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The Feeding Ecology of Paddlefish in the Mermentau River, Louisiana

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Abstract.—We conducted the first comprehensive study of paddlefish *Polyodon spathula* feeding ecology in Louisiana by examining 129 stomachs collected from the Mermentau River. Paddlefish were sampled monthly using gill nets from March 2002 to February 2003. Copepods and cladocerans occurred more frequently in the stomachs than any other prey, with a frequency of occurrence of 90% and 82%, respectively. Feeding peaked in summer and winter and appeared to shift from copepods in the summer to cladocerans in the winter. There appeared to be no size selectivity of prey, suggesting that paddlefish were indiscriminate planktonic feeders. Calculations of apparent ingestion time indirectly suggest that paddlefish were able to locate dense patches of zooplankton. This study concurs with previous studies of northern and other southern paddlefish populations that paddlefish feed primarily on zooplankton crustaceans such as copepods and cladocerans, although diatoms and other plant material may be periodically important.

Introduction

Early studies described adult paddlefish *Polyodon spathula* as bottom feeders that consumed minute vegetable and animal organisms found by stirring up the mud and vegetation with their spatulate snout (Stockard 1907; Alexander 1914). This thought was later dismissed by Eddy and Simer (1929) who discovered that paddlefish were planktivorous feeders. Gerking (1994) described paddlefish as ram or tow-net filterers who swim with their mouth agape and use gill rakers as a sieve to catch plankton. Most contemporary publications on paddlefish report the diet as consisting of crustacean zooplankton (Rosen and Hales 1981; Hageman et al. 1986; Hoxmeier and DeVries 1997) while a few have noted other items being found in the stomachs, including fish (Fritz 1966).

Age-0 paddlefish typically feed on zooplankton in the northern part of its range. Ruelle and Hudson (1977) found age-0 paddlefish (less than 200 mm in length) in Lewis and Clark Lake, Nebraska

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and South Dakota, selected for the largest available zooplankter (*Daphnia pulex*). Their diet was composed of crustacean zooplankton (76%), six species of aquatic insects (21%), and terrestrial insects (3%). Age-0 paddlefish may gradually switch from particulate to filter feeders at about 120 mm in total body length, which may support faster growth rates. Filter feeding was not dependent upon the full development of the gill rakers and resulted in the ingestion of smaller sized prey items than was evident during the particulate feeding stage. Kozfkay and Scarnecchia (2002) determined that age-0 paddlefish selectively fed on larger prey organisms in a Montana reservoir. Moreover, age-0 paddlefish negatively selected cyclopoid copepods and large cladocerans and fed on small cladocerans less than or equal to their availability, indicating negative selection or random feeding. This study also indicated that age-1 paddlefish negatively selected small cladocerans and cyclopoid copepods. Their research showed that juvenile paddlefish were able to acquire large numbers of preferred prey and may delay their switch to filter feeding until they reach a total body length of 300 mm.

Adult paddlefish also may be indiscriminate feeders. Studies in the paddlefish northern range (Rosen 1976; Rosen and Hales 1981) and southern range (Hageman et al. 1986; Hoxmeier and DeVries 1997) found that adult paddlefish fed almost entirely on crustacean zooplankton. These studies classified paddlefish as indiscriminate filter feeders on particles greater than 0.20–0.25 mm in length and 0.10–0.12 mm in width (Rosen and Hales 1981). However, studies of seasonal food habitats of paddlefish have been mixed. Rosen and Hales (1981) indicated higher rates of ingestion in spring and fall, with a cessation of feeding in late June to early September in the Missouri River, whereas Hageman et al. (1986) noted that midges were common in September to October and May to June, plant matter was common in October, and stomach contents were reduced in February in a Kentucky reservoir. However, there is no information on the feeding ecology of adult paddlefish in Louisiana except for early descriptive reports (Alexander 1914; Tulian 1916). The objectives of this study were to examine the feeding habits of subadult and adult paddlefish in the Mermentau River, Louisiana to identify and determine size distribution of the prey items by functional groups and compare these results to northern populations.

Methods

Paddlefish were collected in the Mermentau River (29.86°N, 92.85°W), in the old river loop, near the headquarters of Lacassine National Wildlife Refuge in southwest Louisiana (Smith 2004). The Mermentau River flows into the Gulf of Mexico between Calcasieu Lake and Vermillion Bay on the Chenier coastal plain of Texas and Louisiana. The Mermentau River is approximately 114 km long and is formed by junction of Nezipique and des Cannes bayous (Cohen 2000). We believe Bayou Nezipique to be the spawning ground for Louisiana paddlefish in the Mermentau system.

Paddlefish were sampled monthly with the goal of obtaining up to 15 digestive tracts and gonads per month. Gonads and digestive tracts were taken for the purpose of determining sex and stage of sexual maturity and for conducting gut content analysis. Fish were collected from March 2002 to February 2003, with two 91 × 3 m monofilament gill nets. Each net contained two panels of either 127 or 154 mm bar mesh. Two nets (one of each mesh size) were set perpendicular to the shore in the morning and were lifted hourly to check for and remove paddlefish. The first 15 paddlefish caught were placed in an ice slurry to be euthanatized. Once euthanatized, paddlefish were measured and weighed before dissection. The measurements included

- Eye-to-fork length (EFL), which was measured in millimeters from the anterior orbit of the eye to the fork of the caudal fin;
- Mouth top to bottom (MTB), taken from the midline of the dentary bone on lower jaw to the midline of the dentary on the upper jaw; and
- Mouth side to side (MSS), taken between the junction of the upper and lower jaw.

The fish were then weighed using a field spring scale to the nearest 25 g. Stomachs were removed, placed in labeled bags in a cooler, and returned to the laboratory to be processed (Smith 2004).

Prior to stomach content analyses, cross sections of one of the full frozen stomachs at the anterior, middle, and posterior positions were taken to determine if there were different stages of digestion within the stomach. We removed the gut contents from each of these cross sections and examined each section separately with a dissecting microscope for indications that the contents or their condition differed by stomach region. There did not appear to be any partitioning of food items by region; the stomach contents were a homogenous mix of largely crustacean zooplankton. Moreover, the contents were tightly compact, suggesting that ingestion had not been accompanied by a large intake of water (Smith 2004). Based on these results, the entire frozen content of each stomach was removed and weight of the frozen mass was recorded as an index of the maximum gut content at the time of capture. Each frozen stomach was dissected from the esophagus to the large intestines. The stomach lining was folded back, and the frozen contents were weighed to the nearest 0.01 g and preserved in 70% ethanol. The ratio of stomach weight (SW) to fish weight (W) was used to derive an index of fullness (I_f):

$$I_f = \mathrm{SW}/W. \qquad (1)$$

Stomach contents were analyzed using the procedures outlined in Postel et al. (2000). Stomach contents were subsampled using a Hensen-Stempell pipette following each displacement volume. Each subsample was placed in a Bogorov tray and examined using a dissecting microscope; organisms were identified as Copepoda, Cladocera, Ostracoda, Amphipoda, Decapoda, Insecta, or diatoms using Pennak (1978). Copepods and cladocerans were the major taxonomic groups found and were enumerated until 100 had been tallied. The percent composition by number (%N based on counts in each stomach) and percent occurrence (%O) across all stomachs were estimated for all invertebrates. Diatoms were not included in the analysis because they were not enumerated.

Length frequency of invertebrate prey was measured from fish collected during November 26, 2002, January 24, 2003, and February 19, 2003 to compare with corresponding zooplankton net tows. Previously counted prey items of each taxonomic group were poured into a petri dish, imaged using a digital camera/microscopy system Pixera VCS 1.2.3, and measured using an image processing software program NIH Image 1.62 (Keenan et al. 2003).

Zooplankton tows were taken on November 26, 2002, January 24, 2003, and February 19, 2003 using a 0.5-m-mouth-diameter, 335-μm-mesh plankton net with a 333-μm cod end equipped with a flowmeter (General Oceanics model 2030; General Oceanics, no date). Three replicate 10-min tows were taken from the boat during each trip, each following the collection of fish from the gill nets. The horizontal tows were collected at and just below the surface of the Mermentau River. Plankton samples were preserved in 70% ethanol.

We used the plankton tow data to estimate the apparent ingestion time, t_p. We defined t_p as the time it would have taken for a paddlefish to ingest the zooplankton found in the heaviest stomachs in each of these months (Table 1). The basic relationship is expressed as

$$\overline{N_n / V_n} = N_p / V_p \, , \qquad (2)$$

where $\overline{N_n / V_n}$ is the mean ratio of the number of organisms in a net tow to the volume filtered by the plankton net, N_p is the total number of organisms in the fullest stomach, and V_p is the volume filtered by the paddlefish. Equation (2) assumes that the plankton tows are representative of the concentration of plankton upon which the paddlefish had fed and that no digestion occurs in the paddlefish stomach. We estimated apparent ingestion time, t_p, as

$$t_p = N_p/(\text{prey density, no./m}^3) * (\text{filter rate, m}^3/\text{d}) \, , \qquad (3)$$

where N_p is the total number of prey in the fullest stomach, prey density is that measured from the zooplankton tow, and filter rate is the volume of water filtered per day by paddlefish. The filter rate of a paddlefish was calculated as

$$\text{Filter rate (m}^3/\text{d)} = 3.14 \times (0.5\text{MSS}) \times 0.5\text{MTB} \times R \text{ (m/d)} \, , \qquad (4)$$

where R = 27,820.8 m/d the speed of a ram filter-feeding paddlefish (converted from Sanderson et al. 1994).

Zooplankton from net tows was examined through silhouette photography (Ortner et al. 1979; Davis and Wiebe 1985). Each net tow was poured onto a piece of labeled photographic film (Kodak, fine grain positive, 8 × 10 in). A strobe light was then flashed to expose the film, which was developed using Kodak developer for 1 min followed by standard stop bath and fixative procedures. Silhouette photographs were then digitized as tagged image file format (TIFF) files at 1,200 pixels/in resolution, and lengths of imaged organisms were measured in a Matlab program Digitizer 1.0 (Little and Copley 2003). Silhouettes were uploaded into a Matlab digitizer, a grid (22 × 18 cells) was superimposed on each image, and 32 cells were randomly

Table 1. Parameters used to calculate t_p, apparent ingestion time, for the heaviest paddlefish stomach contents from November, January, and February. Abbreviations are V_n, volume of water filtered by the plankton net; N_n, number of zooplankton in net; MSS, width of the paddlefish mouth; MTB, height of the paddlefish mouth; and N_p, number of zooplankton found in the stomach.

	Plankton net				Paddlefish			
					Mouth (m)			
Month	Tow	V_n	N_n	N_n/V_n	MSS	MTB	N_p	t_p (d)
November	1	134.46	917.65	6.82	–	–	–	–
	2	129.59	445.50	3.44	–	–	–	–
	Mean			5.13	0.140	0.155	9,664	3.95
January	1	122.57	14,916.00	121.70	–	–	–	–
	2	152.65	17,964.00	117.68	–	–	–	–
	3	184.37	8,712.00	47.25	–	–	–	–
	Mean			95.54	0.107	0.116	27,200	1.12
February	1	134.55	7,191.36	53.45	–	–	–	–
	2	122.54	5,722.20	46.70	–	–	–	–
	3	118.43	3,981.41	33.62	–	–	–	–
	Mean			44.59	0.110	0.109	568,000	48.21

selected for counting. In each cell, organisms were measured with the goal of counting 100 total individuals of copepods and cladocerans. Other taxonomic groups were also counted, but their abundances were typically much lower than copepods and cladocerans. These less abundant taxa were ostracods, insects, and a miscellaneous group that included organisms such as arachnids and phytoplankton. Once all measuring was complete for a silhouette, the lengths were saved in a text file for size-selectivity analysis.

Size selectivity was examined during November, January, and February. Copepod and cladoceran size frequency distributions from net tows were compared to the size-frequency distributions from the fish stomachs. The abundances of insects, ostracods, amphipods, and decapods in stomachs or net tows samples were too low (<3%) to evaluate size selectivity. Diatoms were not included because they were not enumerated. Prey categories were placed in 0.1-mm size-classes and the 3 months were pooled together to increase sample sizes.

Chesson's alpha (Chesson 1983) was calculated to evaluate prey size selectivity:

$$\alpha_i = \frac{(r_i / p_i)}{\sum r_j / p_j} \text{ for } j = 1 \text{ to } m \quad , \quad (5)$$

where α_i is the selectivity for the *i*th size-class for an individual paddlefish, r_i is the numerical proportion of the *i*th size-class in an individual paddlefish stomach, p_i is the numerical proportion of the *i*th size-class in the environment, and *m* is the number of size-classes observed in the zooplankton net tows.

Chesson's alpha values were calculated for each size-class for copepods and cladocerans for each paddlefish caught during November (n = 4), January (n = 3), and February (n = 7). Alpha values for each month were calculated independently from each other and thus could be pooled for analysis (Chesson 1983). Positive selection occurred when $\alpha_i > 1/m$ and negative selection when $\alpha_i < 1/m$. *T*-tests were used to determine significance of the selection.

Results

One-hundred twenty-nine paddlefish stomachs were examined of which 21 were empty, 13 contained only parasitic nematodes, 45 contained food items only, and 50 had food and parasitic nematodes. No evidence of regurgitation was documented because when food contents were found in the esophagus, it was due to a full stomach and at no point did an empty stomach have a distended stomach wall.

Paddlefish were collected in all months between March 2002 and February 2003, except October 2002 when they were absent (Figure 1). Stomach fullness was lowest in March and gradually increased towards the end of spring through the beginning of the summer months. An initial peak in feeding was evident from May through July. A second feeding peak was observed during December and February (Figure 1).

We identified seven different taxonomic groups of prey items: Copepoda, Cladocera, Insecta, Ostracoda, Amphipoda, Decapoda, and diatoms (Table 2). Copepods were the most abundant (%N = 62%) and frequent (%O = 90%) prey item found in the stomachs, followed by cladocerans (%N = 35% and %O = 82%). Insects and ostracods were the third and fourth most abundant prey with low %Ns of 1.56% and 0.80% but comparatively high %Os of 68% and 38%, respectively. Amphipods and decapods were rarely found in paddlefish stomachs.

Copepods exhibited a peak in %N during June and declined from July to February (Figure 2). Cladocerans exhibited an inverse relationship compared to copepods, with a low %N for June, which increased from July to February. This pattern was

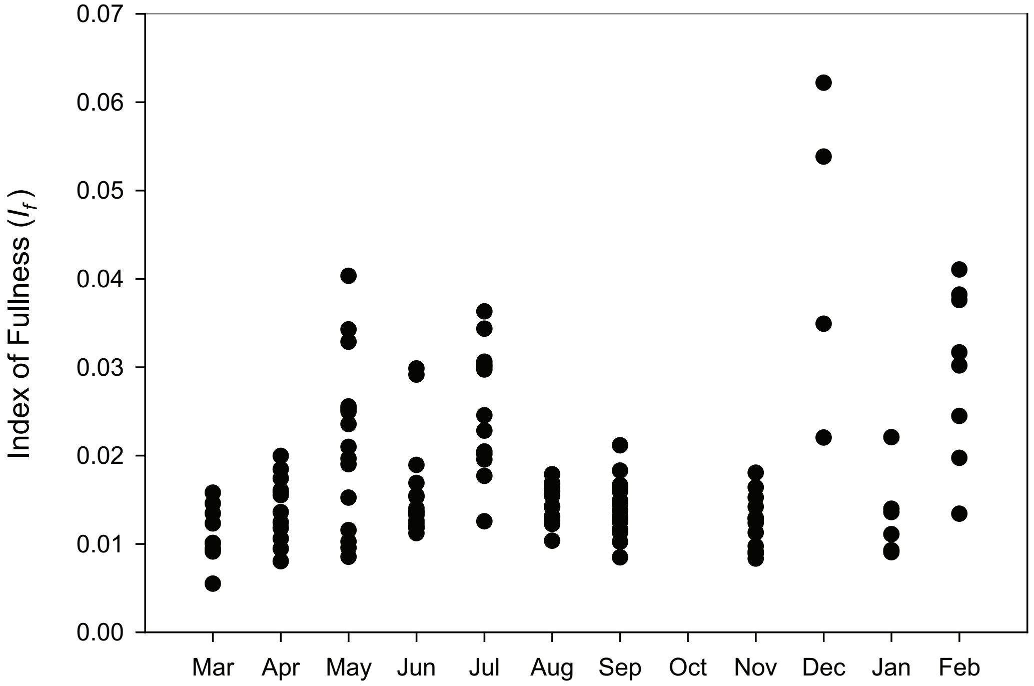

Figure 1. Plot of index of fullness (I_f) versus month of capture for 129 paddlefish caught in the Mermentau River, Louisiana from March 2002 to February 2003. Index of fullness (I_f) is calculated as the ratio of stomach weight to fish weight. Horizontal line represents mean index of fullness.

also observed in the crustacean zooplankton tows taken in November, January, and February, where copepods were dominant in the diets of paddlefish from March 2002 to September 2002 and cladocerans were dominant from November 2002 to February 2003 (Figure 2). Mean monthly abundances of other prey categories never approached those of copepods and cladocerans. Amphipods only occurred in May 2002 (%N = 0.4, %O = 15.4) and February 2003 (%N < 0.1, %O = 28.6). Decapods only occurred in August (%N = 0.1, %O = 12.5) and September 2002 (%N = 0.0, %O = 10.0). Insects occurred in every month with low %N (<4%) but always had %O greater than 50%. Ostracods

Table 2. Percent by number and percent occurrence for all prey categories found in the diet of 129 paddlefish caught in the Mermentau River, Louisiana from March 2002 to February 2003. Filamentous algae were not counted (n.q. = not quantified) and were not included in the calculation of percent by number.

Prey category	Percent by number	Percent occurrence
Copepoda	62.13	90.20
Cladocera	35.44	82.35
Insecta	1.56	68.63
Ostracoda	0.80	38.24
Amphipoda	0.06	3.92
Decapoda	0.01	1.96
Diatoms	n.q.	9.80

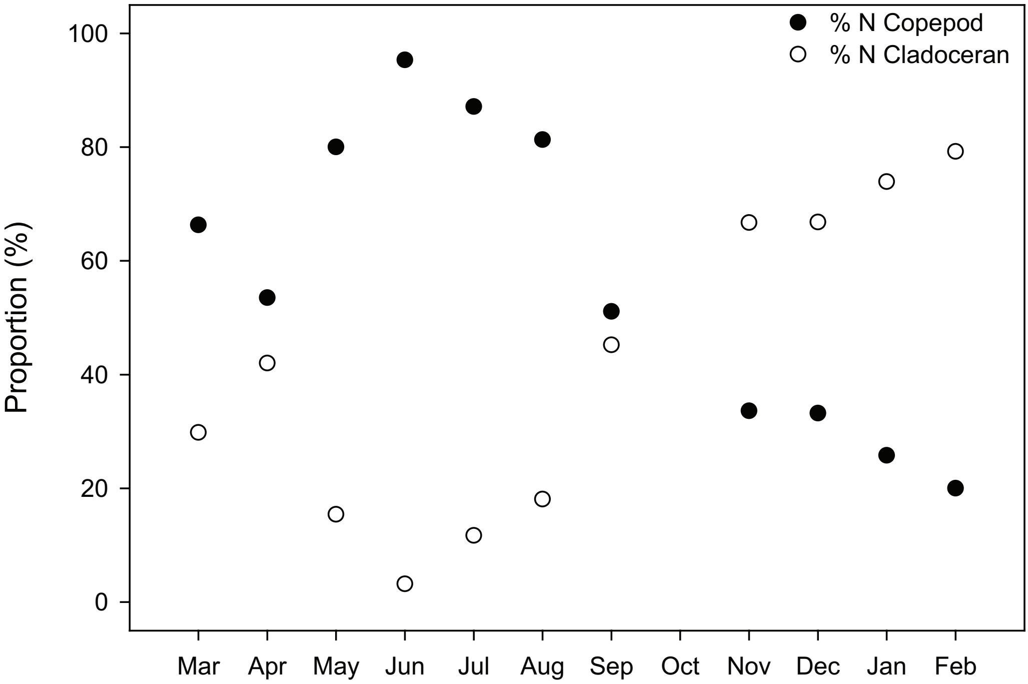

Figure 2. Mean percent number (%N) for copepods and cladocerans from 129 paddlefish collected from March 2002 to February 2003 in the Mermentau River, Louisiana.

occurred in every month except June, July, December 2002, and January 2003. While their %N was low (<4%), in the months they did occur, their %O was always above 30%. Diatoms only appeared in May and were found in 60% of those stomachs.

There was no apparent positive relationship between the abundance of zooplankton in the fullest paddlefish stomachs and average zooplankton concentration in the water column. For example, January's zooplankton concentration (95.54 no./m^3) was twice that of February (44.59 no./m^3), but February's estimate of gut fullness, N_p (27,200), was approximately 20% of January's (568,000). Estimates of apparent ingestion time, t_p, (November = 4 d, January = 1 d, and February = 48 d) are unrealistically long and reflected the apparent lack of a positive association between prey abundance and gut fullness in our limited data. The results, while preliminary, suggest that paddlefish are not random filter feeders, but seek out dense patches of zooplankton.

Paddlefish appeared to feed on slightly smaller sized copepods than found in the plankton in the net tows (Figure 3A). Copepods size distribution peaked at about 0.5 mm in stomachs but 0.7 mm in plankton tows. However, paddlefish appeared to feed on the same sizes of cladocerans found in the plankton (Figure 4A). A peak occurred in the 0.4-mm size-groups of cladocerans for paddlefish stomachs and plankton tows. Paddlefish fed on copepods and cladocerans that were no smaller than 0.2 mm. However, the results of the selectivity analysis indicated that paddlefish were not significant selective feeders for copepods (Figure 3B) and cladocerans (Figure 4B). High variability in Chesson's alpha indicates that individual paddlefish had highly variable diets and that overall selection for a particular size-class of copepods or cladocerans was not evident.

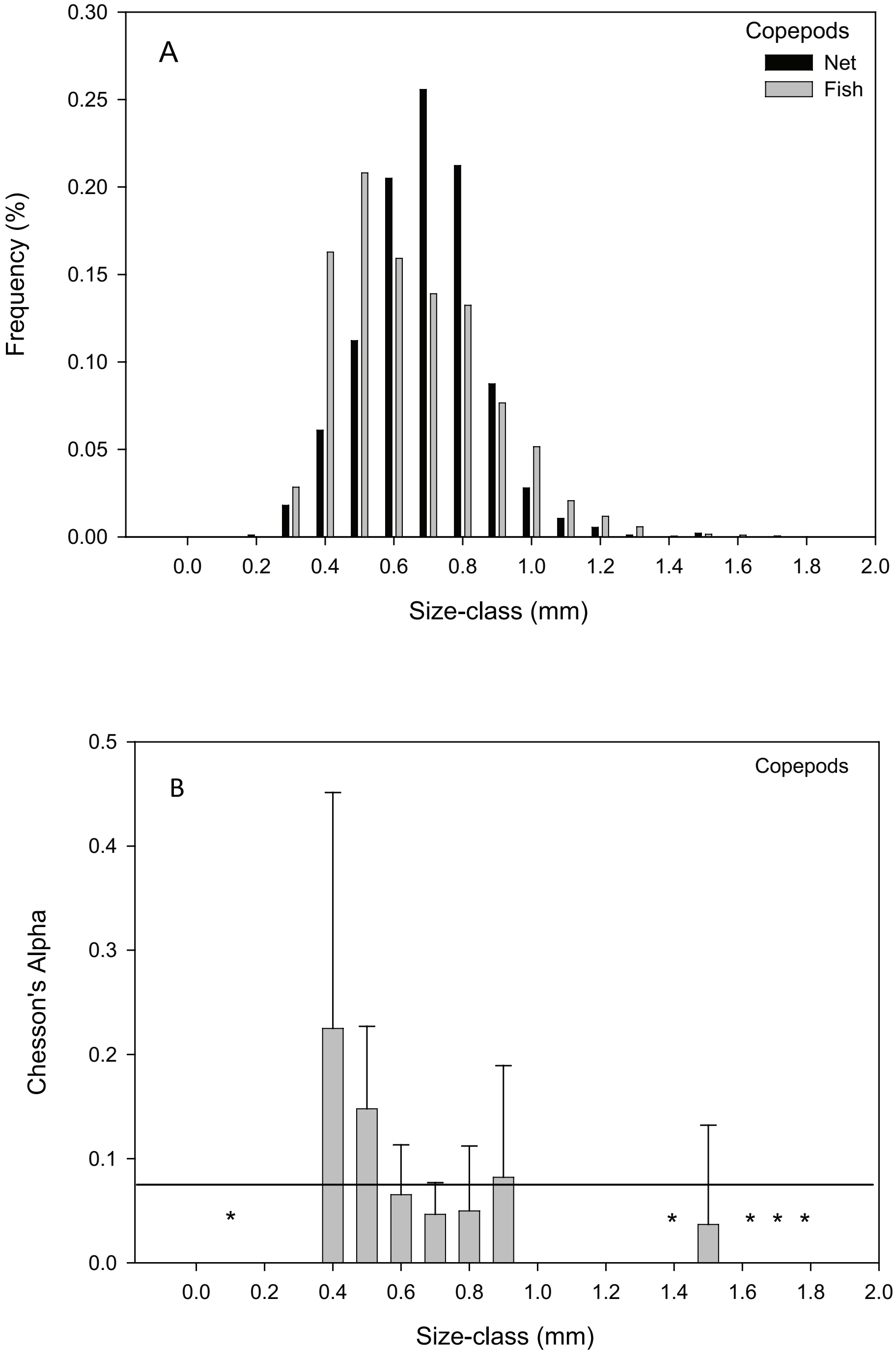

Figure 3. Frequency distributions (A) and size selection of paddlefish using Chesson's alpha (B) for copepods from November 2002, January and February 2003. Horizontal bar indicates unbiased feeding (1/m = 0.0769). A size-class with no bar indicates prey items of that size were not found in the stomachs. Asterisks indicate prey items of that size were not found in the net tows. Error bars represent one standard deviation.

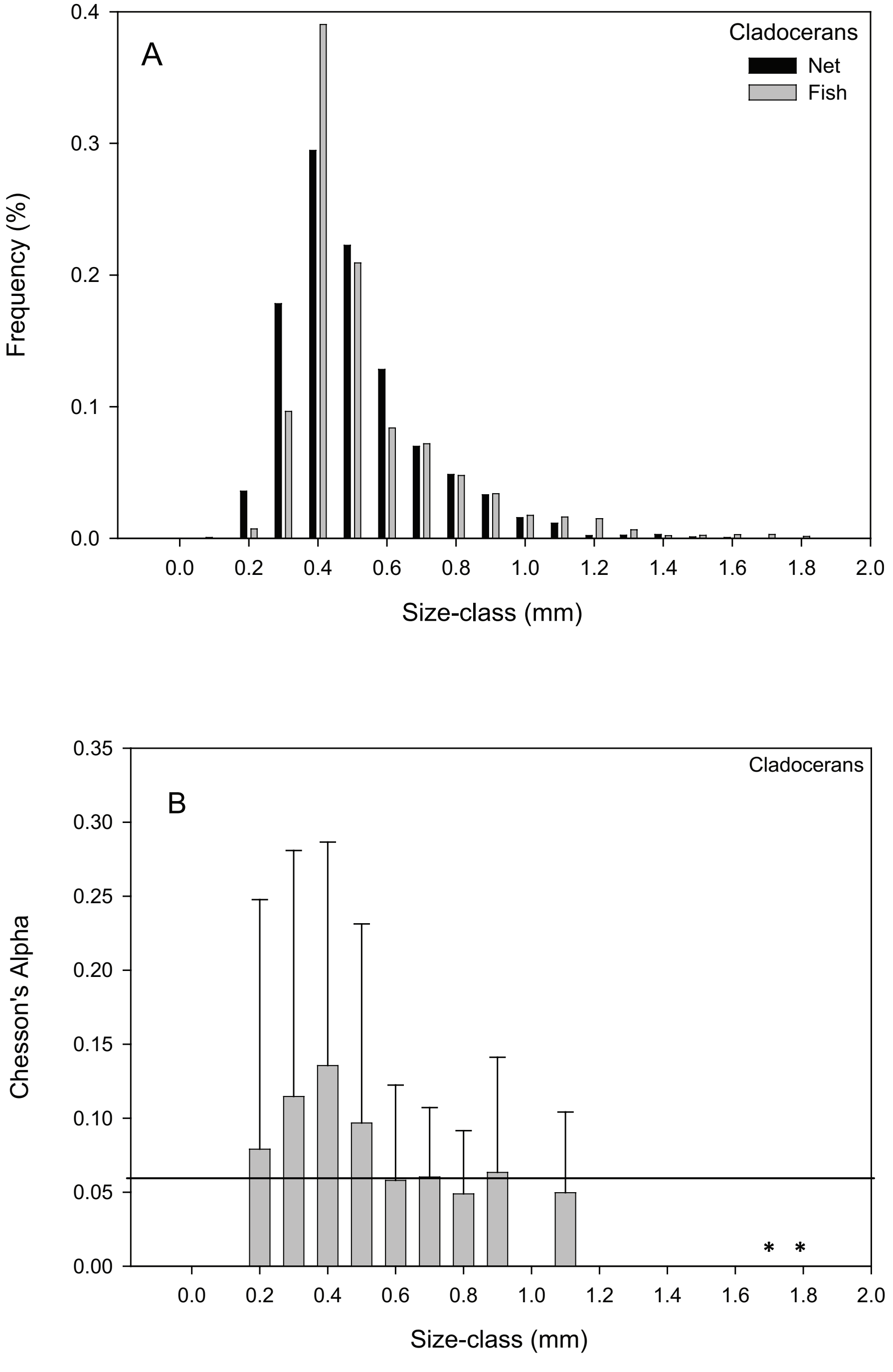

Figure 4. Frequency distributions (A) and size selection of paddlefish using Chesson's alpha (B) for cladocerans from November 2002, January and February 2003. Horizontal bar indicates unbiased feeding (1/m = 0.0625). A size-class with no bar indicates prey items of that size not found in the stomachs. Asterisks indicate prey items of that size not found in the net tows. Error bars represent one standard deviation.

Discussion

This is the first study of the feeding ecology of subadult and adult paddlefish in Louisiana waters. Paddlefish in Louisiana mainly feed on crustacean zooplankton such as copepods and cladocerans, which is similar to northern rivers (Rosen and Hales 1981) and other southern rivers and reservoirs (Hoxmeier and DeVries 1997; Hageman et al. 1986). Our study indicated that copepods and cladocerans comprised most of the diet of paddlefish but shifts from a predominance of copepods in the late spring to early fall to a predominance of cladocerans in the late fall to winter, which was similar to paddlefish in the Missouri River, South Dakota (Rosen and Hales 1981). However, Rosen and Hales (1981) also noted that Diaptomis were important in the fall, which was not evident in our study. The shift from copepods to cladocerans in our study is likely based on the dominance of these organisms in the plankton based on similarities between the gut contents and with the plankton tows taken in November, January and February. Like northern populations of paddlefish (Ruelle and Hudson 1977), we also found aquatic insects in the stomachs. However, Louisiana paddlefish were not similar with other populations of southern paddlefish, specifically Trinity River, Texas (Blackwell et al. 1995), where rotifers and copepod nauplii dominated in the eight paddlefish stomachs they examined.

It is possible that the importance of algae in the diets of subadult and adult paddlefish has been underestimated. We found that diatoms dominated the stomachs of Louisiana paddlefish in May 2003. This is similar to other southern rivers where Hageman et al. (1986) found "prominent green masses of algal and/or plant cells" in one particular month (October). Although few studies have reported algae as a diet item, some paddlefish populations apparently do consume algae during certain times of the year.

Our study supports the argument that paddlefish do not selectivity feed and can be described as indiscriminate feeders. As with Rosen and Hales (1981), paddlefish stomachs contained the same organisms as the plankton, but smaller forms were not in abundance. We also determined, along with Rosen and Hales (1981) that paddlefish were not selectively feeding on plankton. However, there did appear to be seasonal peaks in feeding throughout the year. Our study found two peaks in feeding, one in the summer and one in the winter. Rosen and Hales (1981) also found seasonal paddlefish peaks in the Missouri River, South Dakota, but they occurred during spring and fall. This may be a function of latitude as the fall peaks from Rosen and Hales (1981) were from South Dakota, where water temperatures might be similar to winter temperatures in Louisiana.

Apparent ingestion time of paddlefish ranged from 1 d in January to 48 d in February. Our estimates of apparent ingestion time were inversely related to stomach fullness and clearly demonstrated that paddlefish are not random filter feeders, supporting the argument that they locate and exploit localized concentrations of plankton (e.g., Wilkens et al. 1997; Freund et al. 2002). Wilkens et al. (1997) describe the rostrum as an antenna extended in front of the fish used to detect plankton encountered during continuous ram-ventilating swimming. This "antenna" is unique to the paddlefish and, as Wilkens states, may be a mechanism essential for prey location and capture.

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