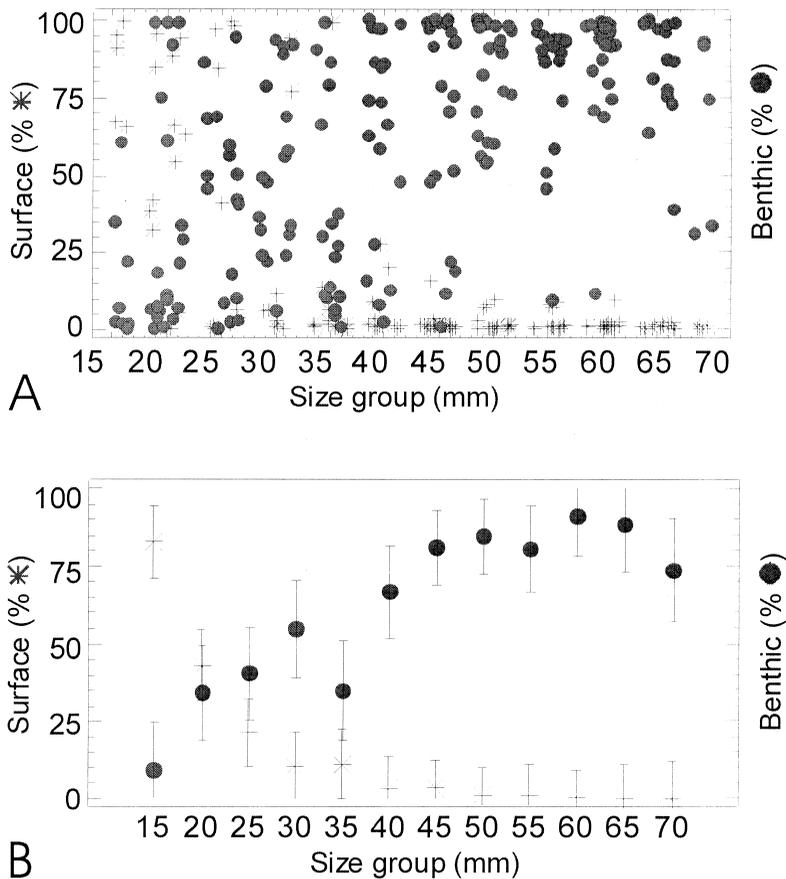
Fig. 2. Percent composition by abundance of surface (✳) and benthic (●) prey taxa in stomachs of larval and juvenile shortnose and Lost River suckers in Upper Klamath Lake, 1999. (A) Distribution of individual data. (B) Group means and 95% Bonferroni confidence intervals.

DISCUSSION

The primary pattern in the diets of these suckers was an ontogenetic transition from surface to benthic feeding between 20 mm and 30 mm (Fig. 2). This shift had the appearance of a change in central tendencies rather than an abrupt shift. At least part of the problem is that the nominal water column categories, especially surface and planktonic, are unlikely to be completely accurate descriptors of prey location in a littoral zone subject to wind-generated waves and turbulence. The major prey during the surface phase were adult chironomids (Fig. 4A), while the major prey during the benthic phase were larval chironomids, chydorids (Fig. 5), and ostracods. During the transition, planktonic prey and eggs were important. In some stomachs, eggs

appeared to have been freed from female *Daphina* during feeding, but we could not confirm the identity of any eggs. The importance of increasing diet breadth with continued growth (Fuiman 2002) is facilitated in a 3-dimensional medium. Although mouth morphology of both sucker species changes from terminal to subterminal during the larval-to-juvenile transition, a fish's body angle in water can change the mouth's orientation to prey (Liem 1990) so that prey location becomes a minor but nonlimiting constraint. Because larvae (<20 mm) and transitional juveniles (20–30 mm) were feeding primarily on surface prey (adult chironomids) or planktonic prey widely distributed in the lake (Bond et al. 1968), this study provides indirect evidence that the sucker's early association with emergent macrophytes (Cooperman and Markle
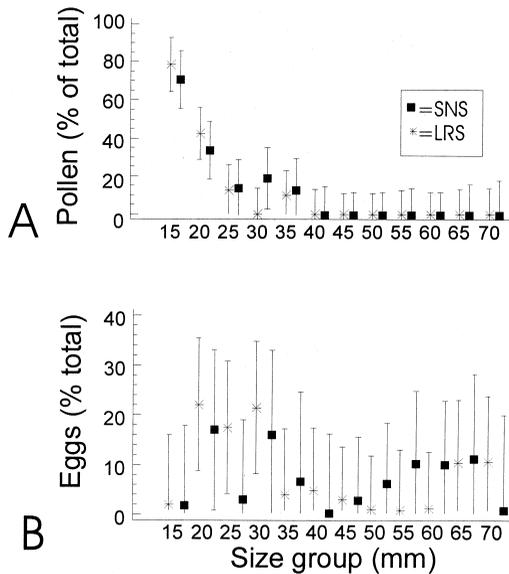
Fig. 3. Percent composition by abundance of (A) pollen and (B) eggs in stomachs of larval and juvenile shortnose (■) and Lost River (✳) suckers in Upper Klamath Lake, 1999. Symbols indicate group means and bars show 95% Bonferroni confidence intervals.
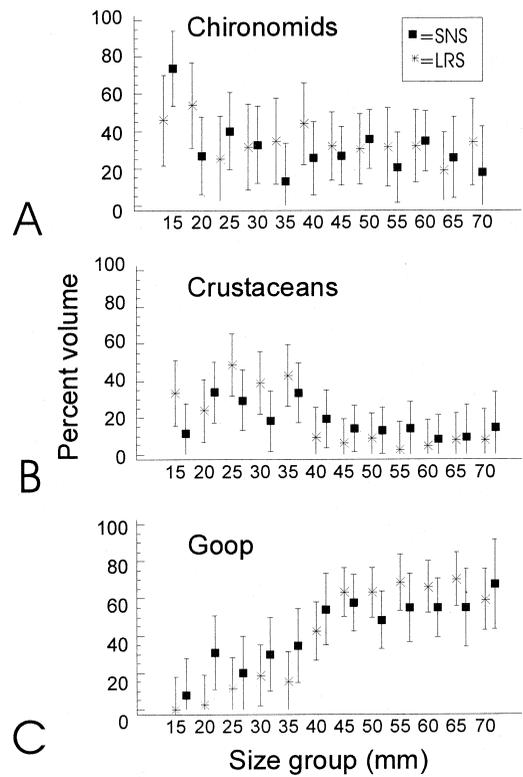

Fig. 4. Percent composition by volume of (A) chironomids, (B) crustaceans, and (C) goop in stomachs of larval and juvenile shortnose (■) and Lost River (✳) suckers in Upper Klamath Lake, 1999. Symbols indicate group means and bars show 95% Bonferroni confidence intervals.

2004) may have more to do with a predation refuge than better feeding opportunities. However, local processes, such as shoreline configuration and winds, might promote accumulation of prey and sucker larvae in or near some shorelines with emergent macrophytes.

Few differences in diet between shortnose and Lost River suckers existed at the taxonomic level of this analysis, and most differences appeared in juveniles >40 mm. Prey abundance may not be a limiting resource in such a highly eutrophic system. Chironomid abundance in Upper Klamath Lake has been at epizootic numbers since at least the 1930s (Bonnell and Mote 1942). Larval biomass was estimated at 635,000 kg in 1932 and 544,000 kg in 1964–1965 (Bond et. al 1968), and minimum average density was estimated at 1195 larvae · m^{-2} and maximum density at 159,000 larvae · m^{-2} (Bonnell and Mote 1942). Because adult chironomids are important for larvae and larval chironomids are important for juveniles, prey may not be limiting generally. However, the match in life cycles (larvae feeding on adult chironomids and juveniles feeding on larval chironomids) could be important to sucker larvae if hatching of some chironomid species was delayed.

Starvation might also be a problem for individuals that consume pollen (Fig. 3A). The outer pollen wall, or exine, is composed of sporopollenin, a biopolymer resistant to enzymes (Wierman and Gubatz 1992). Dunsmoor (Klamath Tribes, personal communication, July 2005) has observed that sucker larvae feeding on pollen in a hatchery do not digest pollen, but simply pass it through their digestive tracts. However, there is a pollen coat on the exine that contains carbohydrates, proteins, and lipids (Wierman and Gubatz 1992); so, although larvae cannot digest pollen, they might gain some potentially useful molecules. It is uncertain whether the pollen coat provides a benefit to larvae or if pollen feeding is a waste of search and feeding time. Pollen has been mentioned in the diet of a nearshore marine anchovy (Vinas and Ramirez 1996), but we can find no other reports of pollen consumption by larval fish in
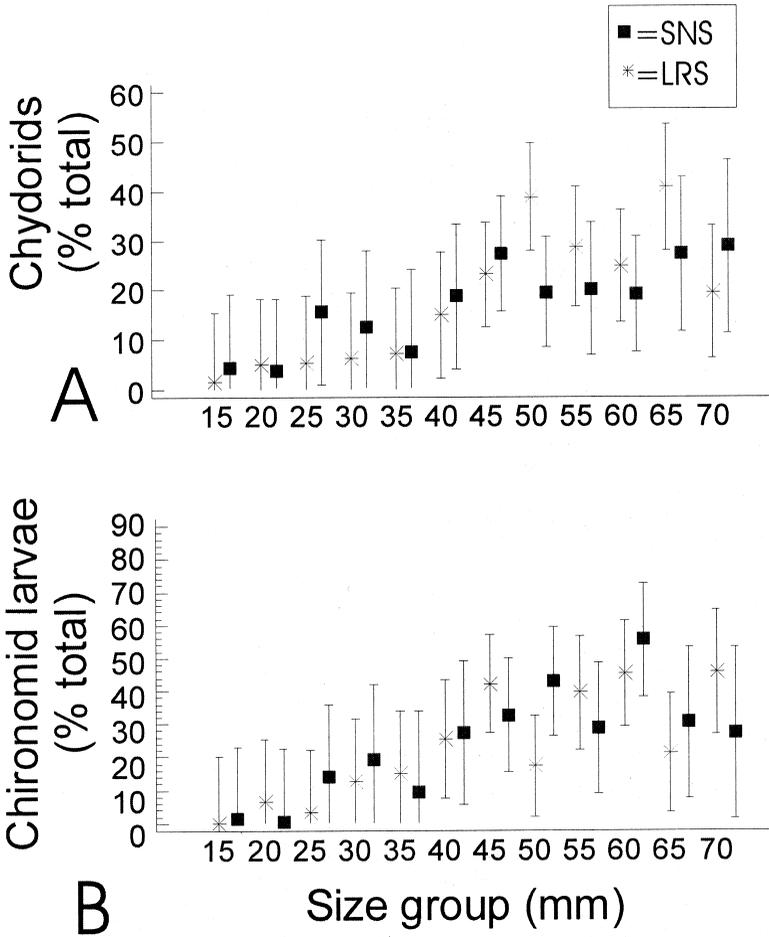
Fig. 5. Percent composition by abundance of (A) chydorids and (B) chironomid larvae in stomachs of larval and juvenile shortnose (■) and Lost River (✳) suckers in Upper Klamath Lake, 1999. Symbols indicate group means and bars show 95% Bonferroni confidence intervals.

nature. Pollen consumption was frequent, and small larvae that had consumed pollen were most abundant on eastern shorelines, a very important early nursery area (Cooperman and Markle 2004). These conditions might suggest the importance of local conditions and processes such as windrow accumulation of pollen and larval drift. Although we do not know the overall mortality effect, high frequency of pollen consumption could potentially contribute to reduced fitness and higher starvation-caused mortality. Marine fish larvae are known to detect ultraviolet wavelengths (Britt et al. 2001). Since zooplankton reflect more shorter than longer wavelengths, this sensitivity should increase prey contrast and detection, and is thought to be a general adaptation of fishes

feeding on zooplankton (Britt et al. 2001). Assuming larval suckers have the visual capability typical of freshwater fish, pollen grains should be very obvious targets because they usually absorb ultraviolet wavelengths (Britt, personal communication, 2005). Based on a lead-dated core, the 260-year pollen record of Upper Klamath Lake is uniform for pines, but total pollen concentration has tended to be higher since 1900 (Bradbury et al. 2004). The latter may be due to redeposition of pollen from marshes (Bradbury et al. 2004) and does not provide convincing evidence of an anthropogenic influence on pollen in the sucker's diet. A better understanding of the particle selection process in larval suckers, the nutritional value of pollen, and the processes that

TABLE 3. Summary of multifactor ANOVA of effect of species, size group, and location on relative abundance of prey of suckers 40–70 mm (n = 163). Prey was expressed as percent composition of all countable prey items. Location for this analysis was offshore versus all onshore locations. Lost River sucker = LRS, shortnose sucker = SNS, offshore = OFF, shoreline = ON.

| | P-value (directional effect) | | |
Prey taxon	Species	Size group	Location
Chironomid pupae	0.03 (LRS > SNS)	0.28	<0.0001 (OFF > ON)
Chironomid larvae			
Chironominae			
Chironomini	0.09	0.007[a]	0.007 (OFF > ON)
Tanytarsini	0.02 (SNS > LRS)	0.30	0.001 (OFF > ON)
Orthocladinae	0.14	0.67	0.006 (OFF > ON)
Tanypodinae	0.64	0.20	0.001 (OFF >ON)
Amphipoda	0.49	0.71	0.15
Copepoda-Harpacticoida	0.29	0.36	0.04 (OFF > ON)
Copepoda-Cyclopoida	0.57	0.27	<0.0001 (ON > OFF)
Cladocera-Chydoridae	0.05 (LRS > SNS)	0.11	0.12
Ostracoda	0.7	0.12	0.33
Trichoptera (Leptoceridae)	0.19	0.30	0.48
Arrenuridae (*Arrenurus*)	0.58	0.26	0.14
Eggs	0.18	0.60	0.03 (ON > OFF)

[a]Chironomines were more abundant in the 60 mm size group than in smaller or larger sizes.

accumulate pollen in this area would help determine the importance of this potential cause of starvation for sucker larvae.

The greatest interspecific diet difference was found in juveniles >40 mm (Table 3). There were significant differences in relative abundances of 3 prey groups. Shortnose suckers ate more Tanytarsini and Lost River suckers ate more chironomid pupae and chydorids. We cannot be confident that this indicates niche partitioning. However, 1999 was a particularly strong year for both species and the offshore abundance of juveniles of both suckers was high (Simon et al. 2000), so the conditions were good for detecting resource partitioning if it existed.

Larger juveniles (40–70 mm) also had a very strong offshore versus onshore pattern in their diet. Both species had significantly more chironomid pupae and larvae and harpacticoid copepods when collected offshore. Relative abundance of prey also had a strong habitat-related component (Table 3). Specimens >40 mm collected in offshore samples had a greater total stomach volume and ate more chironomid pupae and larvae, harpacticoid copepods, and chydorids than onshore specimens. Cyclopoid copepods and eggs, items typical in the diet of smaller juveniles, were eaten in greater numbers in onshore-collected suckers. Onshore specimens also had a significantly greater per-

centage of goop, perhaps a consequence of the different diets. Juveniles were not fixed in formalin, and the increase in goop with fish size may reflect both preservation and more fragile prey.

If stomach volume and increased numbers of prey in stomachs indicate greater food availability in offshore habitats, both species should leave nearshore habitats at the smallest size possible. In 1999 the smallest shortnose sucker collected offshore was 38 mm and the smallest Lost River sucker was 46 mm. The largest collected onshore were 84 mm and 93 mm, respectively (unpublished data). The latter sizes were near the maximum we expected to see after 1 summer's growth (unpublished data). Suckers in shallow onshore habitats would be expected to have a refuge from larger fish predators because of shallow water depth, though they might be subjected to more invertebrate predators. On the other hand, juveniles in onshore habitats would be expected to become more susceptible to avian predation with growth. It would therefore seem that Werner's (2002) tradeoff between maximizing growth rate and minimizing predation risk results in a shift to offshore habitat in both species of suckers that begins when individuals are as small as 40 mm but may be delayed to when individuals become as large as 93 mm.

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