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Year-class strength and feeding ecology of age-0 and age-1 paddlefish (*Polyodon spathula*) in Fort Peck Lake, Montana, USA

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Summary

The paddlefish *Polyodon spathula* stock that inhabits Fort Peck Lake, Montana, and spawns in the Missouri River is among the few remaining naturally-reproducing stocks. For effective management, information is needed on reproductive success and year-class strength, which entails an understanding of the distribution, abundance, and food habits of age-0 and age-1 fish. Sampling was conducted during the late summer and autumn of 1998 and 1999 in a 39.4-km portion of the upper reservoir from river kilometer 3042.5 to 3003.1. Counts of age-0 and age-1 paddlefish indicated that abundance was low in 1998 and even lower in 1999. During 1998, higher numbers of age-0 paddlefish were more often observed near rkm 3024 during late July and early August. By late August, higher counts of age-0 paddlefish shifted to down-reservoir areas where zooplankton abundance had increased from up-reservoir areas. Significant correlations were found between age-0 fish abundance and two of the six habitat measurements; age-0 fish abundance was positively correlated with wave height and negatively correlated with current velocity. Food habits of wild, age-0 and age-1 paddlefish were investigated in July–September, 1998 and 1999. The stomach contents of age-0 and age-1 paddlefish indicated that these age-classes fed selectively, and the diet was composed of some of the larger organisms available. In up-reservoir areas, paddlefish fed heavily on chironomid larvae displaced by wave action or river currents, whereas those paddlefish collected from down-reservoir areas selected for *Leptodora kindtii*.

Introduction

Successful management of paddlefish requires knowledge of factors that influence reproductive success and survival of young fish so that year-class strength may be assessed. Reproductive success is thought to depend heavily on the duration and timing of high spring flows, although this relationship is for the most part untested due to the unavailability of efficient means for sampling eggs or larvae. Furthermore, the abundance of eggs or larvae may not be a good indicator of year-class strength if a critical period occurs later. Critical periods may occur if large zooplankton are scarce, causing slow growth rates (Michaletz et al., 1982) and thereby increasing the length of time that young paddlefish are vulnerable to piscine predators (Mero et al., 1994). Therefore, sampling age-0 in late summer and autumn probably offers the most promise for indexing year-class strength.

Until recently, assessment of year-class strength has been hampered by inefficient methods for capturing age-0 paddlefish (Ruelle and Hudson, 1977; Pasch et al., 1980; Hoxmeier and DeVries, 1997). Since the early 1990s, surface visual counts along transects in Lake Sakakawea, a neighboring Missouri River mainstem reservoir, have allowed estimation of age-0 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. In addition to visual counts, fish have also been sampled effectively with dipnets for life history information (Scarnecchia et al., 1997).

The objectives were to assess the distribution and abundance of age-0 paddlefish in upper Fort Peck Lake during late-summer and autumn and determine correlated abiotic and biotic factors, as well as determine electivity for prey items and determine at what size juvenile paddlefish switch from particulate to filter feeding.

Fort Peck Lake is the uppermost large, mainstem reservoir on the Missouri River and is located in northeastern Montana (Fig. 1). At full pool (685 m. a. s. l.), the reservoir extends 216 km, possesses a surface area of 100 767 hectares, and collects water from over 145 000 km^2 (USACE, 1991). The stock of paddlefish inhabiting Fort Peck Lake is among the few remaining naturally-reproducing stocks in the country. During the spring high-flow period, adult paddlefish migrate to spawning areas in the wild and scenic section of the upper Missouri River (Berg, 1981). By July or August, young paddlefish have dispersed down-river to the reservoir, where they feed and grow for approximately 8–15 years before returning to spawn (D.L. Scarnecchia, unpubl. data). Although several age classes have been known to utilize the entire reservoir, most paddlefish, especially juveniles, are concentrated in the upper portion of the reservoir that possesses a favorable amount of turbidity, abundant food, and proximity to spawning areas.

This study was conducted in a 40 km reach of the upper reservoir. Within the study area, reservoir width averages approximately 1.25 km. The location and relative amount of lotic, transitional, and lacustrine habitats was strongly dependent on reservoir elevation and discharge from the Missouri River (Figs. 2 and 3). In 1999, the study area was narrower, shallower, and more turbid than in 1998 as a result of reduced discharge from the Missouri River and lower reservoir levels.

Materials and methods

Age-0 counts

In 1998–1999, paddlefish were enumerated using visual counts at eight stations placed systematically within the study area. Each station possessed three pre-established transects. Transects were 2 km in length and placed parallel to each other and the reservoir

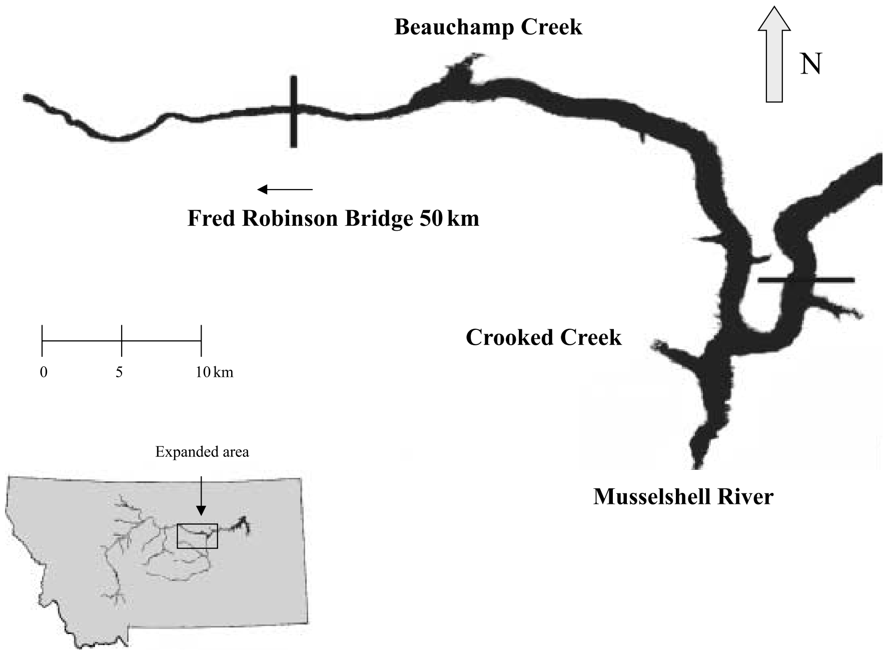

Fig. 1. Fort Peck Lake, Montana, and location of the study site. The thick black lines represent the boundaries of the study area

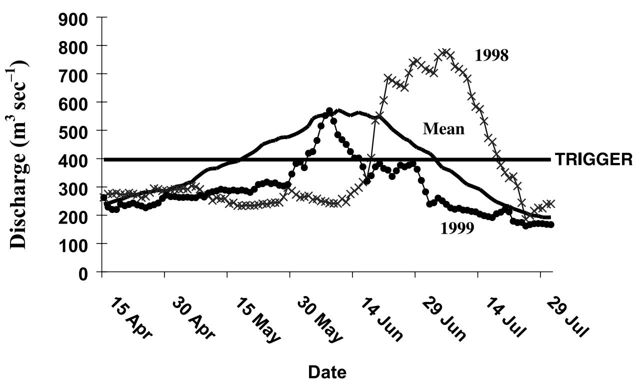

Fig. 2. Discharge of the upper Missouri River measured at the Virgelle gauge near Landusky, MT. This USGS gauge is located near suspected paddlefish spawning areas, and the horizontal line represents the minimum flow necessary for migration to spawning areas, also known as trigger flow (400 $m^3 sec^{-1}$, Berg 1981)

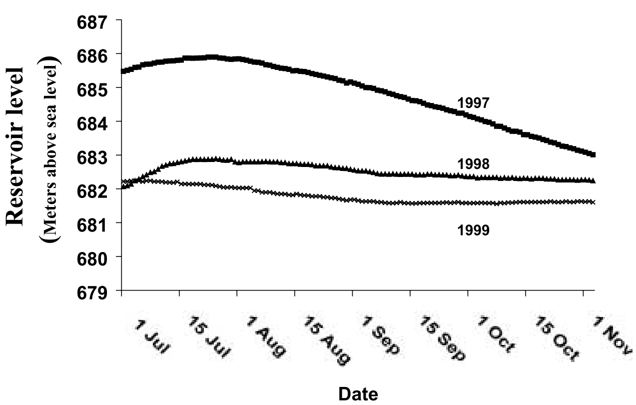

Fig. 3. Elevation of Fort Peck Lake, MT during July through November 1997, 1998, and 1999

or river banks. Paddlefish were counted weekly from late July through September over a 1–2-day period. Boat speed was maintained between 8–9.5 km h^{-1}. A two-person crew equipped with polarized sunglasses counted all age-0 paddlefish within 10 m of either side of the boat. Paddlefish encountering pressure waves or turbulence from the boat typically flee, and at fish sizes greater than about 100 mm body length (BL), their morphology, which includes a long paddle-like rostrum (Thompson, 1933), drives them to the surface where they can be counted. Counts of age-0 fish were expressed as the number of fish per km. During July and August, paddlefish shorter than 200 mm BL were classified as age-0. During September, paddlefish shorter than 250 mm BL were classified as age-0.

Abiotic and biotic measurements

Water temperature, water velocity, depth, water transparency, and zooplankton densities were monitored weekly during transect sampling at the start point of each transect. Wave height and cloud cover were visually estimated 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). Cloud cover was categorized as clear, partly cloudy, or overcast.

At the upstream point of each transect, a horizontal surface tow was made to collect zooplankton with an 80-micron mesh Wisconsin plankton net. All zooplankton samples were preserved with 95% ethanol, diluted, and subsampled. Zooplankton were identified to the genus or species level, and macroinvertebrates to family. Zooplankton counts, dilution volumes, and the volume of water sampled were used to calculate total density of potential prey items.

A repeated-measures factorial analysis of variance was used to assess the influence of sampling period and station on age-0 paddlefish counts. 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.

Fish collection

Age-0 and age-1 paddlefish were captured during 1998 and 1999 with long-handled dipnets. At each capture, sampling continued within a 1–2 ha area surrounding the initial capture location until no fish could be captured. All captured fish were measured for fork length, BL, and weight. Stomachs were removed and the contents diluted and subsampled. Whole organisms were enumerated and identified to the lowest practical taxonomic level. 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 by their head capsule.

To assess possible size-selection of *L. kindtii*, we measured spine length and total length of intact *L. kindtii* 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 $TL = -0.6984 + 8.0553SP$ ($r^2 = 0.9361$, $P < 0.01$, $n = 100$). We compared total lengths of *Leptodora kindtii* in age-0 and age-1 fish stomachs to transect samples with two-sample *t*-tests.

Analysis of Stomach Contents

A linear food selection index (Strauss, 1979) was used to determine electivity and feeding mode. Stomach contents of fish were compared with the three horizontal-surface tows taken at the location of capture. Prey species identified in stomachs and tows were grouped into six categories to allow statistical comparison. Prey items within a category were similar in terms of body shape, agility, or ecological function (Table 1). 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. 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–Wallis 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, we used Mann–Whitney *U*-tests to compare means from the four grouped sampling periods. This analysis could not be performed for the few age-0 paddlefish captured in 1999.

Table 1
Groupings of organisms used in diet analyses for calculation of Strauss linear selection index values

Leptodora	
	Leptodora kindtii
Chironomids	
	Chironomidae
Large cladoceran	
	Daphnia sp.
	Diaphanosoma sp.
	Ceriodaphnia sp.
	Moina sp.
	Sida sp.
	Latona sp.
	Polyphemus sp.
Insects	
	Chaoborus sp.
	Simuliidae
	Hydrachnidia
	Ephemeroptera
	Plecoptera
	Diptera
	Hemiptera
Copepods	
	Cyclopoida
Small cladocerans	
	Bosmina longirostris
	Chydorus sp.

Results

Counts in 1998

During 1998, 97 age-0 paddlefish were enumerated during the 216 transect counts conducted. Age-0 paddlefish were first observed at rkm 3019 on August, 1 at a mean count of 0.67 fish per km. Counts of age-0 paddlefish remained low through August, 23, when most observed fish were located between rkm 3028 and 3019. Counts increased by August, 30 and it appeared that peak counts shifted down-reservoir (Fig. 4). The highest counts of age-0 paddlefish remained in the lower portion of the study area through September, 22. The maximum mean count of 1.44 fish per km was observed on September, 15 at rkm 3010 and at no other time were more than 0.8 fish per km observed at a station. For age-0 paddlefish during 1998, 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 the study area (except the riverine portion) during at least a portion of the year. 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 3024 to 3019. As the season progressed, concentrations of age-0 paddlefish were seen increasingly farther down-reservoir.

No apparent relationship existed between water transparency (Secchi depth), invertebrate density, and age-0 fish counts during 1998. Age-0 paddlefish did not consistently use areas with higher invertebrate densities such as those areas near rkm 3006. 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.

Correlations between age-0 paddlefish per km and habitat variables were evaluated only for 1998. Significant relationships, although weak, were found between age-0 paddlefish per km vs current velocity ($r = -0.19$, $P = 0.0041$), and age-0 paddlefish per km vs wave height ($r = 0.15$, $P = 0.0012$).

Counts in 1999

During 1999, a total of three age-0 paddlefish were counted during the monitoring of 174 transects. Age-0 paddlefish were first observed on September, 9 at rkm 3010 and rkm 3006 at a count of 0.167 fish per km, and were observed on only one more occasion, September, 17, also at rkm 3006 (Fig. 5). We were unable perform the ANOVA and correlation analyses for 1999 because of the few age-0 fish counted.

Diet analysis

During 1998, we collected and analyzed the stomach contents from 77 age-0 and eight age-1 paddlefish captured from July, 27 through September, 23. A strong temporal and spatial trend existed in the location of capture. All fish captured before August, 15 were collected up-reservoir of rkm 3020. After August, 15 all but six fish were taken down-reservoir of rkm

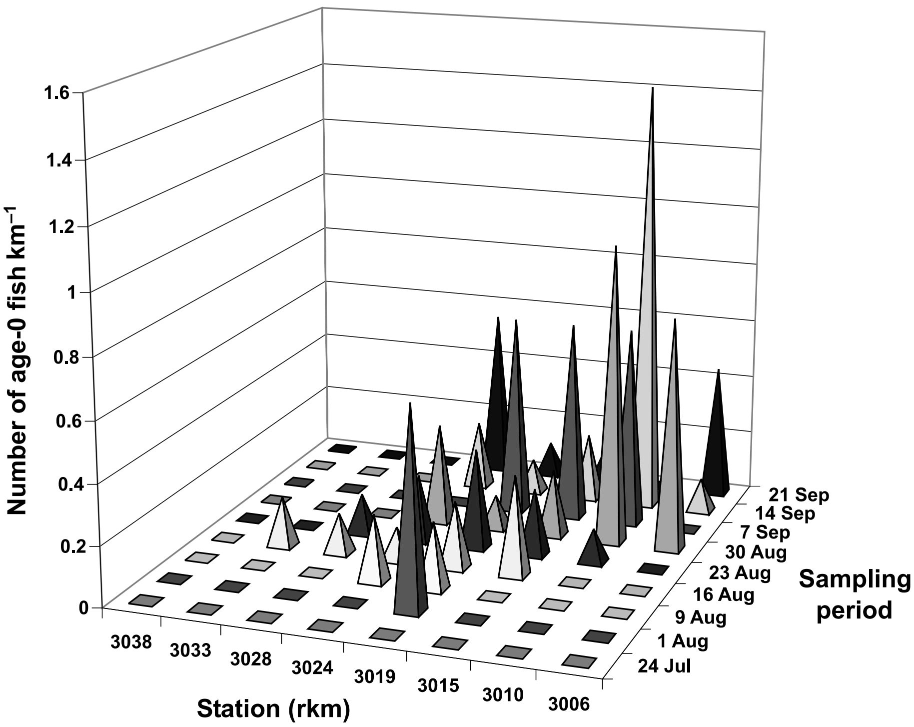

Fig. 4. Counts of age-0 paddlefish km^{-1} observed by date and location in 1998. River kilometer (rkm) 3038 is up-reservoir (near CK Creek), and rkm 3006 is down-reservoir (near Swan Creek)

3020. Age-1 paddlefish were captured for stomach content analysis from July, 27 through September, 18. The five age-1 paddlefish captured in July were captured at rkm 3035, and the remaining three were captured near rkm 3012 during September.

During 1999, the stomach contents of 10 age-0, one age-1, and one age-2 paddlefish were collected and analyzed. All but one of the age-0 paddlefish were captured down-reservoir of rkm 3008 and after September, 1. The age-2 and age-1 paddlefish were captured on August, 25 and September, 8 1999 and at rkm 3011.5 and 3005, 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 fish previously assumed to be age-1 possessed one annulus, except a 328 mm BL individual captured in 1999 that possessed two annuli.

Age-0 paddlefish selectively fed and disproportionately selected organisms from the larger prey. In 1998, age-0 paddlefish selected most strongly for *L. kindtii* and chironomids during all sampling periods (Fig. 6). Mean selection values for *L. kindtii*, the most sought after prey, increased later in the season as fish moved down-reservoir from 0.07 during the period July, 27 through August, 8 to a maximum of 0.84 during the period September, 7 through September, 23. *Leptodora kindtii* were strongly selected after August, 9 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 moved down-reservoir. Insects were positively selected only during the periods July, 27 through August, 8 and September, 7 through September, 23, 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. 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.

We were 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 (Fig. 7). 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 by the ten age-0 fish examined ($L = 0.96$).

Food selection by age-1 fish

During 1998, stomach contents of age-1 paddlefish 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 3035. At this location, *L. 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. 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 3012. When compared with those paddlefish captured earlier in the year, preference shifted from the chironomids to *L. 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 ($L = -0.49$).

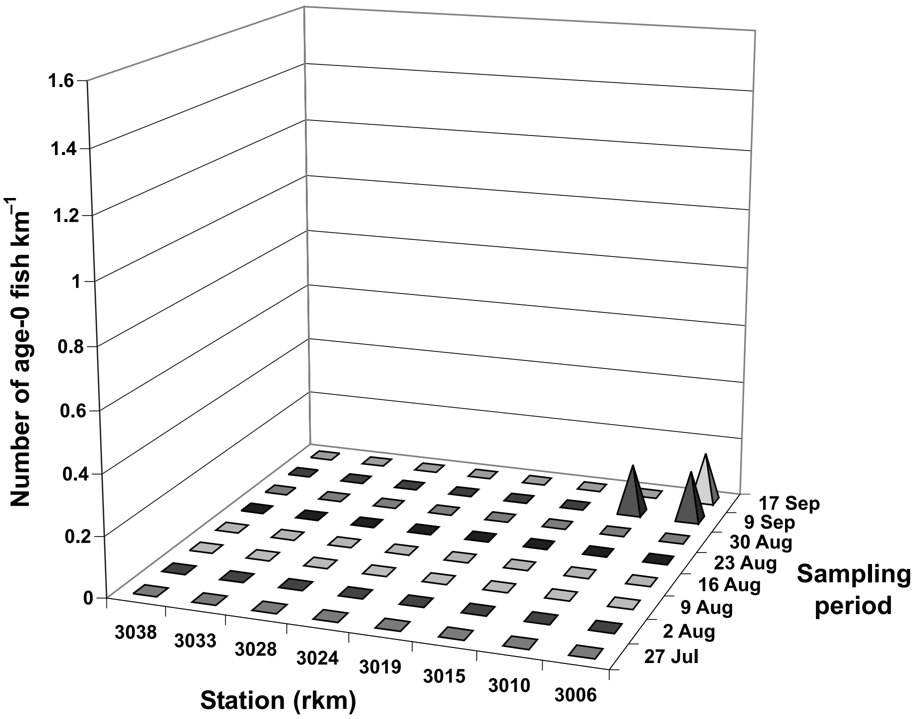

Fig. 5. Counts of age-0 paddlefish km^{-1} observed by date and location in 1999. River kilometer (rkm) 3038 is up-reservoir (near CK Creek), and rkm 3006 is down-reservoir (near Swan Creek)

Stomach contents of the two larger paddlefish captured in 1999 differed substantially. The smaller fish (BL $= 253$ mm), aged as 1+, captured on September, 8 at rkm 3005 fed much like the age-0 paddlefish captured in both years and the age-1 paddlefish captured in 1999; it strongly selected for *L. 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 August, 25 at rkm 3012 was the only fish captured during this study that showed some evidence of filter-feeding. It nevertheless slightly selected for *L. kindtii* ($L = 0.20$), large cladocerans ($L = 0.52$), and cyclopoid copepods ($L = 0.28$).

During 1998, 47 age-0 (61%) and two age-1 (25%) paddlefish stomachs contained *L. kindtii*. The following year, 10 age-0 (100%), one age-1 (100%), and one age-2 paddlefish stomachs contained this organism. During both years, the mean length of *L. kindtii* collected from horizontal surface tows (2.7 and 3.0 mm in 1998 and 1999) was significantly less than the mean length of *L. kindtii* measured from stomachs of age-0 (6.6 and 7.9 mm) and age-1 fish (6.8 and 7.5 mm).

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. Previously on Lake Sakakawea, totals of 220 and 1551 age-0 paddlefish were counted along transects during 1992 and 1993 with mean counts as high as 22.9 fish per km (Fredericks and Scarnecchia, 1997). During 1996, Scarnecchia et al. (1997) captured 2360 age-0 paddlefish from August 2–15 on Lake Sakakawea, despite capturing only about one-third of the age-0 paddlefish observed. Counts on Lake Sakakawea in 1997 and 1998 were 361 and 444 age-0 fish, respectively. In preliminary investigations on Fort Peck Lake during 1997, at least 250 age-0 paddlefish were counted in one afternoon (Bill Wiedenheft, pers. comm.). In the present study, counts of age-0 paddlefish were low (overall mean, 0.15 fish per km) in 1998 and even lower (overall mean, 0.01 fish per km) in 1999.

Paddlefish reproductive success is thought to depend on the characteristics of a natural river, 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 Missouri River flows were below 400 m^3 s^{-1}. As flows exceeded this level, paddlefish moved to areas possessing gravel bars and adequate water velocities, which Berg (1981) assumed as probable spawning areas; he speculated that this flow level during May through mid-June is necessary for successful reproduction, but did not sample early life stages.

In a theoretical average year (calculated from 63 years of historical data measured at the Virgelle gauge), mean daily flow exceeds 400 m^3 s^{-1} (USGS, 1998). When preliminary sampling in Fort Peck Lake was conducted in 1997, mean daily flow exceeded 400 m^3 s^{-1} for 65 days from May 2 to July 5, 1997. High flows during 1998, the first year of intensive sampling, were reduced and delayed compared to 1997 or historical mean daily flows. A mean daily flow of 400 m^3 s^{-1} was first exceded on June 18 remained above this level for 31 consecutive days, and declined below this level on July 19, 1998. The timing of high flows was thus approximately 1 month later than an average year. During 1999, a mean daily flow of 400 m^3 s^{-1} was first exceeded on June 3 remained above this level for only 13 consecutive days, and declined below this level on June 15, 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. If we effectively monitored the relative abundance of age-0 paddlefish, this study suggests that successful reproduction occurs irregularly and is partially influenced by the timing and duration of high spring flows.

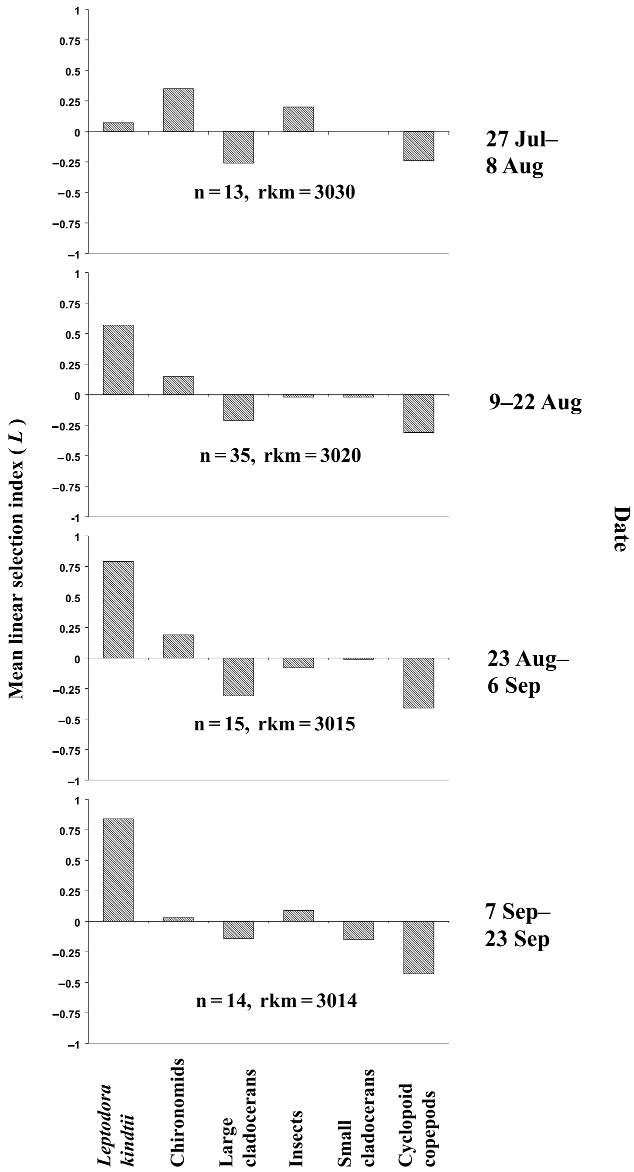

Fig. 6. Mean selection index values (Strauss, 1979), mean capture location, and sample size of age-0 paddlefish captured for stomach content analysis during 1998

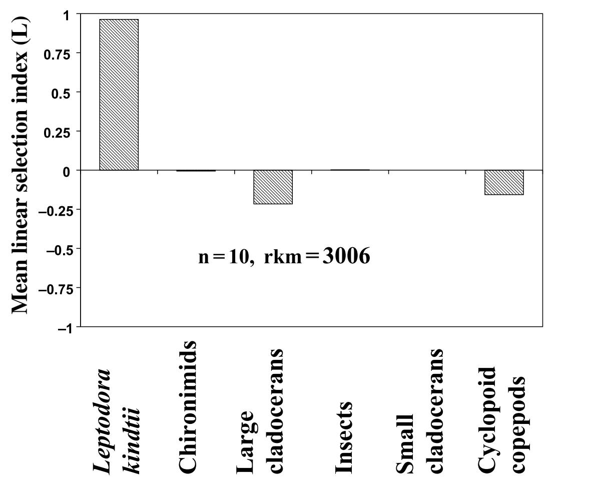

Fig. 7. Mean selection index values (Strauss, 1979), mean capture location, and sample size of age-0 paddlefish captured for stomach content analysis during 1999

Little data exist 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 rkm 2443 to rkm 2438 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. Within the Fort Peck study site, 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).

The tendency noted in this study for age-0 paddlefish to select larger prey, such as chironomids (in up-reservoir areas) and *L. 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 large *Daphnia pulex*, 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.; smaller zooplankton species are utilized only at times when the abundance of *Daphnia* sp. is low (Michaletz et al. 1982). In Lake Sakakawea, *L. 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 *L. kindtii*. Fredericks (1994) found a similar size selectivity, where the range of *L. 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 *L. kindtii* by age-0 paddlefish collected from Fort Peck Lake and Lake Sakakawea is similar to selection of larger *L. kindtii* by the razor bleak (*Pelecus cultratus*) captured from the Neusiedler See, Austria (Liu and Herzig 1996). The mean length of *L. kindtii* (7.11 mm) examined from the stomachs was nearly double the mean length of *L. 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 this study and in Lake Sakakawea by Fredericks (1994). The lengths of *L. kindtii* sampled from the habitats and stomachs, however, were similar in all of these studies.

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 *L. 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; approximately 80 mm BL) with underdeveloped gill rakers. They 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 (approximately 160 mm BL) 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.

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, and delayed 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.

References

Adams, L. A., 1942: Age determination and rate of growth in *Polyodon spathula*, by means of the growth rings of the otoliths and dentary bone. Am. Midland Nat. **28,** 617–630.

Berg, R. K., 1981: Fish populations of the wild and scenic Missouri River, Montana. Department of Fish, Wildlife and Parks. Federal Aid to Fish and Wildlife, Restoration Proj. FW-3-R, Job Number 1–A. 242 p.

Fredericks, J. P., 1994; Distribution, abundance, and feeding ecology of young-of-the-year paddlefish in upper Lake Sakakawea, North Dakota, MS. Thesis. University of Idaho, Moscow, ID.

Fredericks, J. P.; Scarnecchia, D. L., 1997: Use of surface visual counts for estimating relative abundance of age-0 paddlefish in Lake Sakakawea. N. Am. J. Fish. Manage. **17,** 1014–1018.

Hoxmeier, R. J. H.; DeVries, D. R., 1997: Habitat use, diet, and population structure of adult and juvenile paddlefish in the lower Alabama River. Trans Am. Fish. Soc. **126,** 288–301.

Liu, Z.; Herzig, A., 1996: Food and feeding behaviour of a planktivorous cyprinid, *Pelecus cultratus* (L.), in a shallow eutrophic lake, Neusiedler See (Austria). Hydrobiologia **333,** 71–77.

Mero, S. W.; Willis, D. W.; Power, G. J., 1994: Walleye and sauger predation on paddlefish in Lake Sakakawea, North Dakota. N. Am. J. Fish. Manage. **14,** 226–227.

Michaletz, P. H.; Rabeni, C. F.; Taylor, W. W.; Russell, T. R., 1982: Feeding ecology and growth of young-of-the-year paddlefish in hatchery ponds. Trans. Am. Fish. Soc. **111,** 700–709.

Pasch, R. W.; Hackney, P. A.; Holbrook, J. A., 1980: Ecology of paddlefish in Old Hickory Reservoir, Tennessee, with emphasis on first year life history. Trans. Am. Fish. Soc. **109,** 157–167.

Rosen, R.A.; Hales, D. C., 1981: Feeding of paddlefish, *Polyodon spathula*. Copeia **1981,** 441–445.

Ruelle, R.; Hudson, P. L., 1977: Paddlefish *Polyodon spathula*: growth and food of young of the year and suggested technique for measuring length. Trans. Am. Fish. Soc. **106,** 609–613.

Russell, T. R., 1986: Biology and life history of the paddlefish – a review. In: The paddlefish: status, management and propagation, J. G. Dillard, L. K. Graham and T. R. Russell (Eds). No. Cent. Divis. Am. Fish. Soc., Spec. Publ. Nr. 7, Bethesda, MD, pp 2–20.

Scarnecchia, D. L.; Stewart, P. A.; Power, G. J., 1996: Age structure of the Yellowstone-Sakakawea paddlefish stock, 1963–1993, in relation to reservoir history. Trans. Am. Fish. Soc. **125,** 291–299.

Scarnecchia, D. L.; Ryckman, F.; Lee, J., 1997: Capturing and tagging wild age- and age-1 paddlefish in a Great Plains reservoir. N. Am. J. Fish. Manage. **17,** 800–802.

Strauss, R. E., 1979: Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection Trans. Am. Fish. Soc. **108,** 344–352.

Thompson, D. H., 1933: The finding of very young *Polyodon*. Copeia **1,** 31–33.

USACE (U.S. Army Corps of Engineers), 1991: Montana water resources development manual. Missouri River Division, Omaha, NB.

USGS (U.S. Geological Survey), 1998: Montana Current Streamflow Conditions – Missouri River at Virgelle, MT. U.S. Geological Survey, Helena, MT. http://montana.usgs.gov/rt-cgi.gen_stn_pg?station = 06109500.

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