Ecology of Age-0 and Age-1 Paddlefish in Upper Fort Peck Lake, Montana

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master of Science

with a

Major in Fishery Resources

in the

College of Graduate Studies

University of Idaho

by

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December 2000

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ABSTRACT

The paddlefish *Polyodon spathula* stock inhabiting Fort Peck Lake, a Missouri River mainstem reservoir in Montana, is among the few remaining naturally-reproducing stocks. For effective management, information is needed on reproductive success and year-class strength of this stock, which entails an understanding of the distribution, abundance, and food habits of age-0 and age-1 fish. Objectives of this study were to 1) assess the distribution and abundance of age-0 and age-1 paddlefish in upper Fort Peck Lake during late-summer and fall, and determine correlated abiotic and biotic factors; 2) assess growth and condition within and across years (1998 and 1999); and 3) determine electivity for prey items, and determine at what size paddlefish switch feeding mode from particulate to filter feeding.

Sampling was conducted during the late summer and fall of 1998 and 1999 in a 39.4 km portion of the upper reservoir. Results of objective 1 are reported in chapter 1, and results of objective 2 and 3 are reported in chapter 2.

ACKNOWLEDGEMENTS

I would like to thank the Montana Department of Fish, Wildlife, and Parks for providing funding for this project and its employees for providing assistance and acquiring necessary equipment especially Kent Gilge, Bill Wiedenheft, and Mike Ruggles. I would also like to thank Dr. Dennis Scarnecchia for accepting me for this position, patience in editing my work, and all other assistance that allowed me to complete this project. I am grateful for the input, editing, and statistical consulting provided by Dr. Mike Falter, Dr. James Nagler, and Dr. Kirk Steinhorst. Lastly, I would like to express gratitude to Chris Kinzler and Thomas Droz who suffered through heat waves, boredom, and isolation to collect data and specimens.

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INTRODUCTION

The structure and function of most large North American rivers have been extensively altered within the last hundred years for the purposes of flood control, hydroelectric power, navigation, and irrigation (Ebel et al. 1989, Hesse 1993). Consequently, most large rivers now possess an unnatural flow regime, reduced abundance and diversity of some habitat types, and lack connectivity with their respective floodplains (Junk et al. 1989, Poff et al. 1997). Some native large river fish species, especially those with specific ecological requirements, have declined substantially, while other species, often non-natives, with more generalized ecological requirements have increased in abundance (Hesse et al. 1989, Simon and Emery 1995).

The paddlefish *Polyodon spathula* is native to the Mississippi and Missouri rivers, as well as several gulf coast drainages (Carlson and Bonislawsky 1980). Historically, adult and juvenile paddlefish used low-velocity areas found in oxbow lakes, backwaters, side channels, and downstream of islands for feeding and rearing (Stockard 1907, Hoxmeier and DeVries 1997). During spring, adult paddlefish migrated long distances (hundreds of kilometers) to suitable spawning areas (Russell 1986) where spawning occurred over clean-swept gravel bars (Purkett 1961). Throughout much of the paddlefish's range, habitat alterations have severely reduced the availability of low-velocity feeding and rearing areas, and dam construction has blocked spawning migrations (Sparrowe 1986). These factors, along with pollution and overharvest, have reduced the abundance of some stocks while extirpating others (Carlson and Bonislawsky 1980).

As of the twenty-first century, there are few remaining naturally reproducing stocks of paddlefish. These stocks are mostly found in reservoir systems that allow adult paddlefish to access suitable spawning habitat upstream of the reservoir and provide abundant feeding and rearing areas within the reservoir (Sparrowe 1986, Scarnecchia et al. 1995).

The paddlefish stock inhabiting Fort Peck Lake, a Missouri River mainstem reservoir, is among the few remaining naturally-reproducing stocks. Although population size is unknown, harvest rates have remained low. From 1977 through 1997, estimates of average annual harvest rate of tagged fish did not exceed four percent (Gilge 1994).

During the spring high-flow period, adult paddlefish migrate upstream to spawning areas in the wild and scenic section of the upper Missouri River (Berg 1981). Paddlefish stage in the Missouri River and move to spawning areas when discharge exceeds 400 $m^3 \bullet sec^{-1}$. If discharge does not exceed 400 $m^3 \bullet sec^{-1}$, researchers speculate that few adults move to suitable spawning areas (Berg 1981, Kent Gilge, Montana Department of Fish, Wildlife, and Parks, personal communication). Although the relationship between spawning success and the duration of high flows is not fully understood, many investigators believe that the longer the duration of high spring flows, the greater the likelihood of a successful spawning event (Russell 1986, Wallus 1986). Most spawning of paddlefish of the Fort Peck stock is thought to take place in May or early June, and adults return to the reservoir shortly after spawning.

The Montana Department of Fish, Wildlife, and Parks has assessed this stock by tagging migrating adult fish and monitoring the proportion of tagged fish captured by anglers. Male paddlefish of this stock first mature between 9 and 11 years, whereas females first mature between 15 and 18 years (D. L., Scarnecchia, unpublished data). If recruitment of juvenile paddlefish to the spawning stock declines, a monitoring system based only on information from mature paddlefish would thus not indicate a decline until the population was substantially reduced.

Successful management of any fish population, including paddlefish, requires information on factors affecting abundance in early life history stages (Van Den Avyle 1993). The current Montana-North Dakota Paddlefish Management Plan lists the development of age-0, age-1, and spawning adult indices as primary objectives (Scarnecchia et al. 1995).

Until recently, sampling juvenile paddlefish has been hampered by ineffective methods for capturing juveniles. Electrofishing was ineffective at capturing age-0 paddlefish in off-channel habitats of the lower Alabama River: only one age-0 paddlefish was collected from June 1994 through July 1995 (Hoxmeier and DeVries 1997). Pasch et al. (1980) used small mesh (13-38 mm bar) experimental gill nets in the intake canal of a power plant on the Cumberland River and captured 1.5 % of age-0 paddlefish impinged on intake screens. During 1970-1974, Ruelle and Hudson (1977) captured 448 age-0 paddlefish using between 320 and 400 minutes • year^{-1} of benthic trawling effort along the old river channel of Lewis and Clark Lake, a mainstem impoundment of the Missouri River bordering South Dakota and Nebraska.

Since few investigators have been able to capture juvenile paddlefish, there is currently little information available of juvenile paddlefish habitat preferences, especially those of wild, age-0 fish. Crance (1987) compiled information using the Delphi exercise and listed three abiotic factors (depth, velocity, and temperature) that affect the suitability of habitat for early juvenile paddlefish. Habitat was most suitable with current velocities below 20 cm • s^{-1}, temperatures between 15 and 30 °C, and depths between 3 and 12 meters.

In Fort Peck Lake, managers are seeking a method of not only capturing age-0 fish, but also of assessing spawning success and year-class strength. Low catch rates, high cost, and incompatibility with the habitat present in Fort Peck Lake would make methods such as trawling and electrofishing largely ineffective. Information on the timing of first appearance, highest densities, extent of distribution, and disappearance in late fall of juvenile paddlefish from the surface is unavailable, but is essential to the development of the age-0 and age-1 abundance indices.

Since the early 1990s, surface visual counts along transects in Lake Sakakawea, a neighboring Missouri River mainstem reservoir, have allowed estimation of age-0 and age-1 paddlefish year-class strength (Fredericks and Scarnecchia 1997). Visual counts allowed these investigators to monitor the relative abundance of juvenile paddlefish throughout a large portion of the upper reservoir with a small crew and minimal equipment investment. In 1998, for example, 444 age-0 fish and 92 age-1 fish were counted on standard transects in the upper portion of Lake Sakakawea reservoir during summer and late fall (D.L. Scarnecchia, University of Idaho, Unpublished data). In addition to visual counts, fish have also been sampled effectively (>2000 fish • $year^{-1}$) with dipnets for life history information (Scarnecchia et al. 1997). Although these techniques hold promise for enumerating and sampling age-0 and age-1 paddlefish in other reservoirs, to date, no other investigators have reported success. It was unknown how effective these techniques would be in Fort Peck Lake.

Prior to 1997, information on the spatial and temporal distribution of juvenile paddlefish in upper Fort Peck Lake was limited to reports of age-0 and age-1 paddlefish visually located at river kilometer (rkm) 3,035 near the inundated confluence of Beauchamp Creek and the Missouri River during August (Bill Wiedenheft and Kent Gilge, Montana Department of Fish Wildlife and Parks, personal communication). During preliminary sampling in 1997, age-0 paddlefish were counted and captured with dipnets at the same location. At 1997 reservoir levels (approximately 684 meters above sea level, msl), this area was down-reservoir of the river-reservoir transition area and possessed lacustrine habitat 1-3 meters in depth interspersed with dead, flooded willows (*Salix* sp.).

Objectives

In addition to information on abundance and year-class strength, information is also needed on feeding ecology and growth as they may influence year-class strength. Young paddlefish are known to individually select larger zooplankton species (Ruelle and Hudson 1977, Michaletz 1982). If large zooplankton species are unavailable, growth rates decrease, and young paddlefish may switch to filter feeding before their gillrakers are fully developed (Rosen and Hales 1981). Low densities of preferred, large prey and decreased growth rates would increase the time at which these fish are vulnerable to predators and decrease the size at which they enter winter.

My objectives were to:

1) Assess the distribution and abundance of age-0 and age-1 paddlefish in upper Fort Peck Lake during late-summer and fall, and determine correlated abiotic and biotic factors;

2) Assess growth and condition within and across years (1998 and 1999); and

3) Determine electivity for prey items, and determine at what size paddlefish switch feeding mode from particulate to filter feeding.

Objective one will be considered in Chapter One. Since feeding behavior strongly influences growth and condition of juvenile paddlefish, objectives two and three are considered together in Chapter Two.

STUDY AREA

Fort Peck Lake is the uppermost large mainstem reservoir on the Missouri River and is located in northeastern Montana (Figure 1). Fort Peck Dam was constructed between 1933 and 1940, and electricity was first generated during July 1943. The reservoir was constructed to provide navigation, hydroelectric power, and flood control. The project plan also provides for irrigation, municipal water supply, water quality, fish and wildlife conservation, and recreation. At full pool (685 meters above sea level, msl), the reservoir extends 216 kilometers, possesses a surface area of 100,767 hectares, and collects water from over 145,000 km^2 (USACE 1991). Reservoir elevations from 1967 through 1999 ranged between 672 and 686 msl (Figure 3). Over most of these years, reservoir elevation was fairly stable (approximately 680 msl) except during 1987 through 1993 when reservoir level was substantially lower (mean elevation, 676 msl).

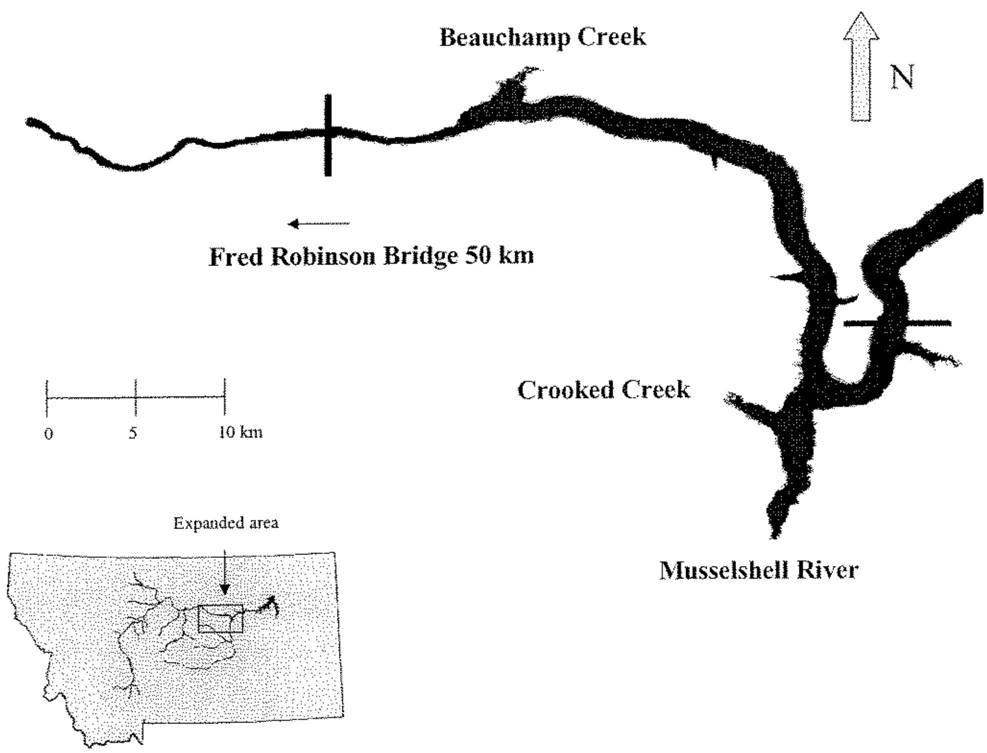

Figure 1. Fort Peck Lake, Montana, and location of the study site.

The geology of the upper Missouri River basin is largely influenced by the recession of the great inland sea approximately 80 million years ago which deposited sediments that are now sandstone and shale (U.S. Department of the Interior 1984). Erosion and the properties of these rocktypes have formed large prairies which are dissected by deeply entrenched, narrow streams. Vegetation is heavily influenced by the arid conditions prevalent; normal annual precipitation does not exceed 30.5 cm (U. S.

Army Corps of Engineers 1991). Sagebrush *Artemisia* sp. and grasses Family Gramineae cover the upland areas. Cottonwood *Populus* sp. and willow *Salix* sp. groves grow in riparian areas bordering the river that are not inundated by Fort Peck Lake, and Douglas-fir *Pseudotsuga menziesii*, juniper *Juniperus* sp., and ponderosa pine *Pinus ponderosa* grow on side slopes and along seasonally-dry channels also known as coulees.

The Missouri River upstream of Fort Peck Lake is one of the last large free-flowing river segments within the United States not significantly altered by humans (Berg 1981). Large amounts of riparian and instream habitat are protected by its wild and scenic river designation (U. S. Department of the Interior 1984), and efforts have been made to provide necessary instream flow protection (Gardner and Berg 1982). Small upstream impoundments and cattle grazing may however, be reducing the regeneration of cottonwood stands and other riparian species, altering sediment cycles, and disrupting the natural flow regime (Hesse 1987). Before significant human modification of the system, the hydrograph rose in April as snowmelt from the plains entered the river and again in May through June from snowmelt from the Rocky Mountains. There is some indication that drought, changing weather patterns, or human influences are reducing the duration and magnitude of high flow events. In the first-half of the twentieth century, the spring rise often had two peaks and discharge exceeded 400 $m^3 \bullet sec^{-1}$ for extended time periods. In contrast from 1980 through 1999, the spring rise exceeded 400 $m^3 \bullet sec^{-1}$ for only forty days in seven different years (Figure 3).

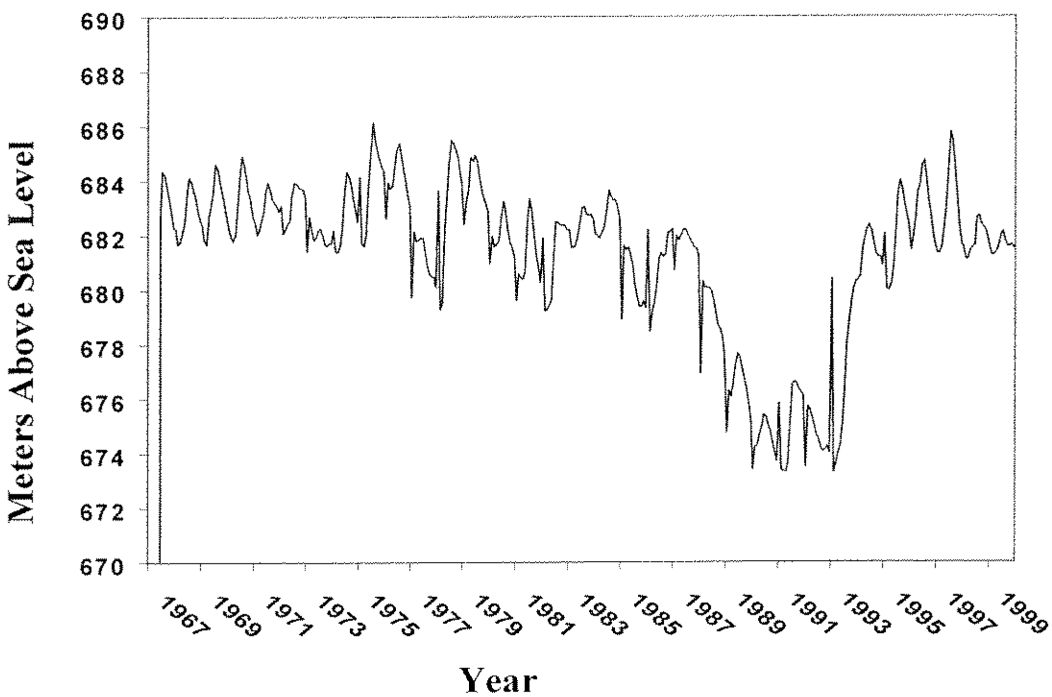

Figure 2. Average monthly midnight elevation of Fort Peck Lake, MT from June 1967 through December 1999. The six large, mainstem reservoirs of the Missouri River were first operated as a system in June,1967.

This study was conducted in the upper reaches of the reservoir. The study site, which is oriented in an east-west fashion, has its upstream boundary 50 kilometers down-reservoir of Fred Robinson Bridge (Montana Highway 191), at rkm 3,042.5 near CK Creek. The study area extends 39.4 kilometers down-reservoir (eastward) to rkm 3,003.1 near Swan Creek. Within the study area, reservoir width varies from less than one km to 1.5 km (Figure 1). This area was studied for two reasons. First, preliminary investigations found that young paddlefish were located here in the late summer of 1995 and 1997 (D. Scarnecchia, University of Idaho, personal communication). In addition, the habitat within this area changes rapidly from lotic to lentic, permitting comparisons between habitats in zooplankton and other invertebrate densities, paddlefish counts, and paddlefish feeding ecology. The location and relative amount of each habitat type in the two years of this study was strongly dependent on reservoir elevation and discharge from the Missouri River upstream of the reservoir. In 1999, the study area was narrower, shallower, and more turbid than in 1998 (Table 3) as a result of reduced discharge from the Missouri River (Figure 4) and lower reservoir levels (Figure 5).

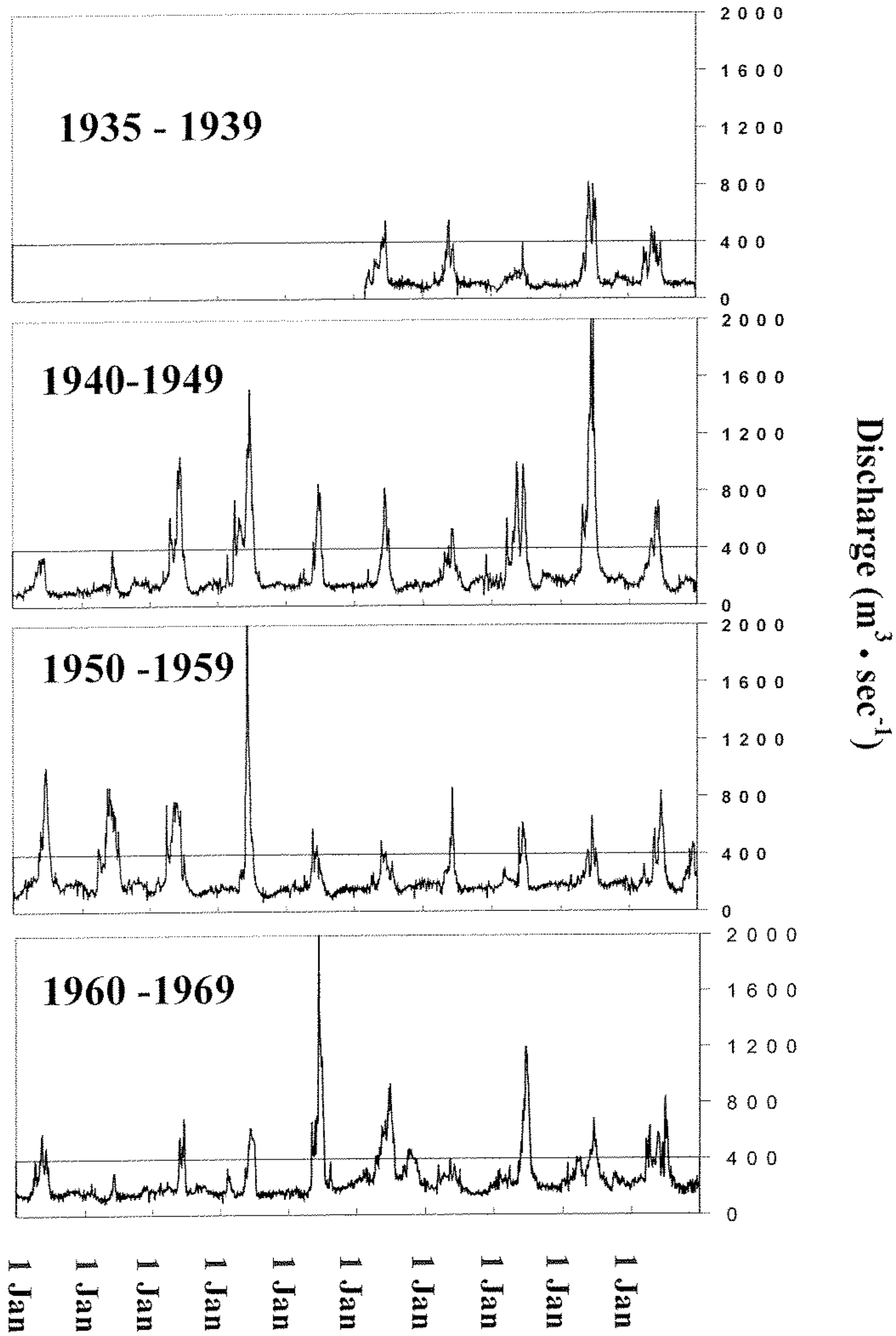

Figure 3. Discharge of the Missouri River from 1935 – 1999 measured at the Virgelle gauge. This USGS gauge is located near suspected paddlefish spawning areas, and the horizontal line represents the suspected minimum flow (400 $m^3 \bullet sec^{-1}$, Berg 1981) for migration to spawning areas.

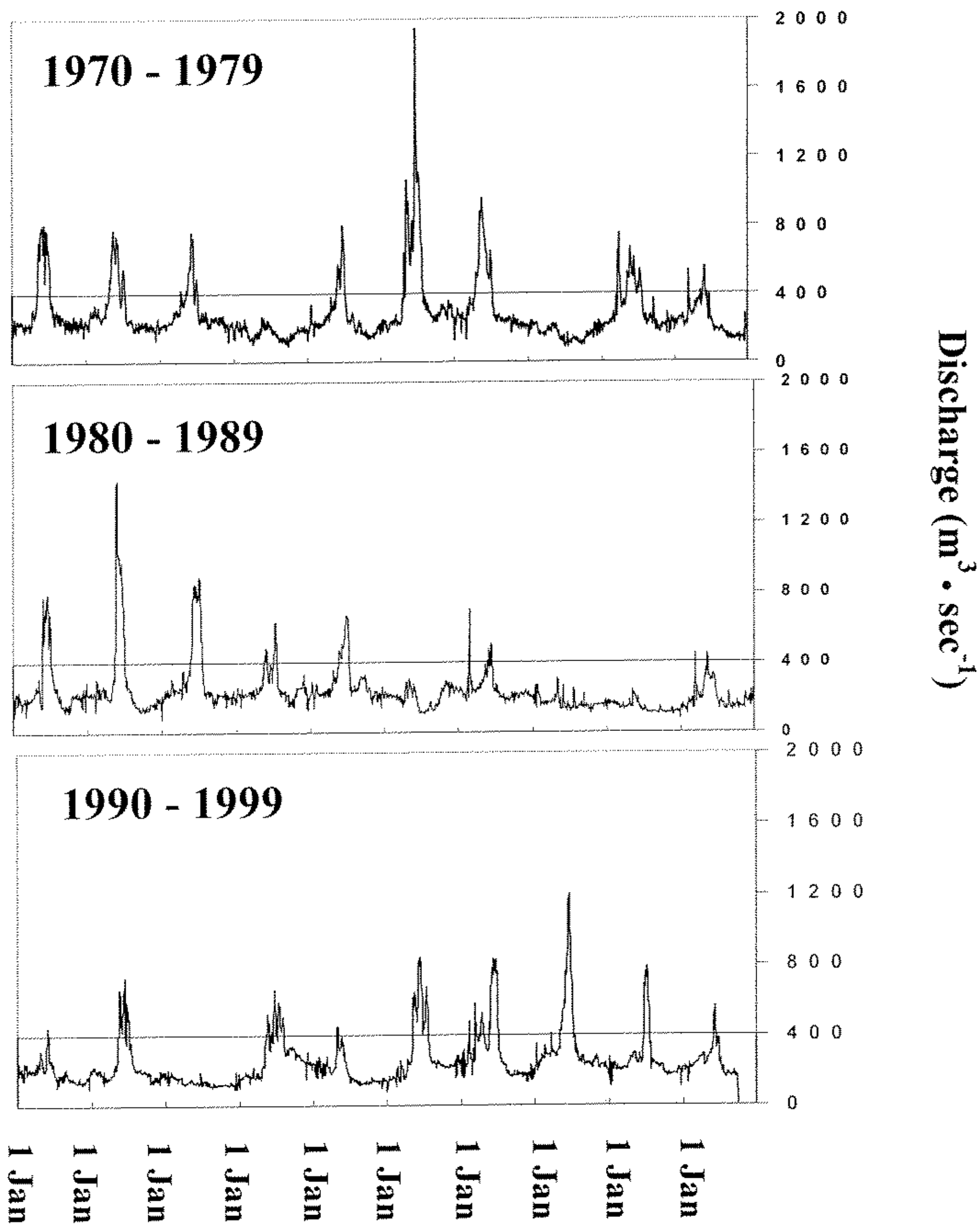

Figure 3 continued. Discharge of the Missouri River from 1935 – 1999 measured at the Virgelle gauge. This USGS gauge is located near suspected paddlefish spawning areas, and the horizontal line represents the suspected minimum flow (400 $m^3 \bullet sec^{-1}$, Berg 1981) for migration to spawning areas.

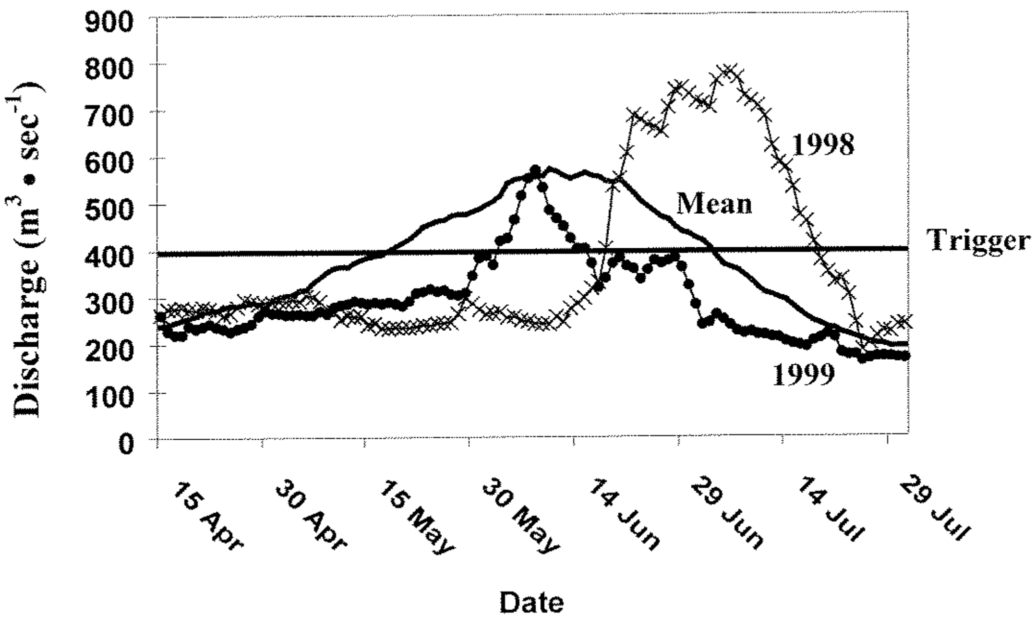

Figure 4. Discharge of the upper Missouri River measured at the Virgelle gauge near Landusky, MT. This USGS gauge is located near suspected paddlefish spawning areas, and the horizontal line represents the minimum flow also known as trigger flow (400 $m^3 \bullet sec^{-1}$, Berg 1981) for migration to spawning areas.

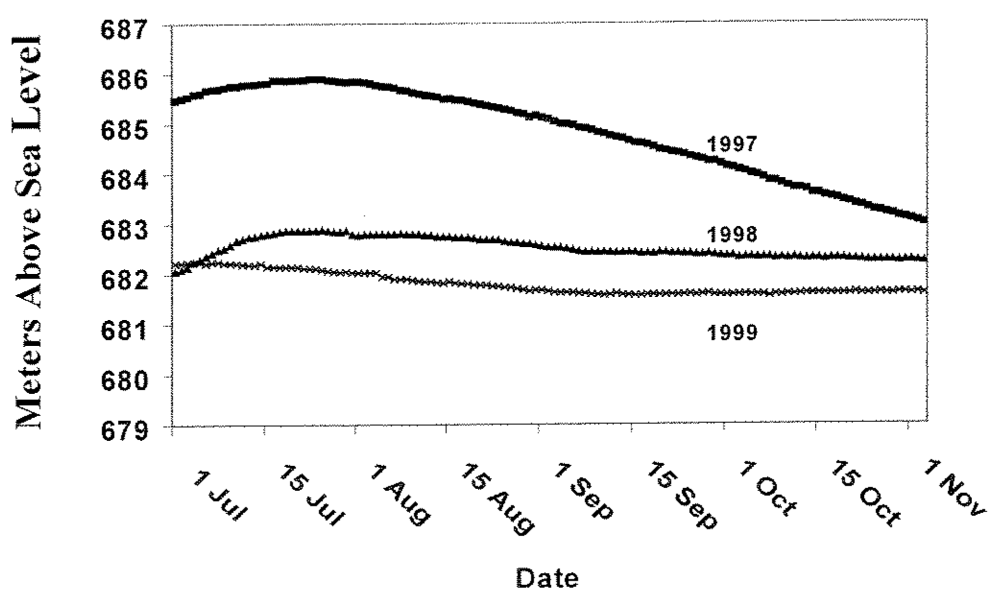

Figure 5. Elevation of Fort Peck Lake, MT during July through November 1997, 1998, and 1999.

CHAPTER 1. DISTRIBUTION AND ABUNDANCE OF AGE-0 AND AGE-1 PADDLEFISH IN UPPER FORT PECK LAKE, MONTANA

ABSTRACT

The distribution and abundance of age-0 and age-1 paddlefish *Polyodon spathula* were evaluated in the late summer and fall of 1998 and 1999 using visual counts over a 39.4 km portion of upper Fort Peck Lake, a Missouri River mainstem reservoir in Montana. Counts of age-0 and age-1 paddlefish indicated that abundance was low in 1998, with a total of 97 age-0 and 54 age-1 fish counted along 216 transects. Counts were even lower in 1999, with a total of 3 age-0 and 10 age-1 fish counted along 174 transects. During 1998, higher numbers of age-0 paddlefish were more often observed near rkm 3,024 than at other sites during late July and early August. By late August, higher counts of age-0 paddlefish shifted to down–reservoir areas (near rkm 3,010) where zooplankton abundance was ten-fold higher than up-reservoir areas (near rkm 3,024). Age-1 paddlefish did not appear to use up-reservoir areas and instead were most often observed down-reservoir of rkm 3,019. Significant correlations were found between age-0 fish abundance and two of the six habitat measurements: abundance was positively correlated with wave height and negatively correlated with current velocity. Although this study shows that age-0 and age-1 paddlefish can be counted at the surface of Fort Peck Lake in the same manner as Lake Sakakawea, counts in 1998 and 1999 were too low to provide detailed information of distribution and abundance of age-0 fish.

INTRODUCTION

Successful stock assessment and management of paddlefish *Polyodon spathula* requires knowledge of annual reproductive success and recruitment, as well as factors that affect reproductive success and recruitment. Practical and accurate indices of abundance of age-0 and age-1 paddlefish depend largely on knowledge of their spatial and temporal distribution when they are most vulnerable to enumeration and capture. In addition, information is needed on how abiotic and biotic factors affect their distribution.

In the past, few researchers were able to capture juvenile paddlefish. Recently, surface visual counts have been used to estimate relative year-class strength of age-0 and age-1 paddlefish (Fredericks and Scarnecchia 1997). Research conducted on Lake Sakakawea, North Dakota indicated that in some years several hundred fish could be counted along standard transects in the upper portion of the reservoir during summer and late fall (Scarnecchia et al. 1997). In other years, fewer age-0 paddlefish were counted. It was not known how effective this technique would be in Fort Peck Lake. The objective of the study reported in this chapter were to assess the distribution and abundance of age-0 and age-1 paddlefish in upper Fort Peck Lake during late summer and fall, and determine correlated abiotic and biotic factors.

METHODS

Fish Sampling

Preliminary studies conducted in 1997 in Fort Peck Lake indicated that a large number of age-0 paddlefish were found near the inundated confluence of Beauchamp

Creek and the Missouri River (rkm 3,036). At 1997 reservoir levels (approximately 684 msl, Figure 5), this area was down-reservoir of the river-reservoir transition area and possessed lacustrine habitat ranging from one to three meters deep interspersed with dead, flooded willows.

In 1998-1999, paddlefish were located and enumerated using visual counts along pre-established transects at stations throughout the upper reservoir. Stations were placed at locations to encompass the full array of habitats available to juvenile paddlefish from lotic habitat through the transitional area to the lacustrine habitat of the reservoir. Since most age-0 paddlefish were located down-reservoir of the river-reservoir transition area during preliminary sampling in 1997, an area with similar habitat during 1998 was chosen as the middle point for placing stations; four stations were then placed both up-reservoir and down-reservoir of this area. The same station locations were used during 1999. A typical station consisted of three, two-kilometer transects placed parallel to the direction of flow evenly spaced from the river or reservoir banks and each other (Figure 6). Due to the narrow channel in the riverine portion of the study area, transects were staggered in the two uppermost stations. The start and end points of each transects were recorded with a GPS unit (Figure 6, Appendices). Paddlefish were counted during a one- to two-day period and the process was repeated weekly. During 1998, I counted along all stations during 9 sampling periods beginning 24 July and ending 22 September. During 1999, I counted stations during 8 sampling periods beginning 27 July and ending 17 September. Shallow water near the transition area in 1999 made it impossible to access the two uppermost stations (1 and 2) from 30 August to 17 September.

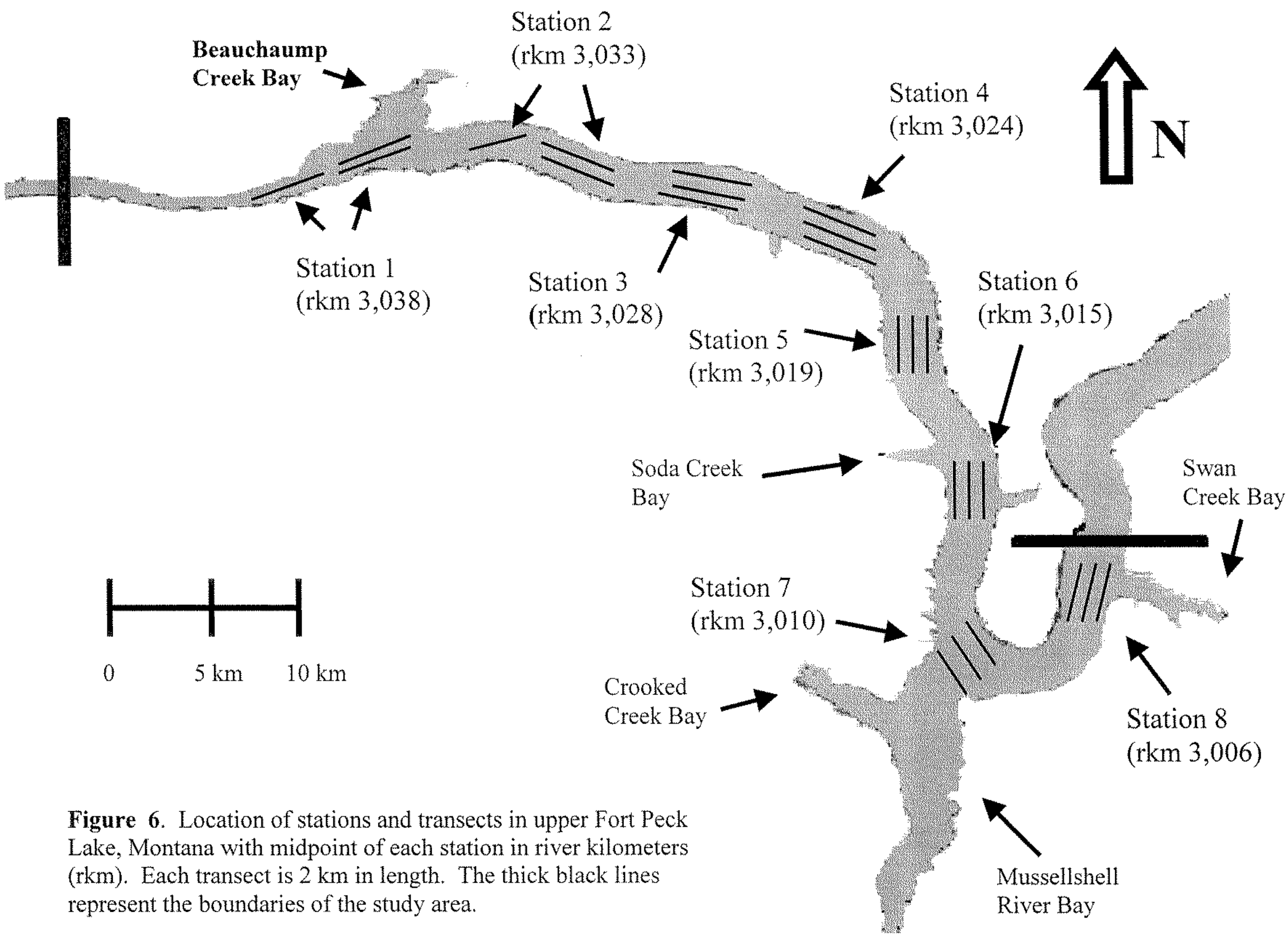

Figure 6. Location of stations and transects in upper Fort Peck Lake, Montana with midpoint of each station in river kilometers (rkm). Each transect is 2 km in length. The thick black lines represent the boundaries of the study area.

Fish were counted using a method described by Scarnecchia et al. (1997). The crew consisted of two people. Boat speed was maintained between 8-9.5 km • h^{-1} with the aid of a global positioning system (GPS) unit. One person drove the boat, and counted all age-0 and age-1 paddlefish within 10 meters of the boat off the starboard side, while the other person counted age-0 and age-1 paddlefish within 10 meters off the port side. Fish encountering pressure waves or turbulence from the boat typically flee, and at fish sizes greater than about 120 mm fork length (FL), their morphology which includes a long paddle-like rostrum (Thompson 1933) drives them to the surface where the fish and their wake are seen. Counts of age-0 and age-1 paddlefish were expressed as the number of fish • km^{-1}. To compare relative abundance of age-0 and age-1 fish, I visually estimated fork length (FL). During July and August, paddlefish shorter than 300 mm FL were classified as age-0. During September, paddlefish shorter than 350 mm FL were classified as age-0. Paddlefish between 300 or 350 mm FL and 550 mm FL were classified as age-1. I did not attempt to classify paddlefish larger than 550 mm FL into age groups.

Abiotic and Biotic Measurements

Water temperature, water velocity, depth, water transparency, and invertebrate densities were monitored weekly during transect sampling at the start point of each transect. Temperature was measured at the surface, using a hand-help thermometer. Surface velocity was measured with a Price AA flowmeter. Depth was recorded with a sonar unit mounted to the boat. Transparency readings were made using a 20-cm Secchi disk attached to a graduated rope (Welch 1948). The disk was lowered until it disappeared from view, and that depth was recorded. After being lowered an additional distance, the Secchi disk was raised slowly through the water column. The second reading was taken when the disk reappeared. The Secchi disk depth consisted of the average of these two measurements.

I visually estimated both wave height and cloud cover at the start of each transect. Wave heights were categorized as calm (0.0-0.15 m), choppy (0.16-0.42 m), rough (0.43-0.73 m), and very rough (0.74-1.00 m). I did not sample in wave heights over 1 m. Cloud cover was categorized as clear, partly cloudy, or overcast.

Zooplankton and other suspended invertebrates were also monitored weekly during the sampling season. At the up-reservoir point of each transect, horizontal surface tows were made with an 80-micron mesh Wisconsin plankton-net with 15.1 cm diameter gape. A General Oceanics flow meter suspended in the mouth allowed the total water volume sampled to be estimated. Tows lasted for 45 seconds. During 1999, benthic invertebrates were also sampled. Two benthic samples were collected in the middle transect at each station with a petite ponar grab. All zooplankton and benthic samples were placed in vials, preserved with 95% ethanol, and returned to the laboratory for identification and enumeration. All invertebrate samples were diluted and subsampled. Invertebrates were identified to various taxonomic levels. Zooplankton were identified as *Daphnia sp.*, *Bosmina longirostris*, *Chydorus* sp., *Leptodora kindtii*, *Moinadaphnia* sp., *Ceriodaphnia* sp., *Diaphanasoma* sp., and both adults and nauplii from the family Cyclopoida. Aquatic macroinvertebrates were identified from the orders Ephemeroptera, Plecoptera, and Tricoptera, as well as from the families Culicidae, Chaoboridae, Simuliidae, and Chironomidae. The combined zooplankton and suspended invertebrate density was expressed as organisms • $liter^{-1}$.

Analysis

Two statistical procedures were used to evaluate the influence of various factors on the distribution and abundance of age-0 and age-1 paddlefish. A repeated-measures factorial analysis of variance was used to assess the influence of sampling period and station on age-0 and age-1 paddlefish counts. In this analysis, each of the three transects was nested within a station. Since juvenile paddlefish densities were monitored along the same transects over time, these measurements were not independent. Because of this unavoidable pseudoreplication, interpretation of one main effect (station) is confounded and must be interpreted with caution (Hurlbert 1984). In the second analysis, all habitat variables were placed into a Pearson's correlation matrix that allowed comparison of all possible correlation coefficients between paddlefish counts and habitat variables.

RESULTS

Counts in 1998

During 1998, 97 age-0 and 54 age-1 paddlefish were enumerated during the 216 transect counts conducted. Age-0 paddlefish were first observed at rkm 3,019 on 1 August at a mean count of 0.67 fish • km^{-1} (Figure 7). Counts of age-0 paddlefish remained low through 23 August, and most observed fish were located between rkm 3,028 and 3,019. Counts increased by 30 August, and it appeared that peak counts shifted down-reservoir. The highest counts of age-0 paddlefish remained in the lower portion of the study area through 22 September. The maximum mean count of 1.44 fish •

km^{-1} was observed on 15 September at rkm 3,010 and at no other time were more than 0.8 fish • km^{-1} observed at a station.

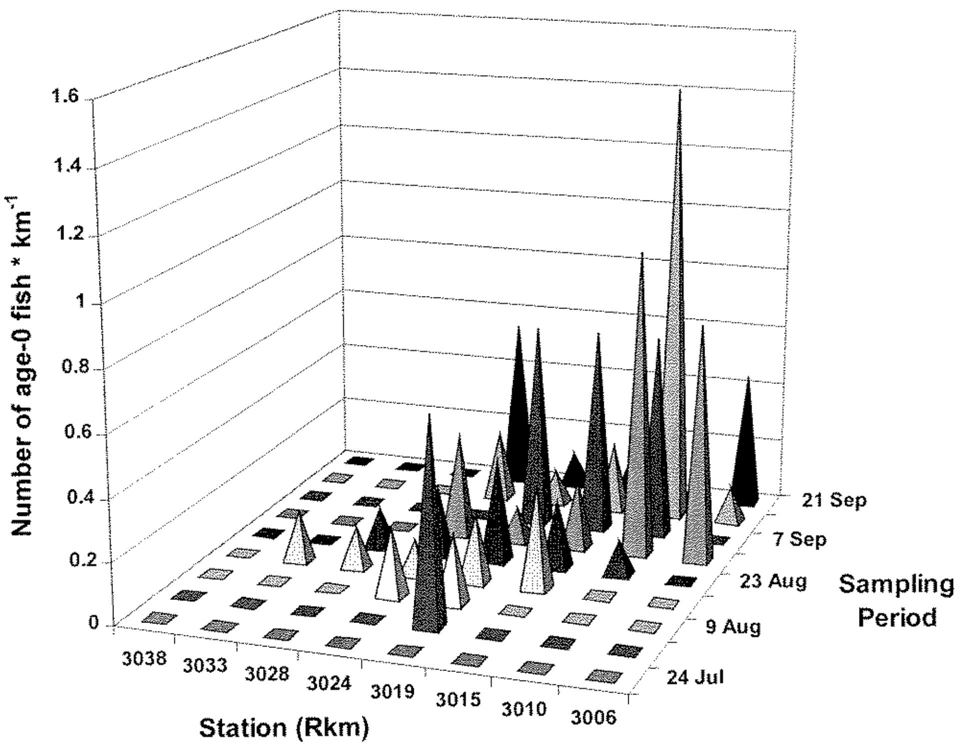

Figure 7. Counts of age-0 paddlefish • km^{-1} observed by date and location in 1998. River kilometer (rkm) 3,038 is up-reservoir (near CK Creek), and rkm 3,006 is down-reservoir (near Swan Creek).

Age-1 paddlefish were first observed at rkm 3,019 on 1 August (Figure 8). Few fish were seen in the up-reservoir stations; no fish were observed in station rkm 3,038 or rkm 3,033 and counts of less than 0.25 fish • km^{-1} were observed on three occasions at rkm 3,028 or rkm 3,024. Higher counts of fish occurred down-reservoir of rkm 3,024 with the highest count of 0.67 fish • km^{-1} appearing at rkm 3,015 on 9 August, 16 August, and 8 September. Few age-1 paddlefish were observed after the first week of September.

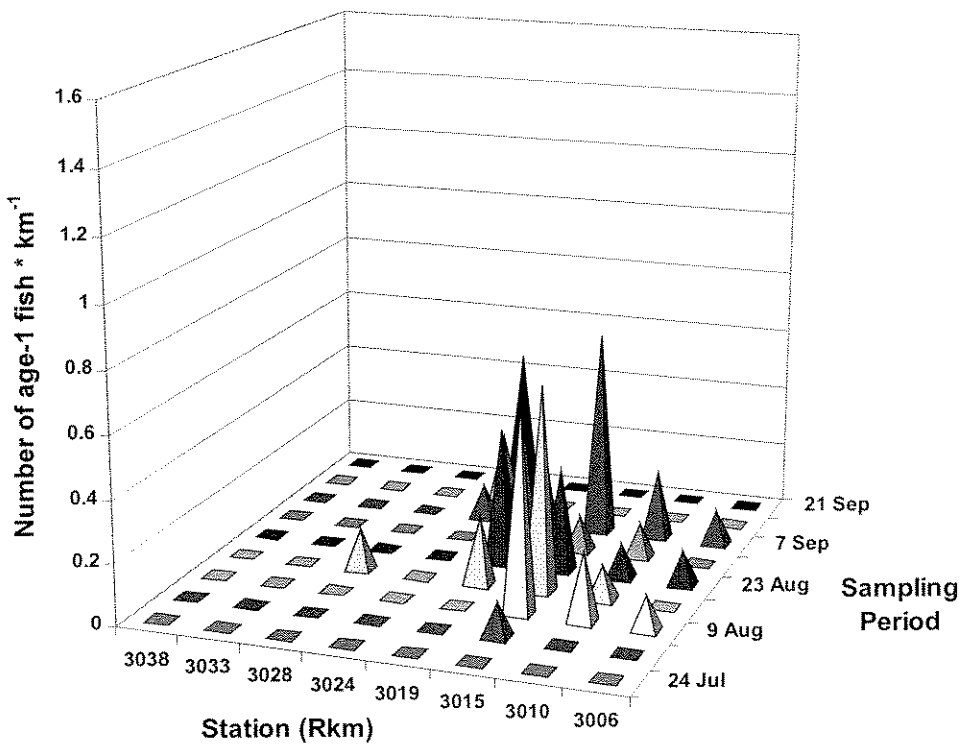

Figure 8. Counts of age-1 paddlefish • km^{-1} observed by date and location in 1998. River kilometer (rkm) 3,038 is up-reservoir (near CK Creek), and rkm 3,006 is down-reservoir (near Swan Creek).

Counts in 1999

During 1999, a total of 3 age-0 and 10 age-1 paddlefish were counted during the monitoring of 174 transects. Age-0 paddlefish were first observed on 9 September at rkm 3,010 and rkm 3,006 at a count of 0.167 fish • km^{-1}, and were observed on only one more occasion, 17 September, also at rkm 3,006.

The assessment of the relationship between water transparency (Secchi depth), organism density, and age-0 counts was not achievable due to the very low age-0 counts (Figure 9). In comparison with 1998, similar habitat, water clarity, and invertebrate densities occurred in 1999, but few age-0 paddlefish were present.

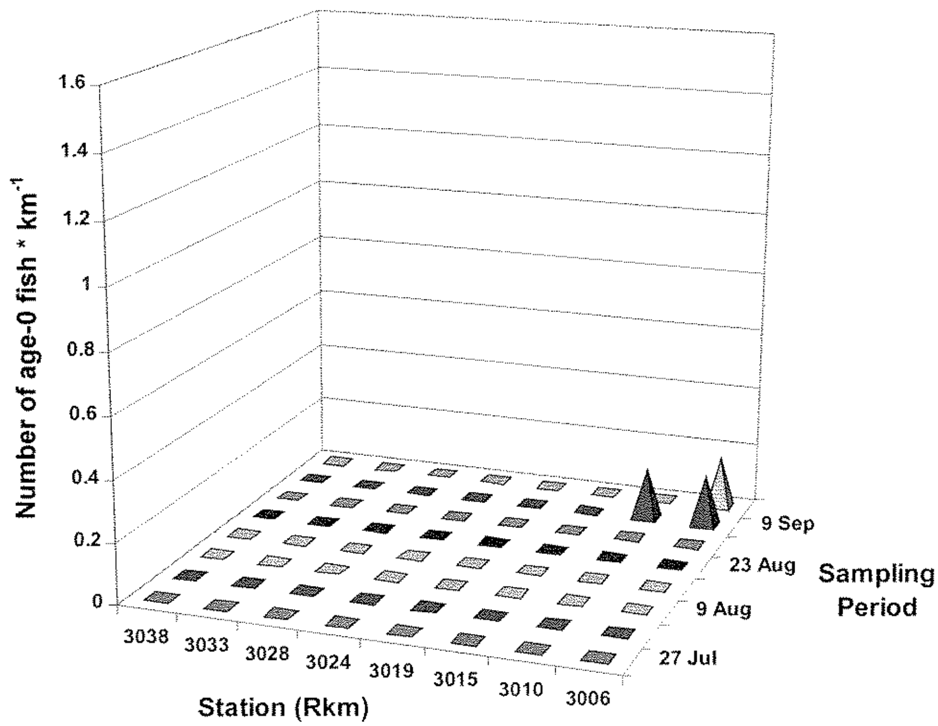

Figure 9. Counts of age-0 paddlefish • km^{-1} observed by date and location in 1999. River kilometer (rkm) 3,038 is up-reservoir (near CK Creek), and rkm 3,006 is down-reservoir (near Swan Creek).

Age-1 paddlefish were first observed on 9 August at rkm 3,024 and rkm 3,015 at 0.33 fish • km^{-1} and 0.17 fish • km^{-1}, respectively (Figure 10). The highest count of 0.5 fish • km^{-1} was observed on 23 August at rkm 3,010. During 1999, few age-0 paddlefish were observed after 30 August. Counts on the surface were concentrated in the lower portion of the study area with no fish observed above rkm 3,024.

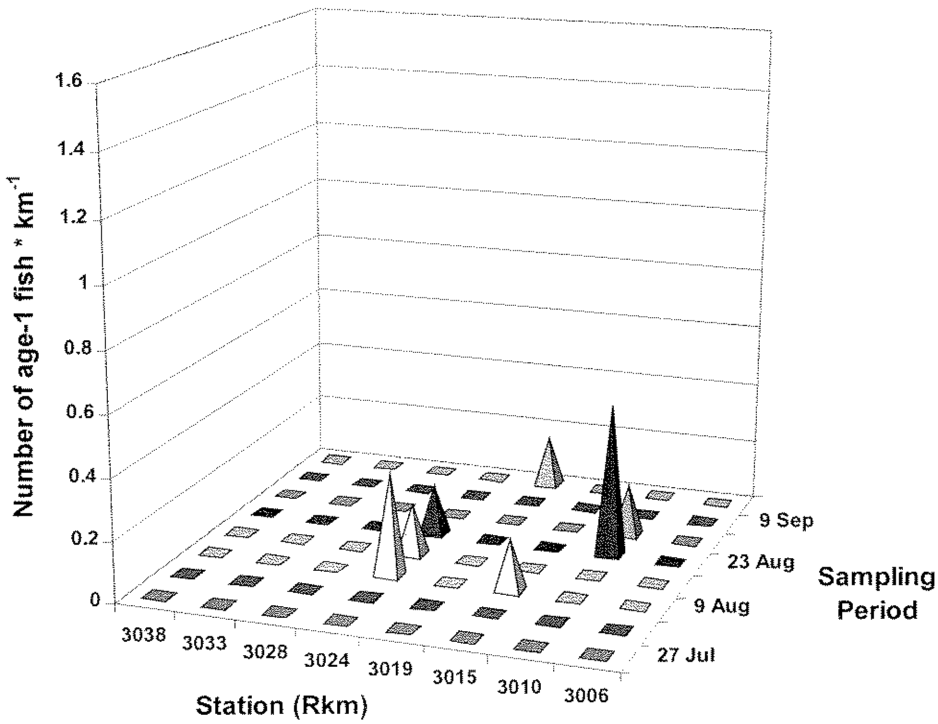

Figure 10. Counts of age-1 paddlefish • km^{-1} observed by date and location in 1999. River kilometer (rkm) 3,038 is up-reservoir (near CK Creek), and rkm 3,006 is down-reservoir (near Swan Creek).

No apparent relationship existed between water transparency (Secchi depth), invertebrate density, and age-0 fish counts during 1998 (Figure 11). Age-0 paddlefish did not consistently use areas with higher invertebrate densities such as those areas near rkm 3,006. They also did not utilize a narrow range of water transparencies, but instead were most often counted in areas with Secchi depths from 20 to 40 cm.

Temporal and spatial aspects of counts

The effect of sampling period, station, and their interaction was not constant across fish ages or years. For age-0 paddlefish during 1998 (Table 1), the interaction between sampling period and station was highly significant (ANOVA; $p = 0.0006$). This result is apparent in that age-0 paddlefish were seen throughout study area (except the riverine portion) during at least a portion of the year (Figure 7). The interaction also implies that the area used by age-0 paddlefish changed as the season progressed; concentrations after first appearance were observed from rkm 3,024 to 3,019. As the season progressed, concentrations of age-0 paddlefish were seen increasingly farther down-reservoir, and the highest count was observed at rkm 3,010 on 14 September.

For age-1 paddlefish during 1998 (Table 2), no interaction between the main effects was found (ANOVA; p = 0.2720). Age-1 paddlefish were rarely observed in stations located in the upper half of the study area from rkm 3,038 through rkm 3,024 and more often seen in down-reservoir areas (ANOVA; p = 0.0193). Counts of age-1 paddlefish were comparable across sampling periods after first appearance and before their disappearance from the surface in fall (ANOVA; p = 0.0809).

Table 1. A repeated measures factorial analysis of variance (ANOVA) for age-0 fish in 1998 with the effects of station, transect, sampling period, and interaction.

Source	DF	S. of Squares	Mean Square	F Value	Pr > F
Model	87	20.0347	0.2303	2.49	0.0001
Error	128	11.8230	0.0924		
Corrected Total	215	31.8577			
Station	7	3.1193	0.4456	1.62	.2017
Transect (Station)	16	4.4143	0.2759	2.99	.0003
Sampling Period	8	2.0236	0.2529	2.74	.0080
Station * Speriod	56	10.4775	0.1871	2.03	.0006

Table 2. A repeated measures factorial analysis of variance (ANOVA) for age-1 fish in 1998 with the effects of station, transect, sampling period, and interaction.

Source	DF	S. of Squares	Mean Square	F Value	Pr > F
Model	87	7.1375	0.0820	1.55	.0114
Error	128	6.7545	.0528		
Corrected Total	215	13.8920			
Station	7	1.8070	0.2581	3.44	0.0193
Transect (Station)	16	1.2010	0.0751	1.42	0.1411
Sampling Period	8	0.7640	0.0955	1.81	0.0809
Station * Speriod	56	3.3656	0.0601	1.14	0.2720

Physical and biotic characteristics of the habitat

In 1998, the up-reservoir section of the study area (rkm 3,042.5-3,030) was characterized by low invertebrate densities (mean for rkm 3,038 and 3,033, 21 organisms • m^{-3}), consisting mostly of drifting macroinvertebrates from the orders of Ephemeroptera, Plecoptera, and Diptera (Chironomidae). Depth averaged 2.5 meters. Water transparency showed a temporal trend with measurements below 25 cm through mid-August, but increasing to more than 40 cm by 14 September (Figure 11). Current velocity measurements were consistently higher than the rest of the study area (mean, 0.56 m • s^{-1}). Surface water temperature was stable through August (mean, 21.5 ° C), and decreased to 17° C by 21 September.

The down-reservoir section of the study area (rkm 3,020-3,003.1) was characterized by higher invertebrate densities (mean for rkm 3,019 through 3,006, 7461 organisms • m^{-3}), especially down-reservoir of rkm 3,010 where density commonly exceeded 10,000 organisms • m^{-3}. The invertebrate community in this section of the reservoir was numerically dominated by crustacean zooplankton, mainly *Daphnia sp.* and cyclopoid copepods. In addition, the few *Leptodora kindtii* captured were collected at or down-reservoir of rkm 3,010. Depth in this section ranged from 2 m at the up-reservoir portion to 8.4 m near the down-reservoir boundary of the study area (mean, 5.3 m). Water transparency reached its maximum (76 cm) and highest mean (mean, 33.9 cm) in this section (Figure 11). Current velocity was lower than in upstream transects (mean, 0.09 m • s^{-1}). Overall, surface temperature (mean, 22.9° C) was one Celsius degree higher than in the up-reservoir and transition sections, as well as more variable, increasing rapidly to 29° C by 16 August then declining to 17° C by 21 September.

The transitional area (rkm 3,030-3,020) was intermediate compared to the down-reservoir and up-reservoir portions of the study area in current velocity (mean, 0.18 m • s^{-1}) and invertebrate density (mean, 319 organisms • m^{-3}). Depth (mean, 5.66 m), water transparency (mean, 22.26 cm), and temperature (mean, 21.33° C) were lower than the lotic section. Depth decreased to a point where modest winds continually redistributed accumulated, benthic sediments in the water column, resulting in reduced water transparency compared to the down-reservoir section.

In 1999, overall trends for current velocities, invertebrate densities, depths, water transparencies, and temperatures were similar to those measured in 1998 (Figure 12). Substantial differences were found in measurements of invertebrate densities, depths, water transparencies, and temperatures, and overall, the study area was shallower, colder, supported less secondary production, and the water was less transparent than in 1998 (Table 3).

Table 3. Descriptive statistics for variables measured in 1998 and 1999.

Variable	Year 19--	N	Mean	Standard Deviation	Minimum	Maximum
Age-0 fish • km^{-1}	98	216	0.15	0.38	0.00	2.33
	99	174	0.01	0.07	0.00	0.50
Depth	98	216	12.1	7.32	2.30	27.40
	99	174	10.1	7.08	1.50	25.00
Secchi depth	98	216	30.0	13.35	2.00	76.00
	99	174	28.4	12.70	5.00	77.00
Current Velocity	98	216	0.23	0.22	0.00	0.70
	99	174	0.24	0.20	0.01	0.77
Temperature	98	216	22.2	2.55	16.00	29.00
	99	174	20.6	2.89	14.44	27.78
Invertebrate	98	216	3,828	11,262.00	0.00	78,569.00
Density	99	174	2,462	5,628.00	0.00	34,332.00

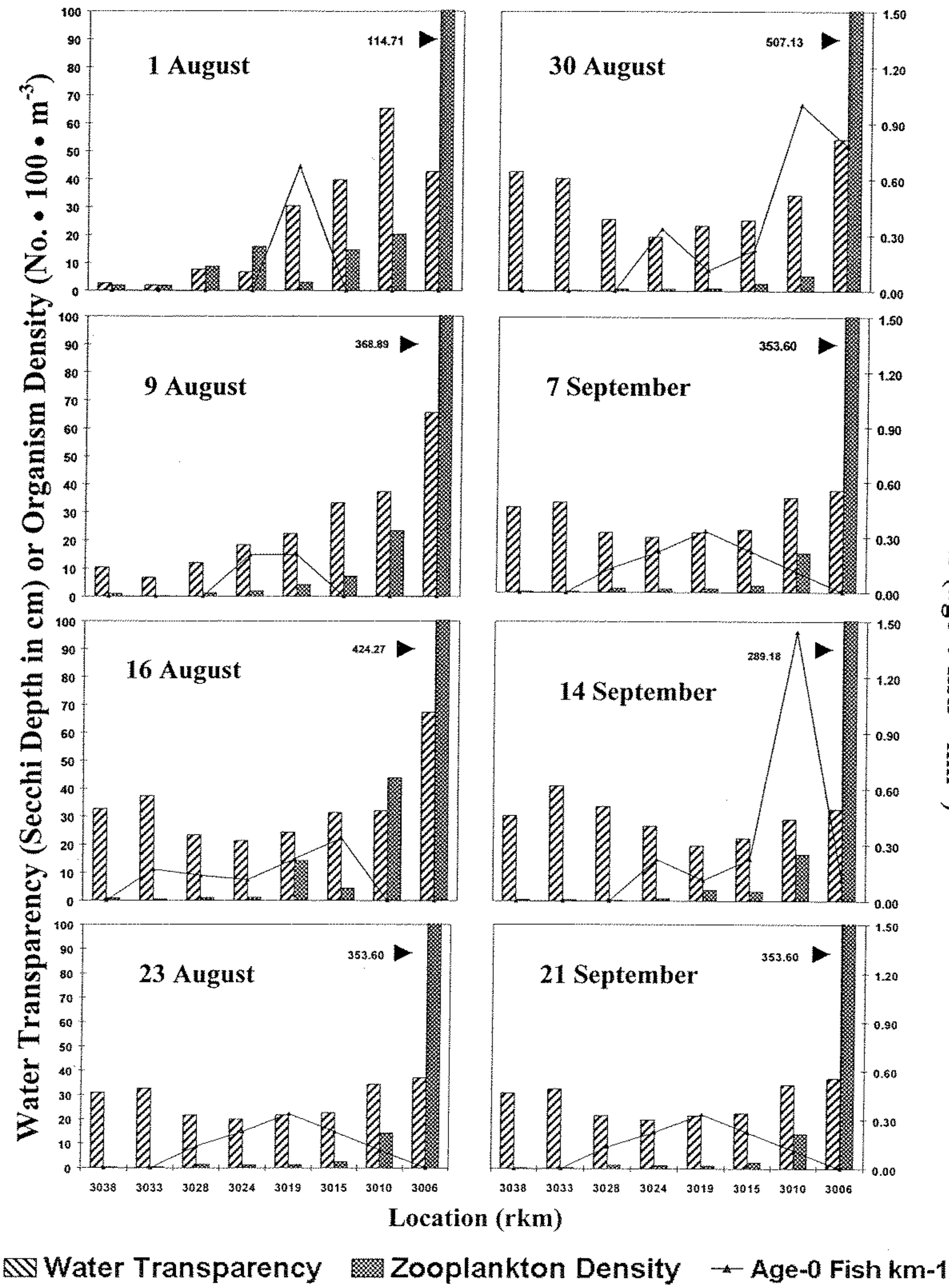

Figure 11. Plots of water transparency, zooplankton and suspended invertebrate density (combined), and age-0 fish • km^{-1} in 1998. If invertebrate density exceeds the graph scale, the density is displayed in the upper right.

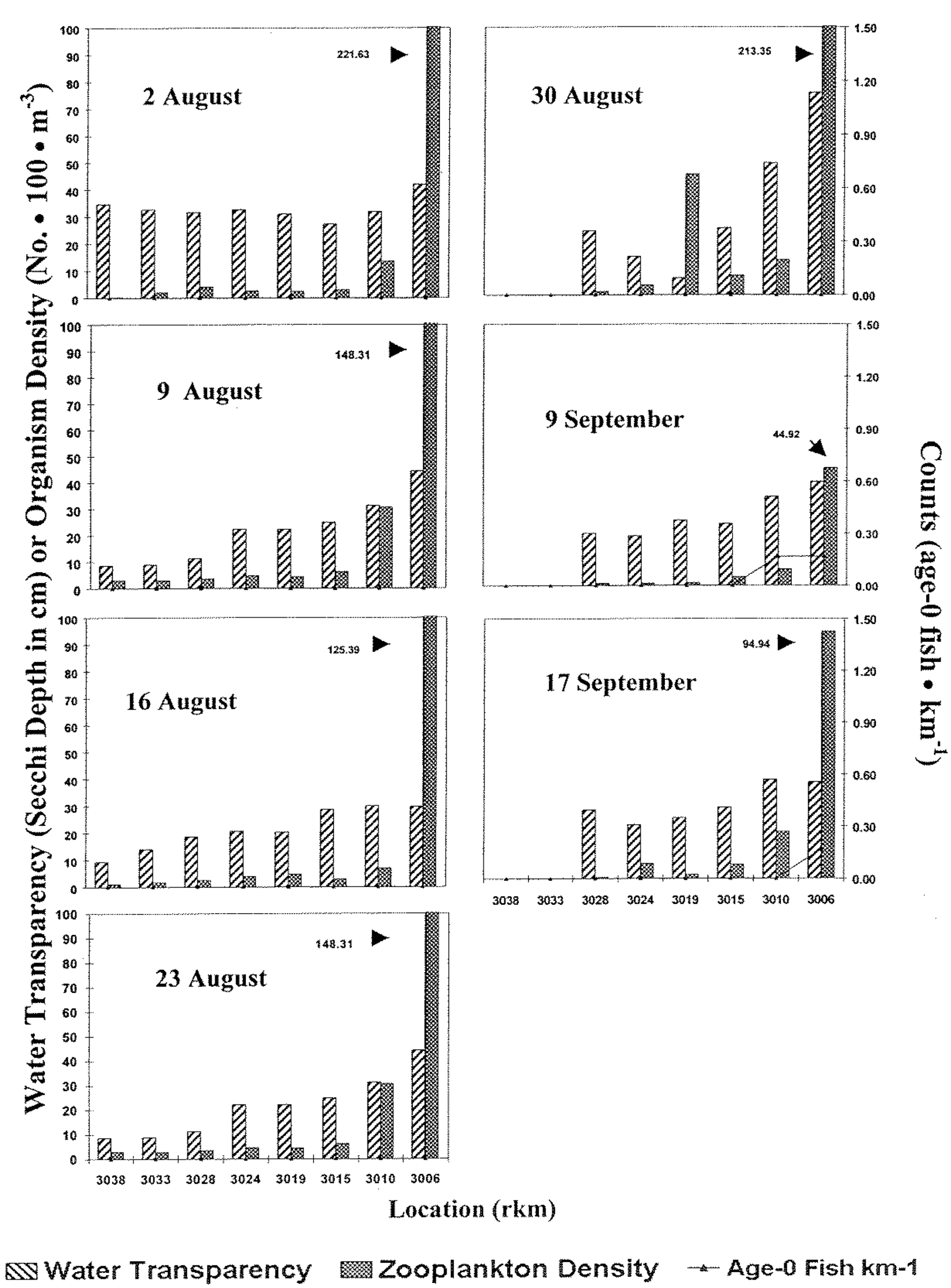

Figure 12. Plots of water transparency, zooplankton and suspended invertebrate density (combined), and age-0 fish • km^{-1} in 1999. If invertebrate density exceeds the graph scale, the density is displayed in the upper right corner.

Relationship between habitat characteristics and age-0 counts

Significant, positive correlations were found between depth vs. Secchi depth, depth vs. invertebrate density, Secchi depth vs. invertebrate density, and wave height vs. cloud cover during both 1998 and 1999 (Table 4). Significant, negative relationships were found between depth vs. current velocity and current velocity vs. invertebrate density in both years. All other correlations were insignificant ($p > 0.05$) in both years.

Correlations between age-0 paddlefish • km^{-1}, the main variable of interest, and habitat variables were only evaluated for 1998. Significant relationships were found between age-0 paddlefish • km^{-1} vs. current velocity ($r = -0.19$, $p = 0.0041$), and age-0 paddlefish • km^{-1} vs. wave height ($r = 0.15$, $p = 0.0012$).

Table 4. Correlation coefficients for age-0 paddlefish counts and habitat variables for 1998 and 1999. Significant correlations (rejection of $r = 0$ at $p = 0.05$) are in bold.

	Year 19--	Age-0 km^{-1}	Depth	Water Transparency	Wave Height	Cloud Cover	Current Velocity	Surface Temperature	Organism Density
Age-0 Fish • km^{-1}	98	1.00							
	99								
Depth	98	0.12	1.00						
	99		1.00						
Water Transparency	98	-0.01	**0.50**	1.00					
	99		**0.58**	1.00					
Wave Height	98	**0.15**	0.05	-0.06	1.00				
	99		**0.16**	-0.06	1.00				
Cloud Cover	98	0.02	**0.23**	-0.06	**0.22**	1.00			
	99		**-0.17**	-0.11	**0.17**	1.00			
Current Velocity	98	**-0.19**	**-0.44**	-0.07	-0.11	0.08	1.00		
	99		**-0.36**	**-0.30**	**-0.16**	0.11	1.00		
Surface Temperature	98	-0.05	**0.27**	-0.01	-0.01	**0.30**	**-0.31**	1.00	
	99		0.05	0.11	-0.01	**-0.38**	-0.10	1.00	
Organism Density	98	0.00	**0.54**	**0.46**	0.11	**0.21**	**-0.22**	**0.17**	1.00
	99		**0.64**	**0.54**	0.01	-0.11	**-0.26**	0.09	1.00

Zooplankton and suspended invertebrate community structure

Relative dominance of particular taxa, based on percent composition, shifted from up-reservoir to down-reservoir areas (Figure 13, 14). Chironomids often represented over fifty percent of the community above rkm 3,028, but declined below ten percent by rkm 3,019 and to near zero percent in more down-reservoir areas. Cladocerans were nearly absent in up-reservoir areas (above rkm 3,033), but by rkm 3,028, cladocerans became the most common organisms sampled. Cyclopoid copepods and cyclopoid copepod nauplii replaced chironomids as the most abundant taxon down-reservoir of rkm 3,028. *Daphnia*, one of the larger zooplankton taxa present in the study area, were never common, but did reach their maximum near rkm 3,006 through the first eight weeks and declined rapidly during the last two weeks of sampling. *Leptodora kindtii* were included in the other category and were never common in surface tows. In fact, *Leptodora* were identified in only five surface samples during the two-year study. In each case, these organisms were collected at rkm 3,006, the most down-reservoir station.

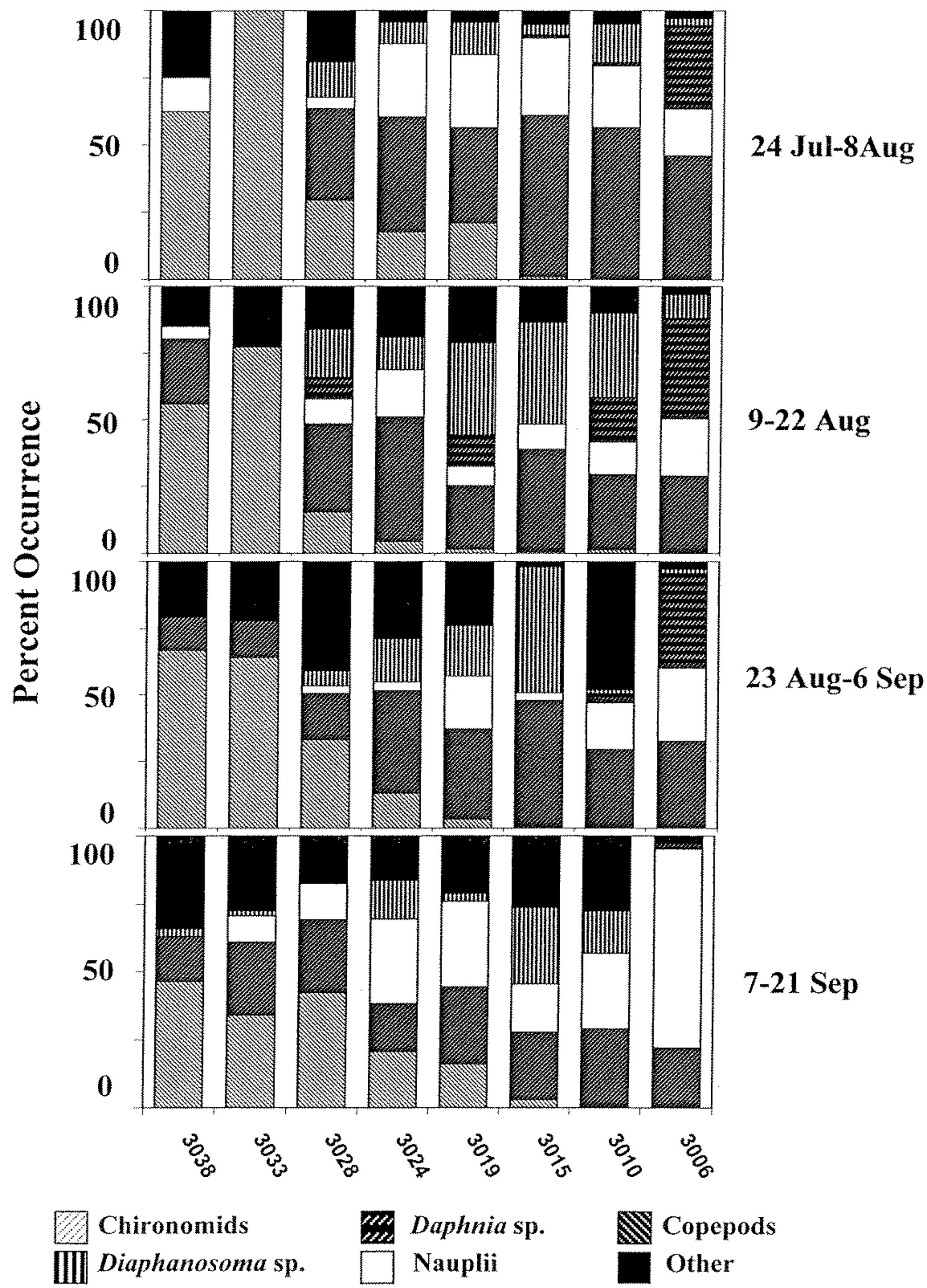

Figure 13. Frequency of occurrence of zooplankton and suspended invertebrates in 1998. The most common taxa are shown individually and remaining taxa are combined (Other). Samples are combined into four successive sampling periods and by station.

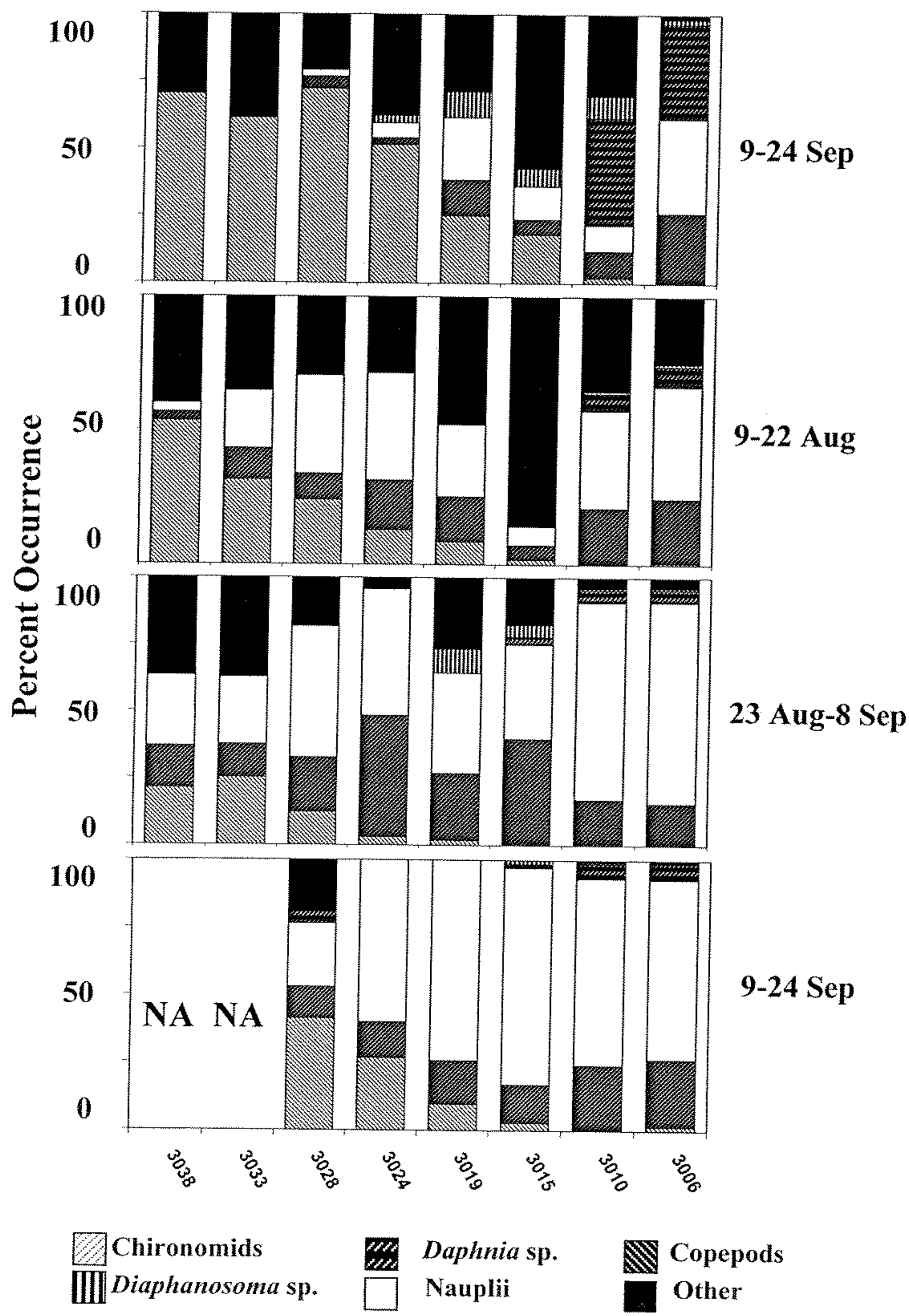

Figure 14. Frequency of occurrence of zooplankton and suspended invertebrates in 1999. The most common taxa are shown individually and remaining taxa are combined (Other). Samples are combined into four successive sampling periods and by station.

DISCUSSION

Prior to this study, the ability to count age-0 paddlefish as a means of assessing year-class strength had been reported only for the stock of paddlefish residing in Lake Sakakawea, North Dakota, the Missouri River mainstem reservoir downstream of Fort Peck Lake. Previously on Lake Sakakawea, a total of 220 and 1,551 age-0 paddlefish were counted along transects during 1992 and 1993 with mean counts as high as 22.9 fish • $transect^{-1}$ (Fredericks and Scarnecchia 1997). During 1996, Scarnecchia et al. (1997) captured 2,360 age-0 paddlefish from 2-15 Aug on Lake Sakakawea, despite capturing only about one-third of the age-0 paddlefish observed. Counts in 1997 and 1998 were 361 and 444 age-0 fish, respectively

During preliminary investigations for this study in 1997 in the upper reaches of Fort Peck Lake, at least 250 age-0 paddlefish were counted in one afternoon. In this study, counts of age-0 paddlefish were low (overall mean, 0.15 fish • km^{-1}) in 1998 and even lower (overall mean, 0.01 fish • km^{-1}) in 1999.

There are several possible explanations for the low number of age-0 paddlefish observed during the two years of this study. Paddlefish reproductive success is thought to depend on the characteristics of a naturally functioning river system, especially the spring hydrograph. A somewhat predictable spring rise serves as a spawning migration cue, inundates additional spawning areas, and may be necessary for final egg deposition (Russell 1986). Upstream of Fort Peck Lake, Berg (1981) noted that adult paddlefish could be found in staging areas when river flows were below 400 $meters^3$ • sec^{-1}. As flows increased above 400 $meters^3$ • sec^{-1}, paddlefish moved to areas possessing gravel bars and adequate water velocities, which he thought to be probable spawning areas.

Berg speculated that this critical flow level, also known as trigger flow, during May through mid-June is necessary for successful reproduction. Berg was unable to relate the number of age-0 fish produced to the number of spawners, and thus could provide no evidence in support of this claim.

In a theoretical average year (calculated from 63 years of historical data measured at the Virgelle gauge), mean daily flow exceeds 400 $meters^3 \bullet sec^{-1}$ for 47 days from 18 May to 3 July (USGS 1998). Within the last twenty years, flows exceeding 400 $meters^3 \bullet sec^{-1}$ for over forty days occurred in only 7 years and four of those years were 1980, 1981, 1982, and 1984. When preliminary sampling in Fort Peck Lake was conducted in 1997, mean daily flow exceeded 400 $meters^3 \bullet sec^{-1}$ for 65 days from 2 May to 5 July 1997. High flows during 1998, the first year of intensive sampling, were reduced and delayed compared to 1997 or historical mean daily flows (Figure 4). A mean daily flow of 400 $meters^3 \bullet sec^{-1}$ was first exceeded on 18 June, remained above this level for 31 consecutive days, and declined below this level on 19 July 1998. The timing of high flows was thus approximately one month later than an average year. During 1999, a mean daily flow of 400 $meters^3 \bullet sec^{-1}$ was first exceeded on 3 June, remained above this level for only 13 consecutive days, and declined below this level on 15 June 1999. Thus, high spring discharge in 1999 was later and of shorter duration than a theoretical average year, providing even poorer spawning conditions than the sub-optimal spawning conditions available in 1998. Research efforts should continue until the relationship between spring spawning conditions and strong or weak year classes is better understood.

Another possible explanation for low counts of age-0 paddlefish is that the upper Fort Peck stock of paddlefish is substantially smaller than the Lake Sakakawea stock.

Although accurate population estimates are unavailable for either stock, in the absence of these data, total adult harvest may reflect relative stock size. Although less fishing effort is expended on the upper Fort Peck stock, paddlefish harvest has never exceeded 712 individuals • $year^{-1}$ from 1973 to1998 (Gilge and Liebelt 1999). An estimated 236 adult paddlefish were harvested from the upper Fort Peck stock during 1998. Since most adult paddlefish are harvested while migrating to spawning areas, it is probable that a relatively low number of fish migrated to spawning areas in 1998.

In contrast, the Lake Sakakawea stock is substantially larger with harvest averaging 2,721 individuals from 1995 through 1998. During 1998 and 1999, approximately 1800 adult fish were harvested from this stock. In both of these years, large numbers of age-0 paddlefish were captured and enumerated in Lake Sakakawea throughout late July, August, and early September.

Lastly, the behavioral tendency for age-0 paddlefish to concentrate at the surface may differ among reservoirs due to reservoir morphology or other reasons. The valley width of the Missouri River in what is now Lake Sakakawea is substantially wider than the valley width of upper Fort Peck Lake. Therefore, The Missouri River changes relatively slowly into Lake Sakakawea and has more available rearing habitat below five meters. In contrast, the habitat in upper Fort Peck Lake changes from riverine to reservoir with depth exceeding five meters in approximately 15 kilometers and provides less rearing habitat in the transitional area.

If I effectively monitored the relative abundance of age-0 and age-1 paddlefish, this study suggest that successful reproduction occurs irregularly and is at least partially influenced by the timing and duration of high spring flows.

Little data exists on the spatial and temporal distribution of age-0 paddlefish in river or reservoir habitats. Fredericks (1994) observed concentrations of age-0 fish in lentic habitats from RM 1518 to RM 1515 during late August 1993. As the season progressed, concentrations of age-0 paddlefish became more uniform and encompassed most of his 34 km study area. In this study, we selected the study site so that it would contain both lentic and lotic habitat. Within this study site, the null hypothesis of equal spatial and temporal distribution of age-0 and fish was rejected. Age-0 paddlefish rarely used lotic habitat. Instead, concentrations were observed in the middle portion of the study area during August. As the season progressed, concentration of age-0 paddlefish moved farther down-reservoir similar to the results observed by Fredericks (1994).

Although this study shows that age-0 and age-1 paddlefish can be counted at the surface of Fort Peck Lake in the same manner as Lake Sakakawea (Fredericks and Scarnecchia 1997), counts in 1998 and 1999 were too low to provide detailed information of distribution and abundance of age-0 fish. When spawning conditions are better in future years, sampling will hopefully yield more fish and permit a more detailed assessment of distribution and abundance.

CHAPTER 2. FEEDING ECOLOGY OF AGE-0 AND AGE-1 PADDLEFISH

ABSTRACT

Food habits of wild, age-0 and age-1 paddlefish *Polyodon spathula* were investigated in July-September, 1998 and 1999 from fish captured over a 39.4 km protion of upper Fort Peck Lake, a Missouri River mainstem reservoir in Montana. The stomach contents of age-0 and age-1 paddlefish indicated that these age-classes feed selectively, and the diet was composed of some of the larger organisms available. In up-reservoir areas, paddlefish fed heavily on chironomid larvae, but paddlefish collected from down-reservoir areas selected for *Leptodora kindtii*. In addition, it appeared that paddlefish selected larger individuals of *Leptodora kindtii*. The use of filter-feeding was observed in only one 328 mm body length (BL) individual. A stomach fullness index indicated that age-0 paddlefish were able to feed efficiently in both up-reservoir and down-reservoir areas when large preferred prey items were available, but fed less efficiently in the middle portion of the study area where few large prey were available. The size of age-0 paddlefish in 1998 was smaller than reported in the literature, but growth was rapid and age-0 fish averaged 136.5 mm BL by 10 September, an average similar to those reported in the literature for stocks from northern latitudes.

INTRODUCTION

Optimal foraging theory suggests that predators will attempt to maximize benefits through the intake of quality food while minimizing costs (Krebs 1978). Costs may involve increased energy expenditures to capture and ingest a particular food item or increased vulnerability to predation while feeding. O'Brien (1979) described predation as a series of steps that include the location, pursuit, attack, and capture of prey and suggested that for zooplanktivorous fish, the act of locating prey is the most critical aspect of successful feeding.

Paddlefish possess two distinct foraging behaviors (Rosen and Hales 1981). Adult paddlefish are ram filter-feeders that swim through concentrations of prey with their mouths open. Prey items larger than the paddlefish filtering mechanism are impinged and swallowed (Rubenstein and Koehl 1977). Prey species found in adult paddlefish stomachs represent a wide range of body sizes, evasion abilities, and pigments (Eddy and Simer 1929, Hoopes 1960, Hoxmeier and DeVries 1997). Very small organisms such as rotifers and copepod nauplii, which are smaller than the spaces between the gillrakers, are nearly absent in stomach contents (Rosen and Hales 1981).

Small paddlefish are particulate feeders that select and attack individual prey items, and stomach contents often contain relatively large, conspicuous zooplankton species and invertebrates (Ruelle and Hudson 1977, Michaletz et al. 1982). Due to the small size of their prey, turbid foraging habitat, and the paddlefish's poorly developed eyes (Hussakof 1910), prey location by paddlefish is not primarily visual (Sanderson et al. 1994). Instead, the paddlefish's rostrum functions as an electrosensory antenna that detects individual prey items during particulate feeding life stages, and detects differing concentrations of prey during filter-feeding (Wilkens et al. 1997). When large zooplankton species are unavailable, small paddlefish may switch to the filter-feeding strategy before their gill rakers are fully developed (Michaletz et al. 1982), which may result in reduced growth rates.

Slow growth rates may negatively affect year-class strength by increasing the amount of time small paddlefish are vulnerable to predators or by reducing condition and decreasing over-winter survival.

My objectives were to determine which prey age-0 and age-1 paddlefish selected, and at what size or age paddlefish switched from particulate to filter-feeding. In addition, growth, condition, and stomach fullness index were assessed in relation to the food habits of the fish to focus on the need for understanding the relationship between paddlefish feeding success, condition, and growth as it relates to over-winter survival and year-class strength.

METHODS

Fish Collection

Age-0 and age-1 paddlefish were captured during 1998 and 1999 with long-handled dipnets as described by Scarnecchia et al. (1997). I attempted to collect and analyze paddlefish from throughout the study area, at different times of the day, and from dissimilar habitat conditions. The sampling boat was driven between 8-9.5 $km \bullet h^{-1}$ in areas where paddlefish were counted during transect sampling or during other reconnaissance. At each capture, the fish was placed in a livewell and a marker buoy was placed at the capture location. I continued sampling within a 1-2 hectare area surrounding the initial capture location until no fish could be captured. All captured fish were measured for fork length or FL (tip of the rostrum to fork of the caudal fin), body length or BL (anterior edge of the orbit to fork of the caudal fin), and weight. Age-0 and age-1 fish were visually distinguished by size. A total of 77 age-0 and 8 age-1 fish captured in 1998 were retained for stomach content analysis. During 1999, only 10 age-0, 1 age-1, and 1 age-2 paddlefish were preserved for analysis. Paddlefish retained for stomach analysis were immersed in a lethal dose of MS-222. After death occurred, a small slit was made in the abdominal cavity to insure fixation of the stomach contents (Haedrich 1983). A sequentially numbered tag was attached to each fish for identification purposes, and each fish was preserved in formalin.

During 1998, I collected and analyzed the stomach contents from 77 age-0 and 8 age-1 paddlefish captured from 27 July through 23 September. A strong temporal and spatial trend existed in the location of capture. All fish captured before 15 August were taken up-reservoir of rkm 3,020. After 15 August, all but six fish were taken down-reservoir of rkm 3,020. Age-1 paddlefish were captured for stomach content analysis from 27 July through 18 September. The five age-1 paddlefish captured in July were captured at rkm 3,035, and the remaining three were captured near rkm 3,012 during September.

During 1999, the stomach contents of 10 age-0, 1 age-1, and 1 age-2 paddlefish were collected and analyzed. All but one of the age-0 paddlefish were captured down-reservoir of rkm 3,008 and after 1 September. The age-2 and age-1 paddlefish were captured on 25 August and 8 September 1999 and at rkm 3,011.5 and 3,005, respectively.

Although paddlefish of age-0, age-1, and age-2 can in most cases be reliably separated by length, the dentaries of sacrificed fish were also used for age determination. The left jaw bone of each paddlefish considered on the basis of length to be age-1 or age-2 was removed, cleaned and sectioned with a low-speed saw (Adams 1942, Scarnecchia et al. 1996). All of the fish previously assumed to be age-1 possessed one annulus, except a 328 mm BL individual captured in 1999 that possessed two annuli.

Invertebrate Monitoring

When paddlefish were collected for stomach sampling, three, horizontal surface tows were made at the location of capture. Sampling was conducted with an 80-micron-mesh Wisconsin plankton net with 15.1 cm diameter gape. A General Oceanics flow meter suspended in the mouth allowed estimation of the water volume sampled. Tows lasted for 45 seconds. Invertebrate samples were placed in vials and preserved with 95% ethanol. All invertebrate samples were diluted, subsampled, and identified to the same taxonomic level described in chapter 1. An estimated total number of organisms • m^{-3} was computed as well as the percentage by number of each taxon present.

Stomach Removal

Preserved fish were removed from formalin and rinsed in 95% ethanol. After enlarging the ventral incision, the stomach was manipulated so that it remained outside of the body cavity. The stomach was separated from the gastrointestinal tract by making incisions at the sphincter junctions anterior and posterior of the stomach. After removing excess fluids by blotting the stomach on a paper tower, the full stomach weight was determined. The contents of the stomach were then transferred to a specimen container by cutting along the ventral surface of the stomach and rinsing the interior of the stomach with a squirt bottle. The blotted wet weight of the empty stomach was then determined. Parasitic worms were removed from the stomach contents and weighed. I then calculated the weight of stomach contents by subtracting the summed weight of parasites and the empty stomach from the full stomach weight. A stomach fullness index (SFI) was calculated by multiplying the stomach content weight by a scaling constant (10,000) and dividing by body length. The data were square root transformed to homogenize variances among the four grouped sampling periods. A one-way analysis of variance was used to test the null hypothesis of equal SFI across grouped sampling periods, and Fisher's protected LSD test was used to make pairwise comparisons.

Microscopic Analysis of Contents

After removing parasitic worms and the stomach lining from the sample container, I placed the contents into a beaker and separated large clumps of organisms. The contents were then diluted so that a 2 ml sub-sample, after being placed in a counting tray, would contain a manageable number of organisms. Whole organisms were enumerated and identified to the same taxonomic level described in objective 1. Most zooplankton were identified to genus, and most macroinvertebrates were identified to family. Some species such as *Leptodora kindtii* and chironomids were rarely found whole. *Leptodora kindtii* were identifiable by their persistent caudal spines, and chironomids were identified to family when a head capsule was found. Since each *Leptodora kindtii* contains 2 spines and pairs of spines are often separated, the total number of spines counted per sub-sample was divided by two. After enumerating the entire tray, I then selected the first 10 intact pairs of spines, and measured each spine from the point of articulation from the abdomen to its termination.

To assess possible size-selection of *Leptodora kindtii*, I measured spine length and total length of intact *Leptodora kindti* from transect samples in which this organism was identified. Spine and total length measurements were then converted to millimeters, and parameters were estimated with linear regression by fitting spine length (**SP**) to total length (**TL**) with the equation **TL** = -0.6984 + 8.0553 * **SP** ($r^2 = 0.9361$, $p < 0.01$, $n = 100$). I compared total lengths of *Leptodora kindtii* in age-0 and age-1 fish stomach versus transect samples with two-sample t tests that assumed unequal variance.

Analysis of Stomach Contents

A linear food selection index (Strauss 1979) was used to determine electivity and feeding mode. The stomach contents of a fish were compared to the three, horizontal-surface tows taken at the location of capture. Prey species identified in stomachs and tows were grouped into 8 categories to allow statistical comparison. Prey items within a category were similar in terms of body shape, agility, or ecological function (Table 5).

Table 5. Groupings of organisms used in the calculation of Strauss linear selection index values.

Leptodora	Insects	Copepods
Leptodora kindtii	*Chaoborus* sp.	Cyclopoida – sub order
	Simuliidae	
Chironomids	Watermite	**Nauplii**
Chironomidae	Ephemeroptera	Immature Cyclopoida
	Plecoptera	
Large Cladoceran	Diptera	
	Hemiptera	
Daphnia sp.		
Diaphanosoma sp.	**Small Cladocerans**	
Ceriodaphnia sp.		
Moina sp.	*Bosmina longirostris*	
Sida sp.	*Chydorus* sp.	
Latona sp.		
Polyphemus sp.		

Electivity (L) for each prey group was calculated as $L = r_i - p_i$, where p_i is the proportion of a prey group sampled from the environment and r_i is the proportion of that prey group sampled from the stomach (Strauss 1979). L can range from –1 to +1, where a value of –1 indicates strong avoidance or inaccessibility, and a value of +1 indicates strong preference. Electivity values were compared by prey group across time using the Kruskal-Wallus test. For age-0 paddlefish captured in 1998, fish were grouped into four sampling periods. If the null hypothesis of equal population distributions was rejected, I used Mann-Whitney *U*-tests to compare means from the four grouped sampling periods. This analysis could not be performed for age-1 paddlefish in either year or for the few age-0 paddlefish captured in 1999 because of small sample sizes.

Analysis of Size, Growth, and Condition

Changes in growth and condition were compared by using the length and weight data. Growth is often exponential for age-0 fish; therefore, an instantaneous growth coefficient (G) was calculated (Chapman 1968) as

$$G = \frac{\ln W_2 - \ln W_1}{\Delta T},$$

where, W_2 is the mean fish weight at the end of a sampling period, W_1 is the mean weight at the start of a sampling period, and Δ T is the time interval.

A Fulton-type condition factor was used to compare changes in well being (Anderson and Gutreuter 1983). Condition, *K*, was expressed as

$$K = \frac{W}{L^3} X,$$

where, W is weight, L is body length, and X is 100,000, an arbitrary scaling constant.

A one-way analysis of variance was used on logarithmic transformed data, which homogenized variances between sampling periods, to determine if changes in mean condition were associated with sampling periods. Pairwise comparisons of means were made with Fisher's Protected LSD (Ott 1993).

RESULTS

Food Selection by Age-0 Fish

Age-0 paddlefish selectively fed and disproportionately selected organisms from the larger prey groups (Figure 15, Appendices). In 1998, age-0 paddlefish selected most strongly for *Leptodora kindtii* and chironomids during all sampling periods (Appendix 2). Mean selection values for *Leptodora kindtii*, the most sought after prey, increased later in the season as fish moved down-reservoir from 0.07 during the period 27 July through 8 August to a maximum of 0.84 during the period 7 September through 23 September. *Leptodora kindtii* were strongly selected for after 9 August, and mean selection values were not significantly different across the final three grouped sampling periods. Selection of chironomids followed an opposite trend with relative importance decreasing as the season progressed and as mean location of capture in river kilometers (rkm) moved down-reservoir. Insects were positively selected for only during the periods 27 July through 8 August and 7 September through 23 September, and mean selection values did not differ statistically during these two time periods (ANOVA, $p = 0.2816$).

During all four sampling periods, age-0 paddlefish negatively selected the large cladoceran, cyclopoid copepod, and nauplii prey groups (Figure 15, Appendices). The nauplii prey group was strongly avoided by both age groups during both years. In addition, age-0 paddlefish consumed small cladocerans less than or equal to their availability indicating avoidance or random feeding.

I was unable to make comparisons across sampling periods for the age-0 paddlefish captured in 1999; however, their feeding behavior was similar to the age-0 fish captured previously at similar dates and locations. Cyclopoid copepods and large cladocerans were avoided (Figure 16, Appendices). Small cladocerans were absent from all age-0 stomachs and the adjacent surface-invertebrate samples. The chironomids and insects were selected in proportion to their low abundance. *Leptodora kindtii* was strongly selected for by the ten age-0 fish examined ($L = 0.96$).

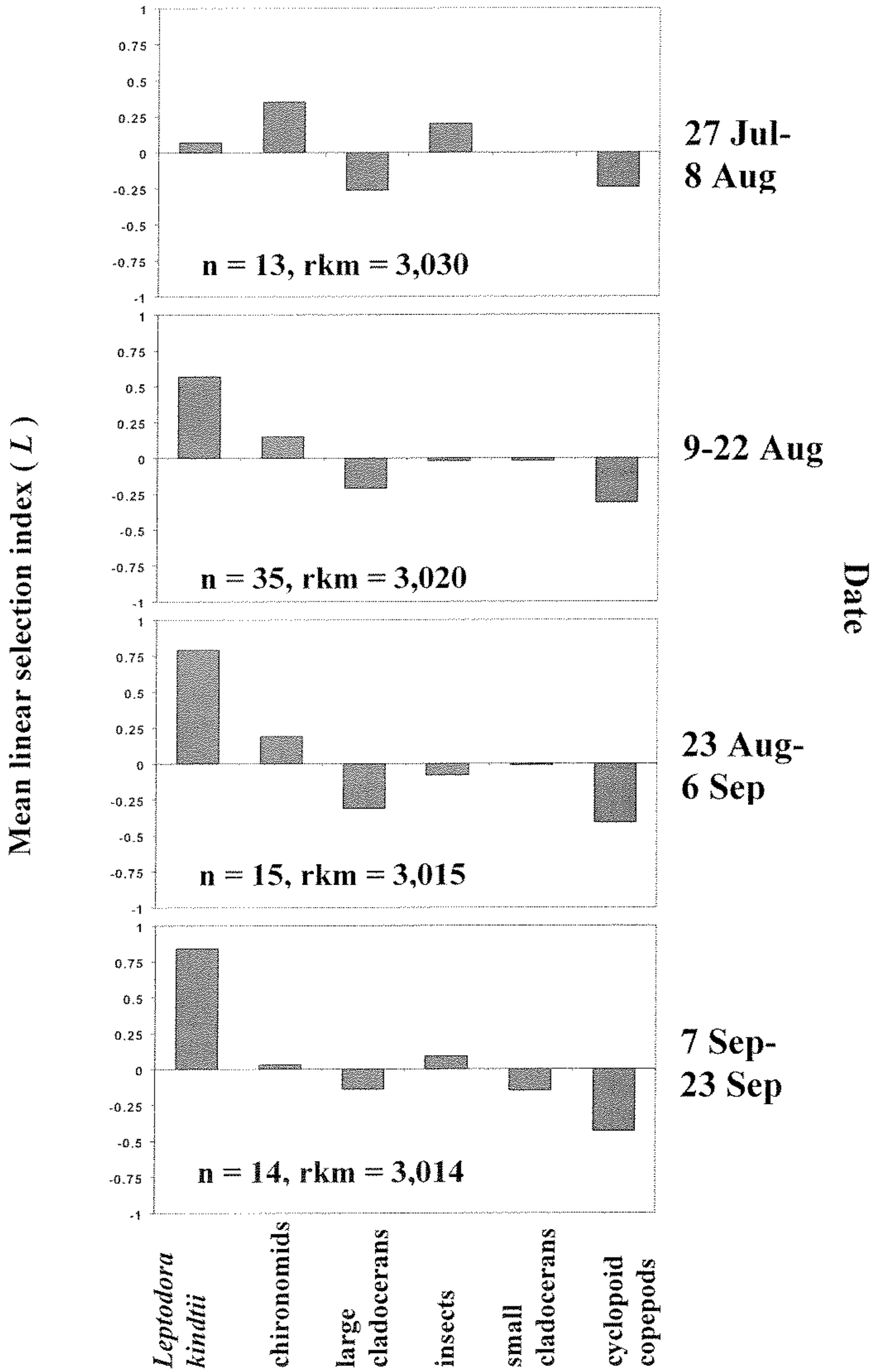

Figure 15. Mean selection index values (Strauss 1979), mean capture location, and sample size of age-0 paddlefish captured for stomach content analysis during 1998.

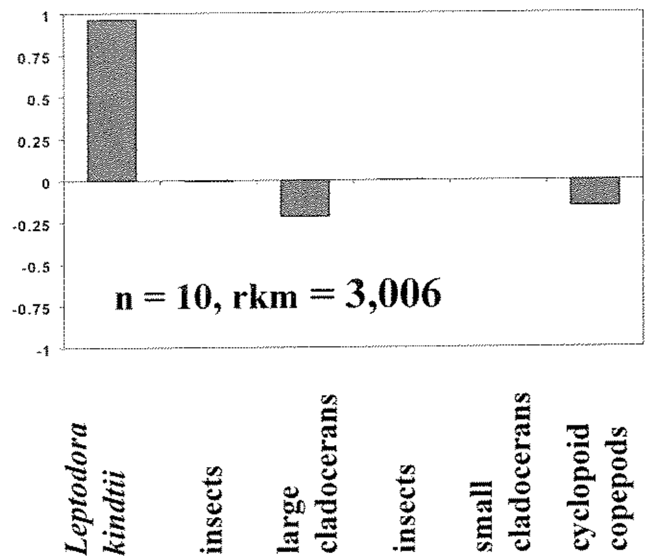

Figure 16. Mean selection index values (Strauss 1979), mean capture location, and sample size of age-0 paddlefish captured for stomach content analysis during 1999.

Food Selection by Age-1 Fish

During 1998, stomach contents of age-1 paddlefish were collected from two distinct time periods in late July (n = 5) and early September (n = 3) differed. Stomachs collected in late July were from fish captured in up-reservoir locations near rkm 3,035. At this location, *Leptodora kindtii* and small cladocerans were absent from stomachs and the surface according to horizontal tows ($L = 0$). Insects ($L = 0.24$) and chironomids ($L = 0.51$) were positively selected (Appendices). Age-1 paddlefish avoided large cladocerans ($L = -0.39$) and cyclopoid copepods ($L = -0.16$). The age-1 paddlefish captured in early September were captured farther down-reservoir near rkm 3,012. When compared to those paddlefish captured earlier in the year, preference shifted from the chironomids to *Leptodora kindtii* ($L = 0.47$), while selection for the insects remained positive ($L = 0.33$). Large cladocerans ($L = 0.03$) and chironomids ($L = -0.01$) were selected in close accordance to their abundance. Age-1 paddlefish avoided small cladocerans ($L = -0.22$)

and cyclopoid copepods (*L* = -0.49).

Stomach contents of the two larger paddlefish captured in 1999 differed substantially (Appendices). The smaller fish (BL = 253 mm), aged as 1+, captured on 8 September at rkm 3,005 fed much like the age-0 paddlefish captured in both years and the age-1 paddlefish captured in 1999; it strongly selected for *Leptodora kindtii* (*L* = 0.94) and avoided large cladocerans (*L* = -0.41) and cyclopoid copepods (*L* = -0.24). The larger fish (BL = 328 mm), aged as 2+, captured on 25 August at rkm 3,012 was the only fish captured during this study that showed some evidence of filter-feeding. It nevertheless slightly selected for *Leptodora kindtii* (*L* = 0.20), large cladocerans (*L* = 0.52), and cyclopoid copepods (*L* = 0.28).

During 1998, forty seven age-0 (61%) and 2 age-1 (25%) paddlefish stomachs contained *Leptodora kindtii*. The following year, 10 age-0 (100%), 1 age-1 (100%), and 1 age-2 paddlefish stomachs contained this organism. The mean length of *Leptodora kindtii* collected from horizontal surface tows was significantly less (t-test, $p < 0.0001$) than the mean length of *Leptodora kindtii* measured from stomachs in both age classes of fish in both years (Table 6).

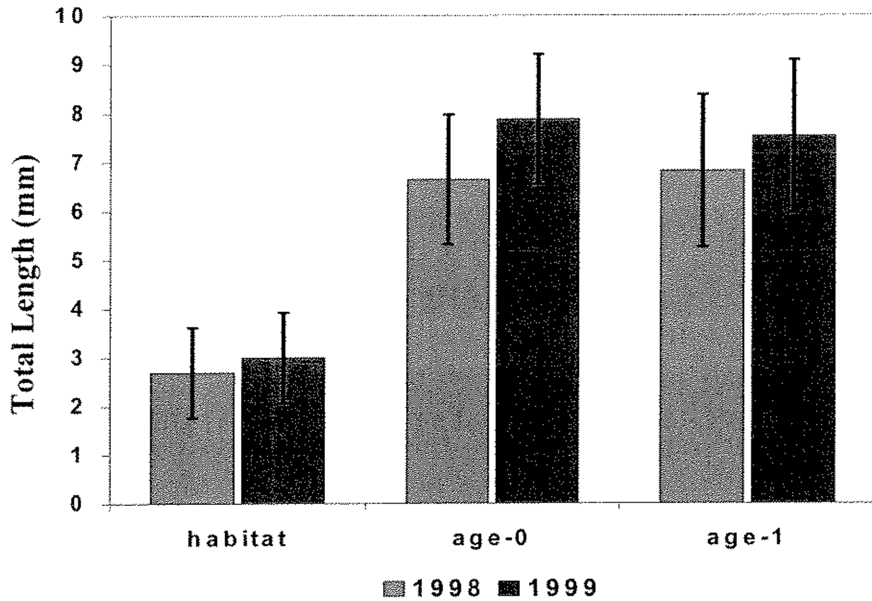

Figure 17. Estimated total length (mm) and standard deviation of *Leptodora kindtii* collected from horizontal surface tows, age-0 paddlefish stomachs, and age-1 paddlefish stomachs during 1998 and 1999.

Variation in Feeding Activity

During 1998, stomach fullness index (SFI) by sampling period varied from 235 to 401. Stomachs were most full from 27 July through 8 August when age-0 fish strongly selected chironomids in up-reservoir areas (Table 6). Stomach fullness was less for 24 August through 6 September and 9 through 23 September when age-0 paddlefish were strongly selecting *Leptodora kindtii* in down-reservoir areas, and did not differ between these sampling periods (ANOVA, $p = 0.2443$). Paddlefish stomachs were the least full during 9 through 22 August, when age-0 paddlefish were concentrated in areas with low prey abundance near rkm 3,020 (Figure 11).

During 1999, age-0 paddlefish captured from 8 to 20 September were fuller than age-0 paddlefish captured at a similar time during 1998 (mean SFI 1999 = 376, mean SFI 1998 = 256). The mean location of capture in 1999 was approximately 8 rkm farther down-reservoir at rkm 3,006. Zooplankton density increased near rkm 3,006, coinciding with paddlefish stomachs from down-reservoir areas that were fuller.

Length, Weight, and Condition

In 1998, 185 age-0 and 27 age-1 paddlefish were captured from 27 July through 24 September. Mean body length and weight of age-0 paddlefish increased throughout the study period, except from 14 September through 24 September when both body length and weight decreased, perhaps a result of the low number (n = 9) of fish captured in the final sampling period (Figure 17). Age-0 paddlefish were most vulnerable to capture with dipnetting at a body length of 110-150 mm (Figure 19).

In 1999, three age-0 paddlefish were captured in each of four sampling periods from 23 August through 22 September. Mean body length and weight, initially 112 mm and 21 grams, increased to a maximum of 165 mm and 61 grams by 1 September (Figure 18). In the following two weeks, mean body length declined. The small sample size and random trend in mean body lengths did not allow me to compare body length or weight within 1999 or across years.

During 1998, condition factor was initially high measuring 1.39 and 1.42 during 24-31 July and 1-8 August, respectively. Afterwards, condition factor was less than 1.30, except during 30 August to 8 September (mean, 1.32). During 1999, mean condition factor exceeded 1.30 in all sampling periods when fish were captured. The corresponding mean condition factors for 23-29 July, 30 July-8 September, 9-16 September, and after 17 September were, 1.30, 1.35, 1.46, and 1.42.

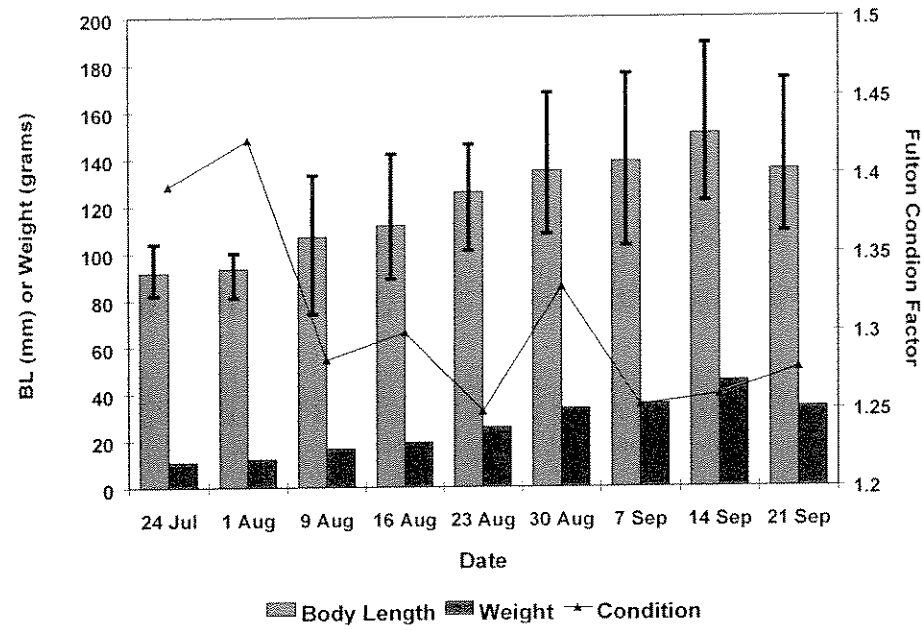

Figure 18. Mean body length, weight and Fulton condition factor for age-0 paddlefish captured in 1998. The dates on the x-axis represent the starting date of a sampling period and the error bars on body length bars represent the maximum and minimum body lengths encountered during that sampling period.

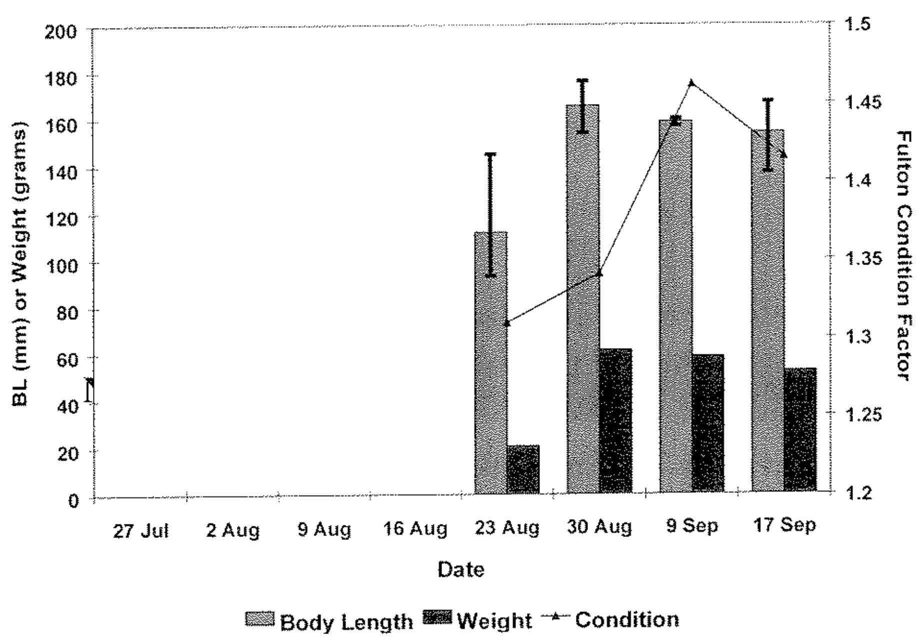

Figure 19. Mean body length, weight and Fulton condition factor for age-0 paddlefish captured in 1999. The dates on the x-axis represent the starting date of a sampling period and the error bars on body length bars represent the maximum and minimum body lengths encountered during that sampling period.

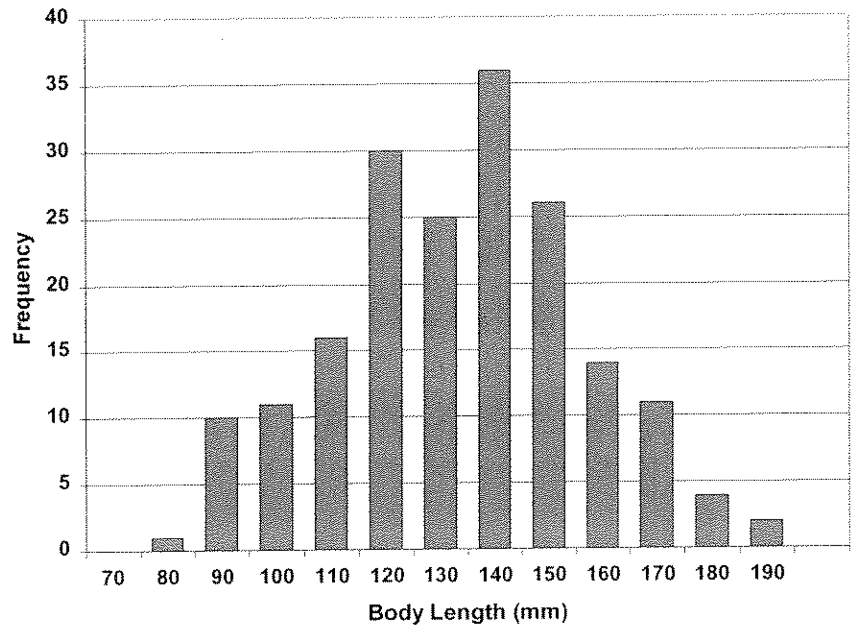

Figure 20. Body length histogram for age-0 paddlefish in 1998. The x-axis labels represent the upper boundary of a 10 mm length group. For example, there were 10 age-0 paddlefish captured greater than or equal to 81 mm and less than or equal to 90 mm.

Growth

Growth of paddlefish was rapid during early August, when paddlefish fed heavily on chironomids in up-reservoir areas. By mid-August, mean increases in body length declined as paddlefish moved into turbid areas near rkm 3,025 that supported low numbers of potential prey (Figure 11). During late August and early September, mean increases in body length averaged nearly 10 mm • sampling period^{-1} (week) when paddlefish were concentrated in plankton rich areas and fed heavily on *Leptodora kindtii*. To assess daily growth rates I compared mean body length early and late in the season. I chose a period between 30 July and 10 September 1998 when a relatively large number of fish were captured on each day. Over the 42 day period, mean body length increased from 94.8 mm to 136.5 mm. The increase of 41.7 mm in body length over this period yielded a daily growth rate of 0.99 mm • day^{-1}.

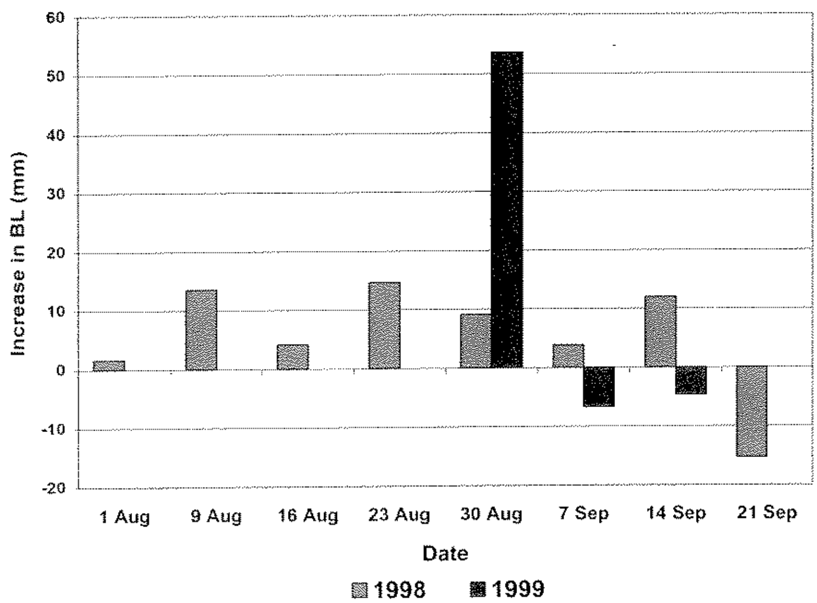

Figure 21. Increase in mean body length (mm) by week for 1998 and 1999. The x-axis labels represent the start date of a sampling period.

DISCUSSION

The tendency noted in this study for age-0 paddlefish to select larger prey, such as chironomids (in up-reservoir areas) and *Leptodora kindtii* (in down-reservoir areas), is supported by the findings of other earlier studies. In Lewis and Clark Lake, a mainstem Missouri River impoundment, young paddlefish fed heavily on *Daphnia pulex*, most of which were the larger gravid females with brood pouches, although this species represented a small proportion (approximately 13%) of the zooplankton community (Ruelle and Hudson 1977). In hatchery ponds, small paddlefish select the largest zooplankton species available, mainly *Daphnia* sp., and smaller zooplankton species are utilized only at times when the abundance of *Daphnia* sp. is low (Michaletz et al.1982). w. In Lake Sakakawea, *Leptodora kindtii* was the most common food item sampled from age-0 paddlefish, representing 90 % of the stomach contents by number (Fredericks 1994).

In addition, this study indicated that age-0 and age-1 paddlefish selected larger than average individuals of *Leptodora kindtii*. Fredericks (1994) found a similar size selectivity, where the range of *Leptodora kindtii* mean body lengths from age-0 paddlefish stomachs (5.0-6.8 mm) was substantially larger than found in the environment (2.5-3.3 mm). Selection of larger *Leptodora kindtii* by age-0 paddlefish collected from Fort Peck Lake and Lake Sakakawea is similar to selection of larger *Leptodora kindtii* by the razor bleak (*Pelecus cultratus*) captured from the Neusiedler See, Austria (Liu and Herzig 1996). The mean length of *Leptodora kindtii* (7.11 mm) examined from the stomachs was nearly double the mean length of *Leptodora kindtii* captured from the lake (3.63 mm). In Liu and Herzig's (1996) study, vertical plankton tows were used in a shallow eutrophic lake as opposed to the horizontal tows used in my study and in Lake Sakakawea by Fredericks (1994). The lengths of *Leptodora kindtii* sampled from the habitats and stomachs, however, were similar in all of these studies.

In clear water, *Leptodora kindtii* exhibit diel vertical migrations (Zettler and Carter 1986), rising to the surface at night to feed and migrating towards the bottom during the day to reduce predation by sight feeding fish. Since paddlefish have poorly developed eyes (Hussakof 1910) and are not sight feeders (Wilkens et al. 1997), water clarity and light penetration should have little effect on paddlefish feeding efficiency. Theoretically, paddlefish should be able to forage on zooplankton through the entire water column; therefore, zooplankton would not benefit by migrating to avoid paddlefish predation. If zooplankton migrated to avoid other zooplanktivores in Fort Peck Lake, I may have over-estimated prey selection for *Leptodora kindtii* by sampling with horizontal plankton tows near the surface during the day. Furthermore, if large individuals exhibit stronger diel vertical migration patterns than small individuals, I may have similarly underestimated the mean size of *Leptodora kindtii* from the habitat and, therefore, overestimated size-selection. It is unlikely, however, that relative selection of the preferred prey would have changed since *Leptodora kindtii* are rarely abundant (LaRow 1975) due to their higher trophic position and vulnerability to planktivorous fish (Smith and Pycha 1960, Voigtlander and Wissing 1974, Repsys et al. 1976, Kempinger 1996). Although I made no assessment of *Leptodora kindtii* vertical migration, the mean sizes from the habitat I reported are similar to those reported by Liu and Herzig (1996) who made vertical zooplankton tows that would be more representative of the total zooplankton community. In turbid water, such as Fort Peck Lake, the benefits of vertical migration and the distance traveled by species such as *Leptodora kindtii* would probably be reduced. In Lake Temiskaming, Ontario which possess a natural turbidity gradient and several species of sight feeding planktivores, large bodied zooplankton species were more abundant, and vertically migrated less in the more turbid, north end of the lake (Zettler and Carter 1986). In the less turbid, south end of the lake, vertical migration increased and some large bodied zooplankton were reduced by sight-feeding predators.

During this study, the contents of all but one juvenile paddlefish stomach indicated selective feeding on large organisms. The only exception was a 328 mm BL, age-2 fish. Although electivity values for this fish did not approach zero, a small, evasive prey group (cyclopoid copepods) was found in large numbers, as well as large cladocerans and *Leptodora kindtii*. Rosen and Hales (1981) speculated that the filtering apparatus of juvenile paddlefish was underdeveloped until a fish reached 225-250 mm BL. In contrast, Michaletz et al. (1982) observed filter-feeding in small juvenile paddlefish (120 mm TL) with underdeveloped gill rakers. He concluded that fully developed, gill rakers were not necessary for this foraging strategy. Two yearling paddlefish (344 and 370 mm BL) captured in Lake Sakakawea used the filter feeding strategy, whereas age-0 paddlefish of up to 252 mm TL fed selectively (Fredericks 1994). The exact time when juvenile paddlefish switch to filter feeding evidently changes with zooplankton abundance or prey size structure. This research indicated that when juvenile paddlefish are able to acquire large numbers of preferred prey, they may delay the switch to filter feeding until after they reach 300 mm BL.

Since, most age-0 paddlefish stomachs were dominated by one species, *Leptodora kindtii*, it is worth asking if age-0 paddlefish were orienting to concentrations of this particular prey item. If so, age-0 paddlefish should have concentrated near rkm 3,006, where overall zooplankton abundance was approximately an order of magnitude higher and the abundance of *Leptodora kindtii* was the highest. *Leptodora kindtii* were sampled by plankton nets only at rkm 3,006. Since, age-0 paddlefish did not concentrate near rkm 3,006, I conclude that age-0 paddlefish were able to locate and capture enough of their preferred prey in areas with lower zooplankton biomass.

In this study, paddlefish stomachs exhibited greater fullness from fish sampled from up-reservoir habitats where chironomids were abundant, declined when sampled from the middle portion of the study area that possessed few preferred prey, and increased again as paddlefish moved down-reservoir where *Leptodora kindtii* was abundant. Fredericks (1994) did not observe a similar trend in either 1992 or 1993. Instead, the SFI values calculated from age-0 paddlefish captured during 1992 decreased as the season progressed, coinciding with a decrease in *Leptodora kindtii*. During 1993, SFI values were initially low, increased to a maximum by late August in down-reservoir areas, and declined through late September. SFI values calculated from Lower Alabama River adult paddlefish did not differ by season, but did differ by habitat (Hoxmeier and DeVries 1997). In that study, stomach samples collected from backwater and oxbow habitats where cyclopoid copepods dominated the diet were significantly fuller than stomach samples collected from paddlefish inhabiting the main channel, where diet was dominated by ephemeropteran nymphs and *Bosmina longirostris*.

Overall growth of age-0 paddlefish was rapid during August and September, approaching 1 mm BL • day $^{-1}$, but was slower than other growth rates reported in the literature. In comparison to growth rates observed during 1998, Michaletz et al. (1982)

reported slower growth rates in hatchery ponds ranging from 0.71-1.24 mm TL • day $^{-1}$ during a similar time period when only small zooplankton were available, but measured higher growth rates ranging from 2.20 to 2.60 mm TL • day $^{-1}$ from May to mid-June when large zooplankton species were present. In Lewis and Clark Lake, Ruelle and Hudson (1977) calculated a higher mean growth rate than encountered in this study of 2.7 mm TL • day $^{-1}$ from 24 June through 31 August for 1970-1974. If natural mortality of age-0 paddlefish is greater for smaller fish, I may have overestimated growth by comparing mean body size by week. Therefore, my calculated growth rates should be viewed as maximum estimates.

Mean body length of age-0 fish reached 150 mm by mid-September 1998, an increase of 50 mm in six weeks. By the following September mean body length of this cohort exceeded 280 mm, an increase of 130 mm in just under a year. Fredericks (1994) observed a similar change in body length (> 100 mm in ten and one-half months). Size of age-0 paddlefish by the end of their first growing season may be influenced by adult spawning time, temperature, competition, and prey size or density. Although the size of Fort Peck age-0 paddlefish at the end of the growing season is substantially less than the 721 mm TL reported by Houser and Bross (1959) for a stock in Oklahoma, they were able to grow quickly and reach sizes similar to other stocks from more northern latitudes.

This study and several other studies have strongly suggested that age-0 paddlefish prefer large zooplankton and grow rapidly when such prey are available. During this study when fish densities were low, young paddlefish were able to ingest large numbers of preferred prey through particulate feeding, grow rapidly, and delay the switch to filter-feeding until after their second growing season. A more detailed assessment of feeding ecology should be made during years when age-0 paddlefish are more abundant to ascertain whether intraspecific competition for food alters feeding behavior, growth rates, or eventual year-class strength.

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APPENDICES

Appendix 1. Location of waypoints, in latitude and longitude, used as start and endpoint for transects and midpoint of transect in rkm. Transect 1 is left of mid-channel (facing upstream), transect 2 is mid channel, and transect 3 is right of mid-channel.

Station		Transect 1	Transect 2	Transect 3	rkm
1	Upstream point	47° 35.12 N 108° 07.98 W	47° 35.46 N 108° 06.31 W	47° 35.46 N 108° 06.24 W	3039.5
	Downstream point	47° 35.45 N 108° 06.45 W	47° 35.64 N 108° 04.73 W	47° 35.67 N 108° 04.64 W	3035.5
2	Upstream point	47° 35.60 N 108° 03.93 W	47° 35.71 N 108° 02.15 W	47° 35.80 N 108° 02.16 W	3034.5
	Downstream point	47° 35.70 N 108° 02.33 W	47° 35.24 N 108° 00.79 W	47° 35.25 N 108° 00.79 W	3030.5
3	Upstream point	47° 34.84 N 107° 59.58 W	47° 34.89 N 107° 59.56 W	47° 34.96 N 107° 59.51 W	3028.5
	Downstream point	47° 34.27 N 107° 58.08 W	47° 34.49 N 107° 58.11 W	47° 34.92 N 107° 57.86 W	3026.5
4	Upstream point	47° 34.16 N 107° 57.70 W	47° 34.43 N 107° 57.67 W	47° 34.66 N 107° 57.46 W	3024.5
	Downstream point	47° 33.79 N 107° 56.42 W	47° 33.85 N 107° 56.34 W	47° 34.07 N 107° 56.12 W	3022.5
5	Upstream point	47° 32.60 N 107° 55.75 W	47° 32.63 N 107° 55.51 W	47° 32.72 N 107° 55.11 W	3019.5
	Downstream point	47° 31.51 N 107° 55.58 W	47° 31.54 N 107° 55.36 W	47° 31.64 N 107° 55.06 W	3017.5
6	Upstream point	47° 30.71 N 107° 54.69 W	47° 30.77 N 107° 54.51 W	47° 30.83 N 107° 54.25 W	3016
	Downstream point	47° 29.66 N 107° 54 .46 W	47° 29.71 N 107° 54.29 W	47° 29.73 N 107° 53.97 W	3014
7	Upstream point	47° 28.11 N 107° 54.70 W	47° 28.15 N 107° 54.53 W	47° 28.21 N 107° 54.35 W	3011
	Downstream point	47° 27.07 N 107° 54.30 W	47° 27.15 N 107° 53.95 W	47° 27.21 N 107° 53.81 W	3009
8	Upstream point	47° 27.59 N 107° 51.67 W	47° 27.64 N 107° 51.90 W	47° 27.85 N 107° 52.16 W	3006.5
	Downstream point	47° 28.64 N 107° 51.27 W	47° 28.68 N 107° 51.50 W	47° 28.90 N 107° 51.78 W	3004.5

Appendix 2. Strauss linear selection index values for 73 age-0 and 8 age-1 paddlefish captured in 1998.

Date	BL	Total Organisms	Leptodora	Chironomids	Large Cladocerans	Insects	Small Cladocerans	Cyclopoid Copepods	Nauplii
Age-0									
7/27/98	82	175.00	0.00	0.44	-0.33	0.35	0.00	-0.19	-0.26
7/27/98	89	166.67	0.00	0.30	-0.33	0.49	0.00	-0.19	-0.26
7/27/98	90	300.00	0.00	0.13	-0.33	0.66	0.00	-0.19	-0.26
7/30/98	89	312.50	0.00	0.62	0.00	-0.09	0.00	-0.42	-0.11
7/30/98	91	300.00	0.00	0.57	-0.44	0.19	0.00	-0.21	-0.10
7/30/98	95	62.50	0.00	0.39	0.00	0.14	0.00	-0.42	-0.11
7/30/98	95	425.00	0.00	0.80	-0.44	-0.04	0.00	-0.21	-0.10
7/30/98	104	208.33	0.00	0.80	-0.44	-0.04	0.00	-0.21	-0.10
7/31/98	83	116.67	0.00	0.91	-0.44	-0.12	0.00	-0.27	-0.07
7/31/98	99	375.00	0.00	0.43	-0.44	0.36	0.00	-0.27	-0.07
8/1/98	81	125.00	0.00	-0.29	-0.05	0.52	0.00	-0.19	0.00
8/1/98	99	62.50	0.00	0.00	-0.05	0.23	0.00	-0.19	0.00
8/1/98	100	312.50	0.93	-0.60	-0.05	-0.10	0.00	-0.19	0.00
8/11/98	74	50.00	0.00	0.49	-0.27	0.26	0.00	-0.04	-0.44
8/11/98	82	125.00	0.00	0.82	-0.27	-0.07	0.00	-0.04	-0.44
8/11/98	101	62.50	0.00	-0.15	-0.31	0.65	0.00	-0.11	-0.07
8/11/98	102	50.00	0.00	0.24	-0.27	0.51	0.00	-0.04	-0.44
8/11/98	108	145.83	0.00	0.15	-0.31	0.35	0.00	-0.11	-0.07
8/11/98	114	20.83	0.00	0.99	-0.27	-0.24	0.00	-0.04	-0.44
8/12/98	85	250.00	0.67	0.25	-0.03	-0.12	-0.01	-0.71	-0.04
8/12/98	103	100.00	0.00	0.62	-0.04	0.07	0.00	-0.31	-0.34
8/12/98	106	62.50	0.00	0.97	-0.03	-0.18	-0.01	-0.71	-0.04
8/12/98	111	75.00	0.00	0.22	-0.03	0.57	-0.01	-0.71	-0.04
8/12/98	113	33.33	0.00	0.29	-0.04	0.41	0.00	-0.31	-0.34
8/12/98	114	575.00	0.90	0.04	-0.03	-0.32	0.00	-0.47	-0.13
8/12/98	115	1104.17	0.98	0.00	-0.03	-0.36	0.00	-0.47	-0.13
8/12/98	115	525.00	0.95	-0.03	0.02	-0.18	-0.01	-0.71	-0.04
8/12/98	117	975.00	1.00	-0.03	-0.03	-0.18	-0.01	-0.71	-0.04
8/15/98	114	925.00	0.00	0.11	0.72	-0.06	0.00	-0.40	-0.36
8/15/98	117	4400.00	0.99	0.00	-0.22	-0.01	0.00	-0.60	-0.16
8/15/98	133	3150.00	0.98	0.00	-0.21	-0.01	0.00	-0.60	-0.16
8/16/98	89	100.00	0.67	0.16	-0.38	0.00	0.00	-0.26	-0.18
8/16/98	100	1325.00	1.00	-0.02	-0.44	-0.04	0.00	-0.15	0.00
8/16/98	102	500.00	0.85	-0.17	-0.23	0.00	0.00	-0.26	-0.18
8/16/98	114	725.00	1.00	-0.17	-0.38	0.00	0.00	-0.26	-0.18
8/17/98	91	62.50	0.00	-0.46	0.00	0.46	0.00	0.00	0.00
8/17/98	112	104.17	0.00	0.80	-0.17	-0.15	0.00	-0.35	-0.13
8/18/98	100	250.00	0.92	0.08	-0.55	-0.15	-0.03	-0.23	-0.04
8/18/98	116	150.00	0.61	0.38	-0.23	-0.15	-0.02	-0.31	-0.29
8/18/98	117	200.00	0.72	0.00	-0.55	0.13	-0.03	-0.23	-0.04
8/18/98	129	1395.83	0.88	0.10	-0.23	-0.13	-0.02	-0.31	-0.29

Appendix 2 continued. Strauss linear selection index values for 73 age-0 and 8 age-1 paddlefish captured in 1998.

8/19/98	90	104.17	1.00	-0.02	-0.46	-0.28	-0.07	-0.12	-0.05
8/19/98	95	50.00	1.00	-0.02	-0.46	-0.28	-0.07	-0.12	-0.05
8/19/98	114	300.00	0.94	0.03	-0.46	-0.28	-0.07	-0.12	-0.05
8/22/98	126	1000.00	1.00	0.00	-0.28	-0.40	-0.02	-0.23	-0.07
8/22/98	136	2675.00	0.87	0.00	-0.52	-0.05	0.00	-0.20	-0.10
8/22/98	142	1325.00	0.98	0.02	-0.28	-0.40	-0.02	-0.23	-0.07
8/25/98	101	625.00	0.00	0.99	-0.36	-0.10	0.00	-0.19	-0.33
8/25/98	106	479.17	0.00	0.99	-0.36	-0.10	0.00	-0.19	-0.33
8/25/98	112	437.50	0.14	0.84	-0.36	-0.10	0.00	-0.19	-0.33
8/25/98	128	3350.00	0.99	0.01	-0.17	-0.14	0.00	-0.46	-0.23
8/25/98	142	1275.00	1.00	0.00	-0.17	-0.14	0.00	-0.46	-0.23
8/25/98	146	300.00	1.00	0.00	-0.17	-0.14	0.00	-0.46	-0.23
8/26/98	121	1325.00	1.00	-0.02	-0.37	-0.24	-0.04	-0.26	-0.07
8/26/98	130	325.00	0.93	0.05	-0.37	-0.24	-0.04	-0.26	-0.07
9/1/98	126	1300.00	1.00	0.00	-0.77	0.00	-0.02	-0.21	0.00
9/1/98	147	1675.00	0.82	0.00	-0.59	0.00	-0.02	-0.21	0.00
9/2/98	111	850.00	1.00	0.00	-0.13	-0.01	0.00	-0.74	-0.12
9/2/98	125	3400.00	1.00	-0.01	-0.30	0.00	-0.03	-0.51	-0.15
9/2/98	134	700.00	1.00	0.00	-0.13	-0.01	0.00	-0.74	-0.12
9/2/98	149	1675.00	1.00	-0.01	-0.30	0.00	-0.03	-0.51	-0.15
9/2/98	163	3850.00	0.99	0.00	-0.13	-0.01	0.00	-0.74	-0.12
9/9/98	122	1708.33	1.00	0.00	-0.12	0.00	-0.08	-0.39	-0.41
9/9/98	126	975.00	1.00	0.00	-0.12	0.00	-0.08	-0.39	-0.41
9/9/98	130	975.00	0.93	0.00	-0.07	0.00	-0.06	-0.39	-0.41
9/9/98	163	1925.00	1.00	-0.01	-0.15	0.00	-0.11	-0.40	-0.34
9/9/98	163	1458.33	1.00	-0.01	-0.15	0.00	-0.11	-0.40	-0.34
9/10/98	120	1104.17	0.98	-0.01	-0.31	0.01	-0.07	-0.38	-0.22
9/10/98	131	1275.00	0.98	0.01	-0.31	-0.01	-0.07	-0.38	-0.22
9/10/98	131	625.00	1.00	-0.03	-0.09	0.00	-0.33	-0.44	-0.12
9/10/98	149	1800.00	0.99	-0.03	-0.07	0.00	-0.33	-0.44	-0.12
9/10/98	173	775.00	0.93	-0.31	-0.01	-0.04	-0.35	-0.22	0.00
9/18/98	131	2200.00	0.96	-0.02	-0.13	0.00	-0.28	-0.29	-0.23
9/18/98	136	2250.00	0.97	0.00	-0.14	0.00	-0.29	-0.30	-0.23
9/18/98	161	2650.00	0.93	-0.02	-0.11	0.00	-0.27	-0.30	-0.23
9/23/98	109	66.67	0.00	0.50	-0.08	0.28	0.00	-0.70	0.00
9/23/98	149	20.83	0.00	0.00	-0.08	0.94	0.00	-0.87	0.00
Age-1									
7/27/98	235	700.00	0.00	0.18	-0.33	0.61	0.00	-0.19	-0.26
7/27/98	253	700.00	0.00	0.36	-0.33	0.40	0.00	-0.16	-0.26
7/30/98	263	1700.00	0.00	0.70	-0.44	0.06	0.00	-0.21	-0.10
7/30/98	264	2600.00	0.00	0.57	-0.40	0.12	0.00	-0.18	-0.10
7/30/98	273	2066.67	0.00	0.75	-0.44	0.01	0.00	-0.21	-0.10
9/2/98	272	1325.00	0.94	0.02	-0.09	-0.01	0.00	-0.74	-0.12
9/10/98	272	50.00	0.00	-0.03	-0.09	1.00	-0.33	-0.44	-0.12
9/10/98	313	9833.33	0.48	-0.03	0.27	0.00	-0.31	-0.30	-0.12

Appendix 3. Strauss linear selection index values for 10 age-0, 1 age-1, and 1 age-2 paddlefish captured in 1999.

Date	BL	Total Organisms	Leptodora	Chironomids	Large Cladocerans	Insects	Small Cladocerans	Cyclopoid Copepods	Nauplii
Age-0									
8/25/99	93	66.67	0.92	-0.06	-0.28	0.02	0.00	-0.23	-0.36
9/8/99	154	3266.67	0.98	0.00	-0.45	0.00	0.00	-0.24	-0.29
9/8/99	166	4066.67	0.92	0.00	-0.39	0.00	0.00	-0.22	-0.29
9/8/99	176	6708.33	0.97	0.00	-0.44	0.00	0.00	-0.24	-0.29
9/10/99	157	4291.67	0.98	0.00	-0.43	0.01	0.00	-0.08	-0.48
9/15/99	159	4458.33	0.99	0.00	0.00	0.00	0.00	-0.08	-0.91
9/16/99	160	4100.00	0.36	0.00	0.13	0.00	0.00	0.07	0.10
9/20/99	137	2950.00	0.95	0.00	0.04	0.00	0.00	-0.09	-0.90
9/20/99	158	4100.00	0.98	0.00	0.01	0.00	0.00	-0.07	-0.92
9/20/99	167	5833.33	0.95	0.00	-0.20	0.00	0.00	-0.18	-0.58
Age-1									
9/8/99	253	11583.33	0.94	0.00	-0.41	0.00	0.00	-0.24	-0.29
Age-2									
8/25/99	328	8533.33	0.20	-0.06	0.52	-0.07	0.00	0.28	-0.36