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**An Investigation of Paddlefish, *Polyodon spathula*, and their prey in Fort Peck Reservoir, Montana**

A Thesis

Presented in Partial Fulfillment of the Requirements for the

Degree of Master in Science

with a

Major in Fishery Resources

in the

College of Graduate Studies

University of Idaho

by

Brett J. Bowersox

March 2004

Major Professor: Dennis L. Scarnecchia

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# AUTHORIZATION TO SUBMIT THESIS

This thesis of Brett Bowersox, submitted for the degree of Master of Science with a major in Fishery Resources and entitled "An Investigation of Paddlefish, *Polyodon spathula*, and Their Prey in Fort Peck Reservoir, Montana", has been reviewed in final form as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

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Steven B. Daley Laursen

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Katherine G. Aiken

# ABSTRACT

The paddlefish, *Polyodon spathula*, stock located on the Missouri River in Fort Peck Reservoir, Montana, is one of a small number of remaining naturally reproducing populations. However, limited information is available with regards to distribution and abundance of paddlefish prey as well as long-term paddlefish growth rates within the reservoir.

The objectives of chapter one were to 1) assess and compare *Leptodora* day/night abundance in three habitat types (riverine, transitional, and reservoir) within the headwaters of Fort Peck Reservoir, Montana, USA, 2) determine if *Leptodora* size differs vertically and horizontally in the study area, and 3) determine if *Leptodora* distribution differed under different turbidities and water temperatures. *Leptodora* abundance displayed a patchy distribution within the three habitat types; however greatest abundances were consistently found within the reservoir habitat type. Minimal differences were found in day/night abundances at depths or *Leptodora* length distribution at depths within the headwaters.

The objectives of chapter two were 1) examine changes in paddlefish weight and body length distributions during three different reservoir time periods (1977-1978, 1992-1993, and 2000, 2002) and 2) examine changes in paddlefish early growth during the three time periods. The analysis indicated that the number of large fish in the population and early growth of both male and female paddlefish have decreased over time. The exact cause of the decrease is not known, however it is hypothesized that a contributing factor is reduced reservoir productivity associated with reservoir aging.

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# INTRODUCTION

The Missouri River has undergone extensive alterations over the past 100 years. As the interior of the United States has developed, the river has been utilized for flood control, navigation, hydro-power, and irrigation (Hesse 1987). The alterations associated with these activities have had negative impacts on many native fish species by blocking migrations to spawning grounds, changing water and temperature regimes within the river, and decreasing the rivers connectivity with the floodplain and its habitat (Hesse 1987, Poff et al. 1997). One fish species that has been greatly affected by these changes is the paddlefish, *Polyodon spathula* (Carlson and Bonislawsky 1981).

The paddlefish is a large zooplanktivorous fish native to the Mississippi and Missouri River drainage (Russell 1986). Paddlefish that historically reared in back-waters and oxbow lakes now mainly rear in reservoirs created by dams (Hoxmeier and DeVries 1997). The species that historically migrated extensively throughout the Missouri-Mississippi hydrosystem is now often confined to river sections between dams (Rosen et al. 1982).

With the extensive changes to paddlefish habitat, many populations are in decline (Dillard et al. 1986). Populations that have remained stable have retained access to spawning habitat above the reservoirs in which the fish rear. One such population is located on the Missouri River in Fort Peck Reservoir, Montana.

Fort Peck Dam, completed in 1938, aids in flood control, river navigation, and hydropower (U.S. Army Corps of Engineers 1991). Paddlefish have been shown to rear within the productive waters of the reservoir and utilize the Missouri River above the reservoir for spawning (Wiedenheft 1992). Recreational snag-fisheries occur on the

Missouri River during spawning migrations in spring. Creel census surveys of this fishery have provided information on age, growth, and size of adult paddlefish and tagging of adult paddlefish in the river has provided information on movements and harvest rates for the stock (Gilge and Liebelt 1997). In addition, dentaries (lower jawbones) taken from harvested individuals provided information on age of the stock. Kozfkay and Scarnecchia (2002) examined recruitment and feeding ecology of age-0 and age-1 paddlefish within Fort Peck Reservoir. Little information has been available, however, on paddlefish ecology within Fort Peck Reservoir as the young paddlefish rear. Information is needed with regards to distribution and abundance of their prey as well as long-term paddlefish growth rates within the reservoir as the reservoir ages.

The objectives of this study were to 1) assess the distribution and abundance of the zooplankton, *Leptodora kindti*, the main prey item of age-0 and age-1 paddlefish, within the headwaters of Fort Peck Reservoir, and 2) determine if changes in growth rates have occurred within the Fort Peck Reservoir paddlefish population over the past three decades. The first objective will be considered in Chapter One and the second objective in Chapter Two.

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# CHAPTER 1. ASSESMENT OF DISTRIBUTION, ABUNDANCE, AND VERTICAL MIGRATION PATTERNS OF THE ZOOPLANKTON *LEPTODORA KINDTI* IN UPPER FORT PECK RESERVOIR, MONTANA

## ABSTRACT

The zooplankton *Leptodora kindti,* a large predaceous cladoceran, has been shown to be highly mobile and to undertake diel vertical migrations (DVM). The objectives of this study were to 1) assess and compare *Leptodora* day/night abundance in three habitat types (riverine, transitional, and reservoir) within the headwaters of Fort Peck Reservoir, Montana, USA, 2) determine if *Leptodora* size differs vertically and horizontally in the study area, and 3) determine if *Leptodora* distribution differed under different turbidities and water temperatures.

*Leptodora* were sampled from July 22 – September 10, 2002, using a bongo net towed at set depths within the three habitat types. *Leptodora* abundance displayed a patchy distribution within the three habitat types; however greatest abundances were consistently found within the reservoir habitat type. Minimal differences were found in day/night abundances at depths or *Leptodora* length distribution at depths within the headwaters. Highest daytime abundances were found at 1.25 m or greater depths for five of six sample periods.

The patchy distribution of *Leptodora* and their lack of a strong consistent pattern of DVM in the headwaters of Fort Peck Reservoir have implications for the assessment of age-0 paddlefish recruitment on the reservoir. Results indicate that if visual transect

counts that are currently utilized to assess age-0 paddlefish recruitment in the headwaters are biased, they are biased somewhat conservatively because many *Leptodora* remain in deeper strata both day and night. Because of the patchy distribution of *Leptodora* in this study and the large surface area that can be covered during visual transect counts, this method is to be preferred over other more localized methods.

# INTRODUCTION

The phenomenon of diel vertical migration (DVM) is recognized as one of the most common and important forms of animal migrations (Bollens 1996, Wetzel 2001). DVM is based upon the idea that by undertaking predictable, consistent movements, individuals can maximize energy gain via feeding while minimizing the probability of death via predators (Bollens 1996). It is widely believed that the main impetus for DVM is predator avoidance (Bollens 1996, Ghan et al. 1998).

DVM has been observed in numerous zooplankton species in lakes and reservoirs (Levy 1991, Loose and Dawidowicz 1994, Ghan et al. 1998, De Robertis and Jaffe 2000). DVM in zooplankton typically consists of an ascent towards the surface waters at dusk and a descent towards greater depths at dawn, although reversed DVM has been reported on numerous occasions (Levy 1990, Vijerberg 1991). In order to avoid sight-feeding predators, zooplankton may make predictable migrations to deeper, less productive waters during the day and ascend to food-rich surface waters to feed at night. The distance of DVM can range anywhere from a few meters to as much as 100 meters or more depending on various environmental conditions (Stewart and Sutherland 1993, Levy 1991).

One zooplankton species that has been shown to undertake DVM is *Leptodora kindti*, hereafter referred to as *Leptodora*. *Leptodora* is a large, (6-12 mm) highly mobile zooplankton belonging to the order Cladocera (Browman et al. 1989; Figure 1). Previous studies have shown *Leptodora* to undertake DVM in lake and reservoir systems (Costa and Cummins 1969, Vijverberg 1991, Stewart and Sutherland 1993, Liu et al. 2002). Liu et al., for example, found that *Leptodora* exhibited DVM in Xujiahe Reservoir, China.

*Leptodora* concentrations were higher at the surface of the reservoir at night than during the day, indicating a nocturnal migration to the surface.

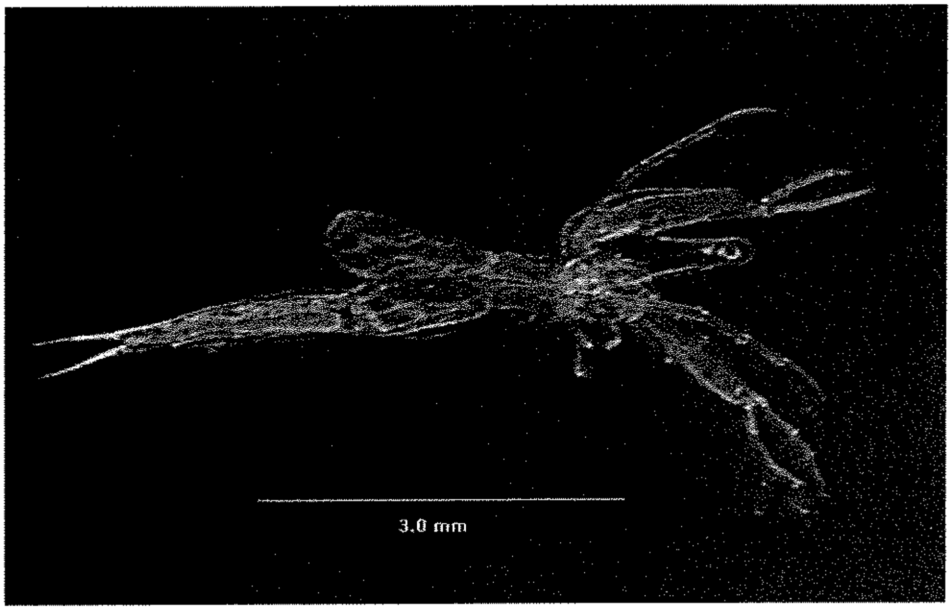



Figure 1. Adult *Leptodora kindti*

*Leptodora* are tactile predators feeding largely on other zooplankton, such as *Diaphanosoma, Bosmina, Daphnia,* and *Ceriodaphnia* (Browman et al. 1989, Herzig and Auer 1990). When a prey item is contacted, the six pairs of legs positioned anterior to the mouth close up around the prey item like a basket, pulling the prey towards the oral parts (Sebestyen 1931). *Leptodora* are voracious predators and can have a significant impact on the abundance and production of their prey. In Canyon Ferry Reservoir, Montana, the average predation rate of *Leptodora* on *Daphnia* was 33% of the net production of *Daphnia* (Wright 1965).

In addition to *Leptodora*'s impact as an invertebrate predator, it is also an important food source for various fish species. Yellow perch, *Perca flavescens*, black crappie, *Pomoxis nigromaculatus*, white crappie, *Pomoxis annularis,* lake chub, *Couesius plumbeus*, and paddlefish, *Polyodon spathula*, have all been shown to positively select for *Leptodora* (Costa and Cummins 1972, Serns and Hoff 1984, Fredericks 1994, Kozfkay and Scarnecchia 2002). Fredericks (1994) reported that in Lake Sakakawea, North Dakota, *Leptodora* constituted 85% of contents by number within age-0 paddlefish stomachs even though they constituted less than 1% of the zooplankton present in the environment. Kozfkay and Scarnecchia (2002) found that both age-0 and age-1 paddlefish in Fort Peck Reservoir strongly selected for *Leptodora* prior to the initiation of filter-feeding at about 300 mm body length (BL, front of eye to fork of caudal fin) (Ruelle and Hudson 1977).

A number of different environmental factors including water temperature and turbidity may influence the abundance of *Leptodora*, as well as the tendency of the species to undertake DVM. *Leptodora* was reported by Cummins et al. (1969) as being temperature-limited at 14 °C and disappearing from samples at any lower temperatures. Garton et al. (1990) found *Leptodora* abundance to decline in Western Lake Erie in water temperatures ranging from 5-15 C° in the fall of the year. Turbidity may also affect the amount of DVM in *Leptodora* within different systems. Zettler and Carter (1986) found that in a turbid lake system in Ontario, zooplankton exhibited an increase in upward displacement corresponding with an increase in turbidity. They also found large zooplankton such as *Leptodora* and the opossum shrimp, *Mysis relicta,* to have greater abundance in high turbidities whereas some smaller cladocerans and copepods had greater abundance in lower turbidities (Zettler and Carter 1986).

In Fort Peck Reservoir, a large mainstem impoundment on the Missouri River, Montana, *Leptodora* was found to be the primary and preferred food item for age-0 paddlefish (Kozfkay and Scarnecchia 2002). In addition, the largest *Leptodora* were eaten preferentially (Kozfkay and Scarnecchia 2002). Despite the evidence of *Leptodora* as the key forage item for young paddlefish, little is known about the ecology and changes in day/night distribution of *Leptodora* in Fort Peck Reservoir. In particular, more information is needed by fisheries managers responsible for the paddlefish stock. Paddlefish reproductive success is estimated annually by counting the number of age-0 and age-1 fish seen at the surface along longitudinal transects (Fredericks and Scarnecchia 1997). Sampling methods for both zooplankton and age-0 and age-1 paddlefish have therefore concentrated on the surface waters of the reservoir. If changes in day/night distribution suggest that *Leptodora* undergoes DVM, these sampling methods may not provide an accurate measure of *Leptodora* abundance nor of age-0 and age-1 paddlefish abundance in the reservoir. Furthermore, if changes in day/night mean lengths indicate that the larger individuals of *Leptodora* undergo DVM; this result may also induce movements of age-0 paddlefish in the headwaters of Fort Peck Reservoir. For a better understanding of the effectiveness of age-0 and age-1 paddlefish transect counts, more information is needed on the changes in day/night abundance of their preferred prey.

The objectives of this study were to 1) assess and compare *Leptodora* day/night abundances in three different habitat types in the headwaters of Fort Peck Reservoir, 2) determine if *Leptodora* size differs vertically and horizontally in the study area and 3) investigate *Leptodora* temporal and horizontal distribution relative to environmental variables, specifically turbidity and water temperature.

## STUDY AREA

Fort Peck Reservoir is located in central Montana and is the uppermost mainstem impoundment on the Missouri River system. The Fort Peck Project was placed in operation in 1938 and when it was finished, it was the largest earthfill hydraulic dam in the world (U.S. Army Corps of Engineers 1991). At full-pool, the reservoir stores approximately 23.4 billion cubic meters of water covering an area of 100,767 hectares (U. S. Army Corps of Engineers 1991). The lake impounds the runoff of approximately 149,000 square kilometers of the Missouri River drainage basin (U.S. Army Corps of Engineers 1991).

Over the most recent five year period (1998-2002), this region of Montana has been subject to a severe drought. Water elevation within Fort Peck Reservoir in the month of August has steadily declined from 685 m msl in 1997 to 676 m asl in 2002 (U.S. Army Corps of Engineers 2003). Because of the significant drawdowns, the shoreline of Fort Peck Reservoir as of 2002 was largely barren with no aquatic macrophytes or fish habitat structure present. In addition, the river-reservoir interface has moved steadily down-reservoir, approximately 20 – 25 km from 1998 to 2002.

Previous paddlefish research conducted on Fort Peck reservoir found that age-0 paddlefish concentrated in the headwaters of the reservoir in late summer after migration down the Missouri River after the late spring and early summer spawning event

(Wiedenheft 1992, Kozfkay and Scarnecchia 2002). This area included the river-reservoir transitional zone as well as more lentic habitat in the reservoir. This entire area has a soft sediment bottom with a range of depths from <1 to 6 m.

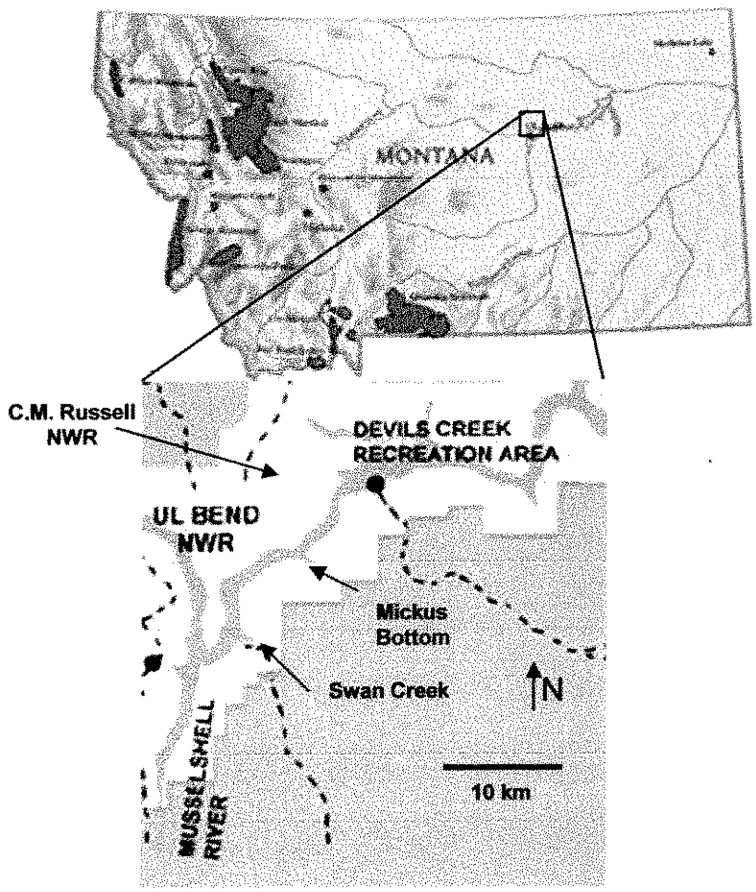



Figure 2. The study area for 2002 *Leptodora* research.

The study focused on the headwaters of the reservoir from the river/reservoir interface at Squaw Creek (rkm 2,997) down-reservoir to slightly above Mickus Bottom (rkm 2,988) within the Charles M. Russell National Wildlife Refuge (Figure 2). The shallow (1-7m), turbid (Secchi depth <1m) headwaters have been shown to be excellent rearing habitat for age-0 and age-1 paddlefish, at least in some years (Wiedenheft 1992). Average width in this section of the reservoir was approximately 1km. There was negligible flow in the area with velocities <1 m/s.

# METHODS

## Zooplankton Sampling

The headwaters of the reservoir were classified into three habitat types arranged longitudinally: riverine, transitional, and reservoir. The riverine habitat type was characterized by high turbidities (median value of 30 NTU), shallow depth (~ 1- 2.5 m), and slight water velocity (< 1 m/s). The transitional habitat type was characterized by mid-range turbidity (median value of 22 NTU), intermediate depth (2.5 - 3.5 m), and negligible velocity. The reservoir habitat type was characterized by low turbidities (median value 15 NTU), greatest depth (< 5.5 m), and no measurable water velocity.

Each habitat type consisted of a 1.5 km long section of reservoir with 1 km separating each section longitudinally. Three waypoints were placed at the uppermost boundary of the habitat type and were spaced at one quarter, one half, and three-quarters across the reservoir. Two additional series of three waypoints were placed 0.75 and 1.5 km below the uppermost waypoints and set across the reservoir in a similar fashion resulting in a total of nine waypoints within each of the three habitat types.

Sampling occurred once every ten days from July 22 – September 10 for a total of six sample periods. For each sample period, three waypoints were selected using a random numbers chart from the nine possible waypoints within each habitat type. At each waypoint, samples were taken both by day (1000 h – 1700 h) and by night (2000 h – 0100 h) during each sample period.

In order to assess *Leptodora* distribution and abundance in the water column, fixed depth tows were conducted at waypoints using a 500-micron Bongo net with a 48.75 cm gape diameter (Figure 3).

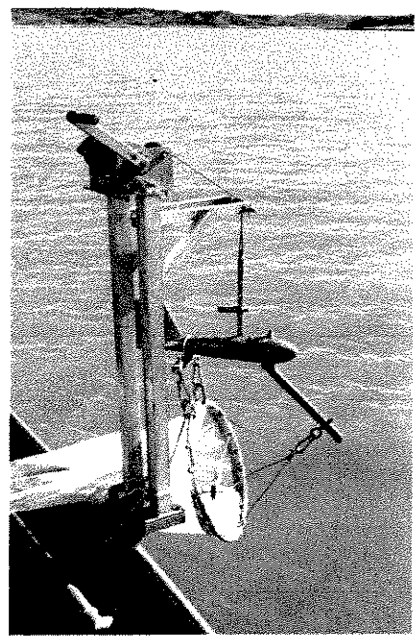


Figure 3. Sampling apparatus used for *Leptodora* tows.

The net was lowered into the water using a winch attached to the side of the boat. Tows were taken in 1 m increments from the surface of the water to within 1 m of the bottom. Since the net sampled 0.5 m of water at each depth, the center of the gape was recorded as the sampled depth 0.25 (surface), 1.25 (1-1.5 m) and so on. Once the net was lowered to the desired depth, the boat was driven at 2 km/h for 1 min. The angle of the cable attaching the net to the winch was measured in order to achieve an accurate sample depth. At the end of a tow, the net was retrieved to the surface after the boat had ceased moving forward. This approach ensured that the amount of water from depths other than that of the tow filtered by the net were negligible. Three replicates were collected for each sample depth. Zooplankton samples were placed in specimen jars labeled with date, waypoint, depth of tow, diurnal period (day or night), and replication and preserved in 90% ethanol.

Zooplankton Analysis

In the laboratory, zooplankton samples were analyzed to estimate the abundance and average length of *Leptodora* found within each tow. Each sample jar was rinsed and the contents diluted into a beaker of appropriate size based upon the amount of zooplankton within the sample jar. Once the sample was diluted, the contents were stirred using a Hensen-Stimple pipette to unstratify the contents of the beaker. Three 2-ml samples were then drawn from the beaker using the pipette and placed into a counting tray. The contents were observed under a dissecting microscope and all *Leptodora* within the tray were tallied. The contents of the counting tray were then rinsed into a strainer. This procedure was repeated three times for each zooplankton tow. Once the *Leptodora* had been tallied for the three subsamples, the average count of the three subsamples was used to obtain an overall mean *Leptodora* count within the tow. Dilution volume of the sample in the beaker was divided by 6 ml to get a total number of subsamples within the beaker. In order to estimate an overall *Leptodora* abundance (organisms/$m^3$) for the tow, the mean number of *Leptodora* tallied from the three recorded subsamples was multiplied by the total number of subsamples within the beaker. This number was then divided by the estimated volume of the sample provided by the flowmeter within the gape of the bongo net. The volume of water strained in a tow (v) was calculated using the following equations:

$$V = \frac{3.14 \times (N)^2 \times D}{4}$$

and

$$D = \frac{F \times R}{Q}$$

where:
N = Net diameter (48.75 cm)
D = Distance of tow
F = Difference in flowmeter counts
R = Rotor constant (26,873)
Q = Set denominator (999999)

In order to compare lengths of *Leptodora* found at various depths, lengths of the first ten individuals observed within each tow were measured using an ocular micrometer in the eyepiece of the dissecting microscope. The ten lengths were recorded and averaged for each tow to arrive at a mean length for each tow. In samples where ten individuals were not found, all individuals present were recorded and measured to estimate abundance and mean length.

<u>Physical Habitat Variables</u>

Total depth, water temperature, and turbidity were recorded at each waypoint sampled during every sample period. Water temperature and turbidity were recorded at each depth interval. All three variables were measured before tows were taken. Depth to the bottom was recorded to the nearest tenth of a meter using a sonar unit mounted at the stern of the boat. Water temperature was recorded to the nearest 0.1°C using an YSI 30 temperature probe lowered from the side of the boat and held at depth for twenty seconds. Water samples were taken from each tow depth using a Van Dorn water sampler.

Turbidity (in Nephelometric Turbidity Units NTU) was measured using a Hach turbidimeter to the nearest 0.1 NTU.

Analysis

Analysis of Variance (ANOVA) was used to test for differences of day/night abundances of *Leptodora* and for length differences of *Leptodora* among sampling strata. The null hypotheses were that no significant differences would be observed among different habitat types and sample depths for both *Leptodora* abundance and length. In addition, no difference in *Leptodora* abundance would be found between night and day samples at the same depth.

Preliminary analysis indicated a positive correlation between the mean and standard deviation in *Leptodora* abundance for the six sample periods (Table 1).

Table 1. Least-square means results for *Leptodora* densities in organisms/$m^3$ for all tows taken during each sample period in the 2002 field season.

| Sample Period | N | SD | SE | Mean | LS Means |
|---|---|---|---|---|---|
| 1 | 207 | 75.708 | 5.26207 | 51.035 | A |
| 2 | 204 | 33.312 | 2.33231 | 22.604 | B |
| 3 | 180 | 1.737 | 0.12947 | 0.561 | D |
| 4 | 198 | 19.133 | 1.35972 | 7.826 | C |
| 5 | 198 | 19.222 | 1.36605 | 15.119 | B |
| 6 | 174 | 0.904 | 0.06853 | 0.468 | D |

As a result, all *Leptodora* abundance data were transformed by the natural logarithms and results are reported as such, unless indicated otherwise. The natural log of *Leptodora* abundance was the response variable and sample period, habitat type, depth of tow, and diurnal period were main effects. Sample period and habitat type (riverine, transitional, and reservoir) were included in the ANOVA model to investigate spatial and temporal trends in natural log *Leptodora* abundance over the course of the field season. In addition to the overall model, separate models were run for each of the six sample periods because of variation among sample periods. The natural log of *Leptodora* abundance was again the response variable and depth of tow, diurnal period, and habitat type were the main effects. A least-squares means slice procedure was used to test for significant differences in mean abundance at different depths and different diurnal periods by habitat type. Regression analysis was used to test for the relation between *Leptodora* abundance and turbidity and water temperature. Data were examined collectively over all six sample periods as well as during each sample period individually because of the variation in turbidity and water temperature throughout the field season.

Differences in the length of *Leptodora* found at different depths during the day and night sample periods were investigated statistically using means of the ten recorded lengths for each of the tows. ANOVA procedures were again employed with *Leptodora* length as the response variable and depth of tow, diurnal period, and habitat type as main effects. The least-squares means slice procedure was used to test for significant differences in mean lengths found at different depths and at different diurnal periods within each habitat type.

Temporal differences in water temperature, turbidity, and *Leptodora* abundance were observed graphically for positive and negative relationships. In addition, an ANOVA procedure was employed to test for differences in both water temperature and turbidity among habitat types. Results were used to determine if *Leptodora* abundance varied longitudinally in the study area with regards to the environmental variables.

# RESULTS

## Overall *Leptodora* Abundance

*Leptodora* abundance by sample period and by habitat type was highly variable. Significant variation was found by sample period (ANOVA; $p < .0001$) (Table 2). Even the waypoints within a habitat type had highly significant overall differences in abundance of *Leptodora* (ANOVA; $p = < .0001$) (Table 2). In addition, high levels of significance were present by habitat type and by waypoint within each of the separate sample periods ($p < 0.05$) (Appendix, Tables 1-6).

Table 2. Overall ANOVA table of log transformed *Leptodora* abundances for entire 2002 field season.

| Source | *df* | Mean Square | *F* | Pr>F |
|---|---|---|---|---|
| Sample Period | 5 | 387.838 | 275.55 | **<.0001** |
| Habitat Type | 2 | 270.119 | 324.72 | **<.0001** |
| Depth | 5 | 30.945 | 3.11 | **0.0086** |
| Diurnal Period | 1 | 0.0018 | 0.49 | 0.9568 |
| Habitat Type x Depth | 5 | 10.006 | 3.24 | **0.0066** |
| Habitat type x Diurnal | 2 | 13.525 | 10.94 | **<.0001** |
| Depth x Diurnal | 5 | 11.338 | 3.67 | **0.0027** |
| Habitat type x Depth x Diurnal | 5 | 6.728 | 2.18 | 0.0544 |
| Water Temperature | 1 | 4.652 | 7.53 | **0.0062** |
| Turbidity | 1 | 0.99 | 1.6 | 0.2058 |
| Water Temperature x Turbidity | 1 | 0.974 | 1.57 | 0.2109 |
| Waypoint(Habitat type) | 22 | 365.582 | 26.23 | **<.0001** |
| Error | 1154 | 0.618 | | |

Considerable variation in *Leptodora* abundance was found by sample periods (Table 2). A significantly greater abundance of *Leptodora* was found during the first sample period (July 22 – July 29) than any later sample period (Figure 4). No difference in abundance was found between the second period (Aug. 1 – Aug. 3) and fifth period

(Sept. 2 – Sept. 4), nor between the third period (Aug. 11 – Aug. 15) and sixth period (Sept. 9 – Sept. 10) (Figure 4).

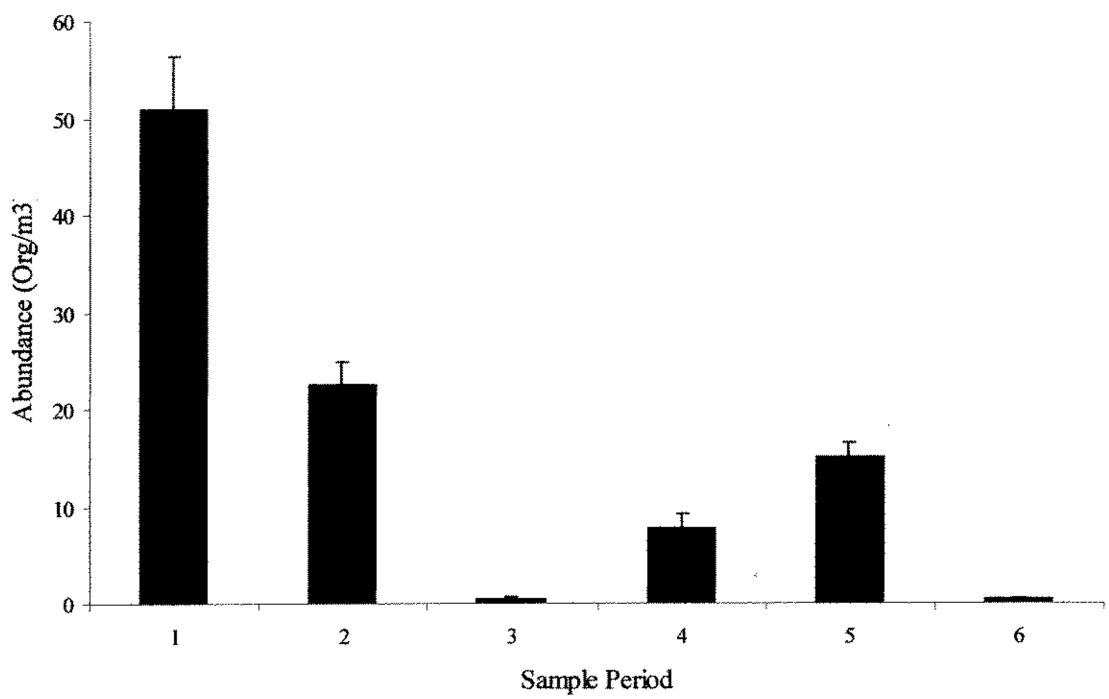



Figure 4. Mean *Leptodora* abundance and standard error (SE) bars for all tows taken during each sample period of the 2002 field season (July 22 - September 10).

Overall *Leptodora* abundance was highest within the reservoir habitat type (Figure 5). Abundance in five sample periods (1, 2, 4, 5, and 6) was higher within the reservoir habitat type than in the riverine and transitional habitat types. During the third sample period however, the transitional habitat type had the highest abundances.

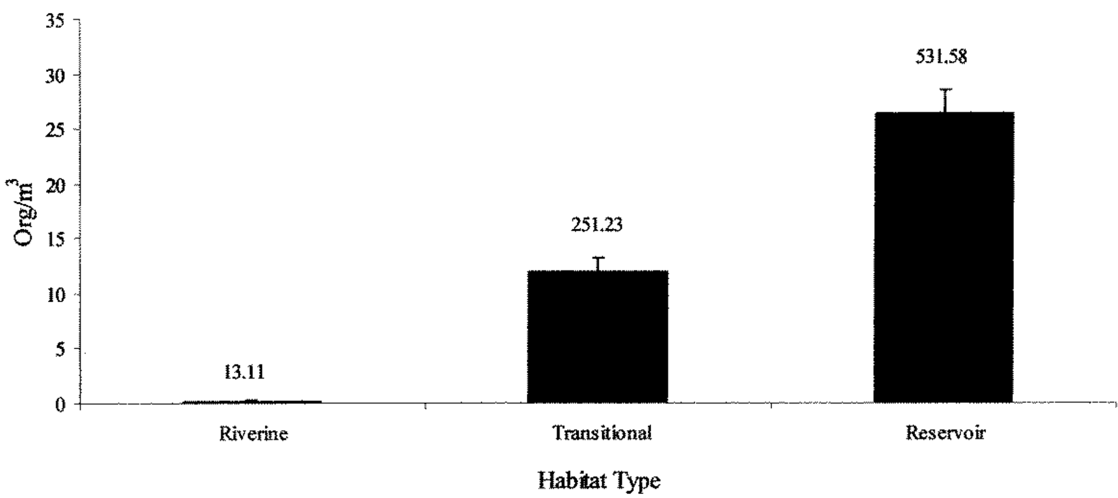



Figure 5. Mean *Leptodora* abundance and standard error bars (SE) for all tows taken in each habitat type during the 2002 field season. Maximum abundances for each habitat type are placed above the SE bars.

Abundance at depth (Day/Night)

No consistent pattern of abundance at depth by day and night was found in *Leptodora* within the headwaters of Fort Peck Reservoir. Diurnal period (day/night) was not significantly related to *Leptodora* abundance within the overall model (ANOVA; $p = 0.9568$) (Table 2). However, the interaction between diurnal period and depth was highly significant (ANOVA; $p = 0.0027$) (Table 2). Significant interaction was found between day/night and depth in five of the six individual sample periods (Appendix, Tables 1-6).

Some evidence of modest differences in abundance at depth by day and night was found within the transitional and reservoir habitat types. For example, within the transitional habitat type, three sample periods had significantly higher abundances of *Leptodora* at the surface by night than by day (Figures 6, 7, and 10). A similar directional pattern was also found during two other sample periods, although the difference was not found to be significant (Figures 8 and 9). Higher abundances were often found in deeper strata both by day and by night. For instance, during sample periods 4, 5, and 6 higher *Leptodora* abundances by night were found within deeper strata (3.25, 1.25, and 3.25 m) than at the surface (Figures 8, 9, and 10). In addition, by day, higher abundances were often observed at 1.25 or 2.25 m rather than at the surface. During sample periods 2 and 3, higher abundances by day were found at the surface, however, abundances by night exceeded those present by day. Thus, abundances in the transitional habitat type at depth by day and night displayed no consistent pattern.

The lack of a consistent pattern also held within the reservoir habitat type. Significantly higher abundances were again found at the surface by night than by day for three of the six sample periods (Figures 6, 9, and 10). However, during four periods (2, 3, 5, and 6) higher abundances by night were found in deeper strata rather than at the surface (Figures 7, 8, 10, and 11). As with the transitional habitat type, higher *Leptodora* abundances by day were found at 1.25 and 2.25 m. Only during the third and fifth sample periods did this pattern change with higher abundances by day recorded at the surface and 3.25 m respectively (Figures 8 and 10).

Within the riverine habitat type *Leptodora* presence was sporadic and the abundance low. Only 11% of tows taken in this habitat type contained *Leptodora* and abundance within those tows was extremely low ($< 1$ org/m$^3$). No significant differences in abundance could be detected.

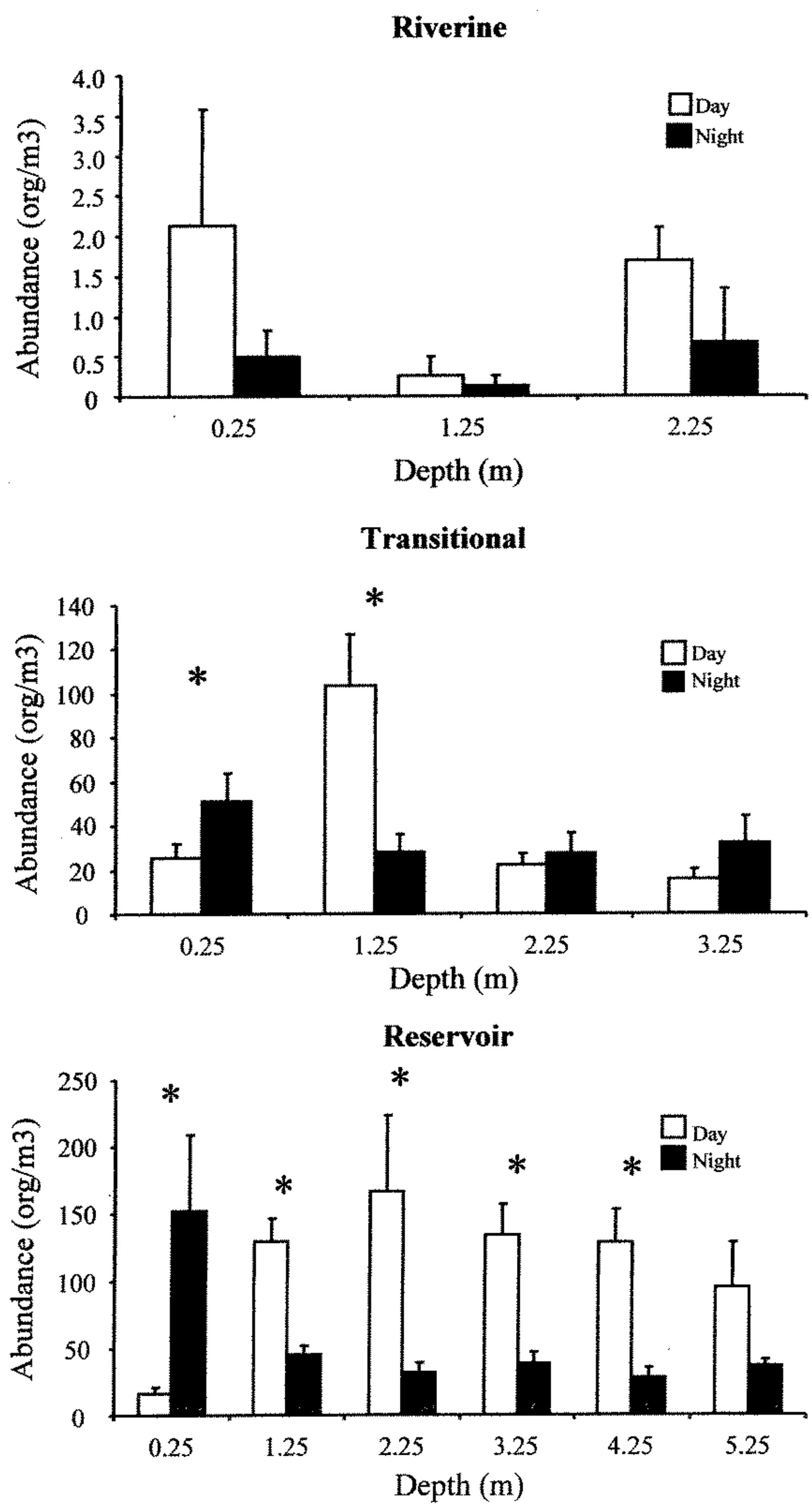



Figure 6. Mean and standard error of *Leptodora* abundance at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 1 (July 22 – July 29). An asterisk (*) indicates a significant (p<= 0.05) difference between day and night means at the specified depth.

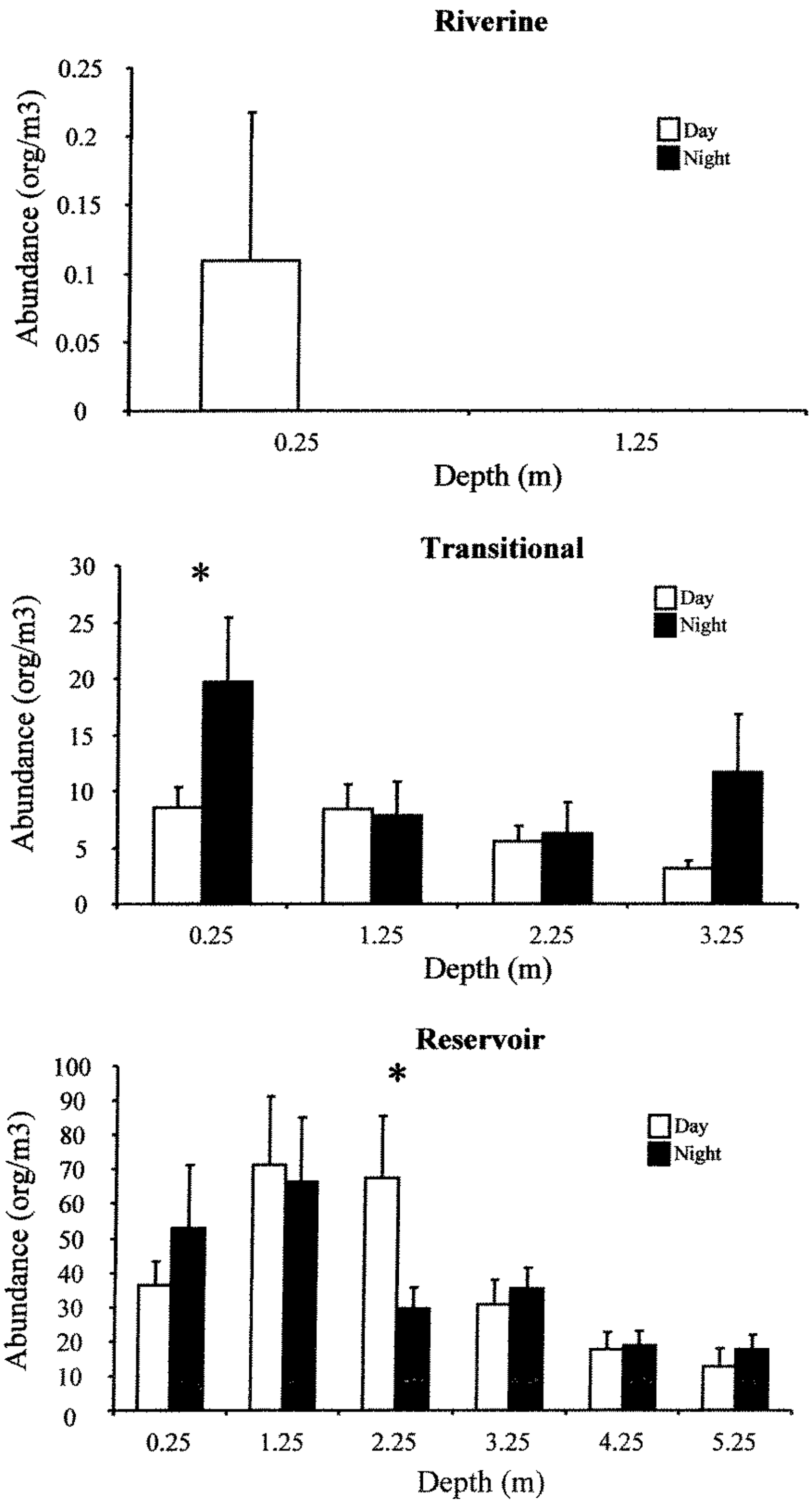



Figure 7. Mean and standard error of *Leptodora* abundance at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 2 (August 1 – August 3). An asterisk (*) indicates a significant ($p <= 0.05$) difference between day and night means at the specified depth.

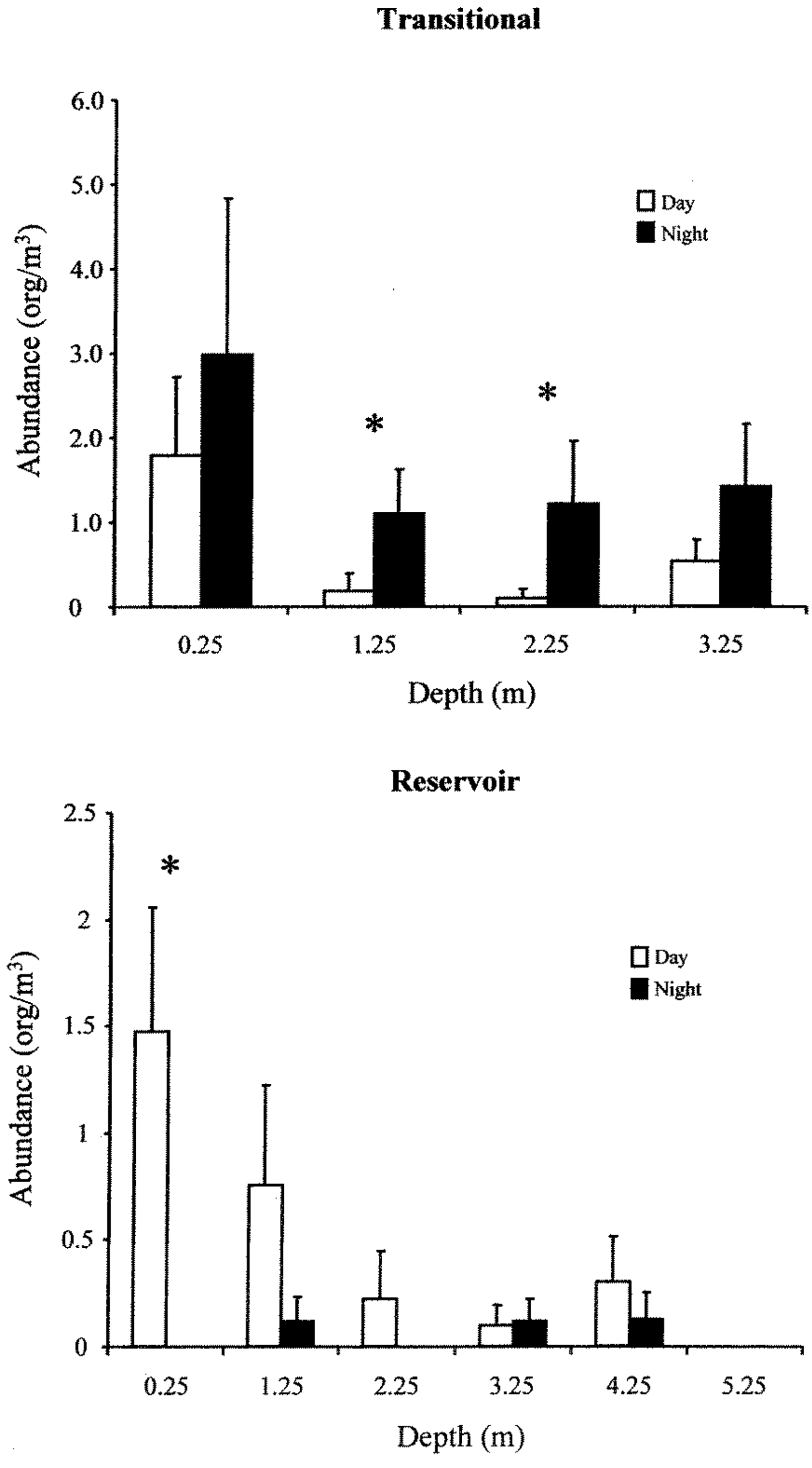



Figure 8. Mean and standard error of *Leptodora* abundance at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 3 (August 11 – August 15). An asterisk (*) indicates a significant ($p <= 0.05$) difference between day and night means at the specified depth.

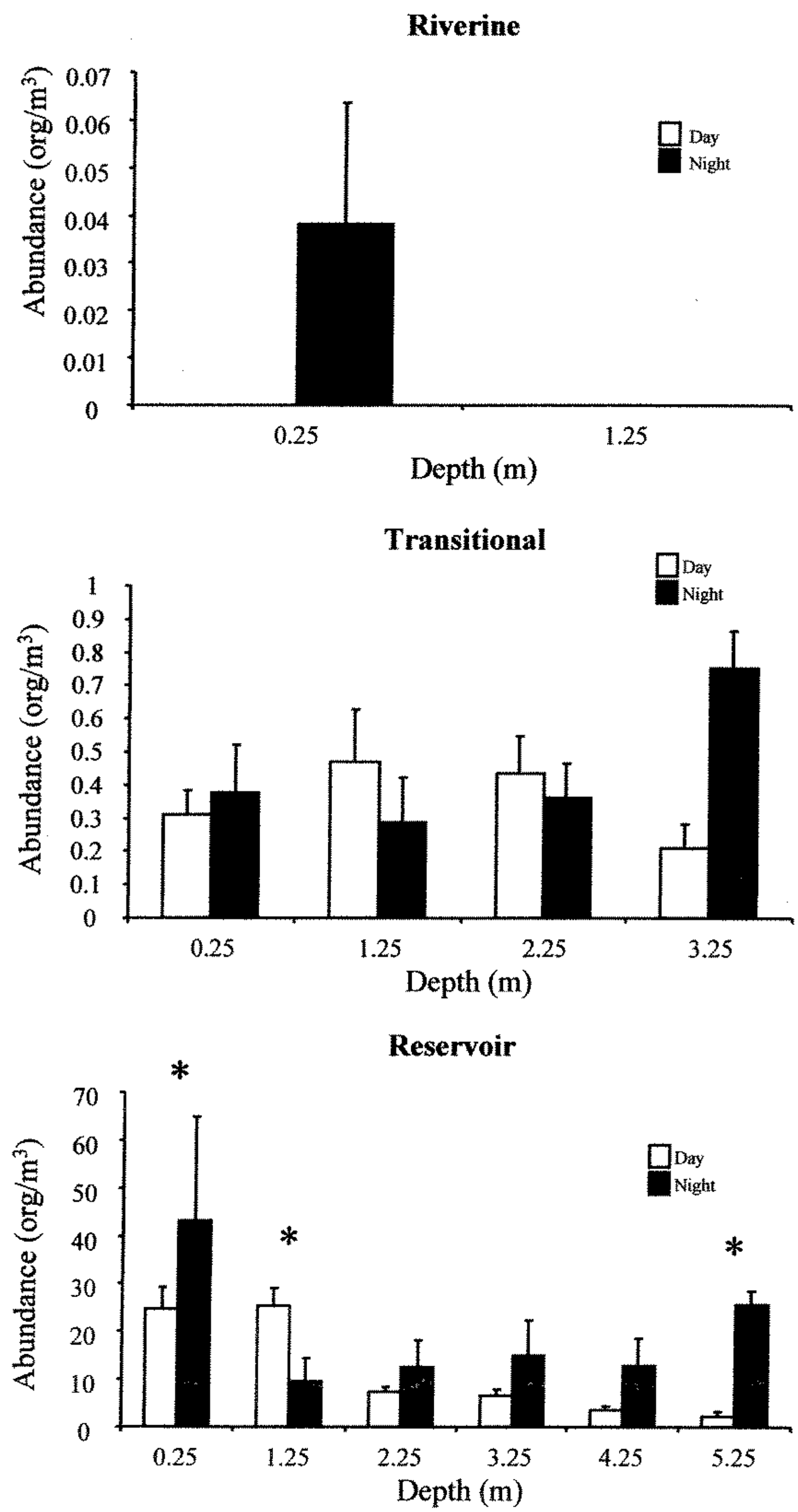



Figure 9. Mean and standard error of *Leptodora* abundance at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 4 (August 21 – August 22). An asterisk (*) indicates a significant ($p <= 0.05$) difference between day and night means at the specified depth.

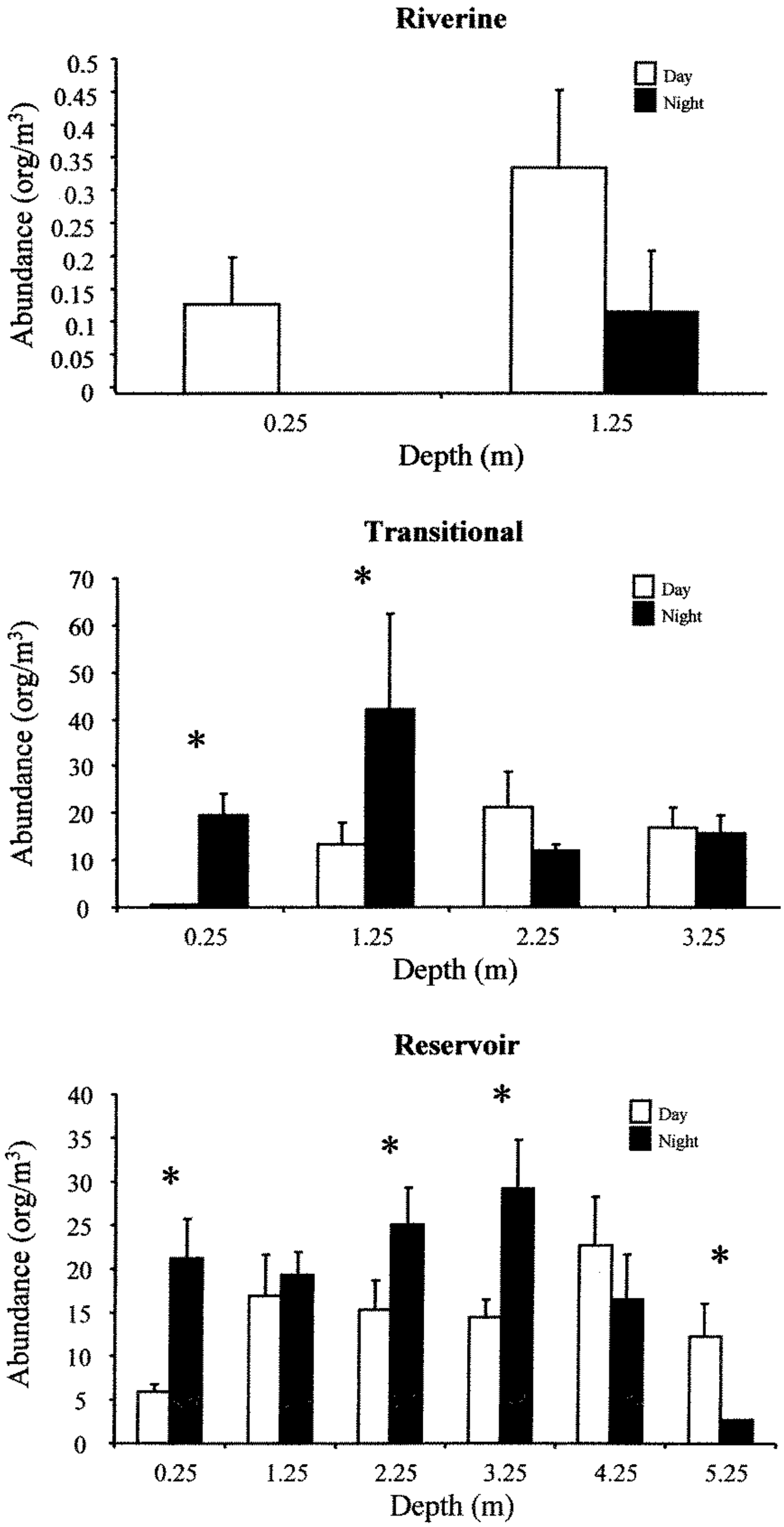
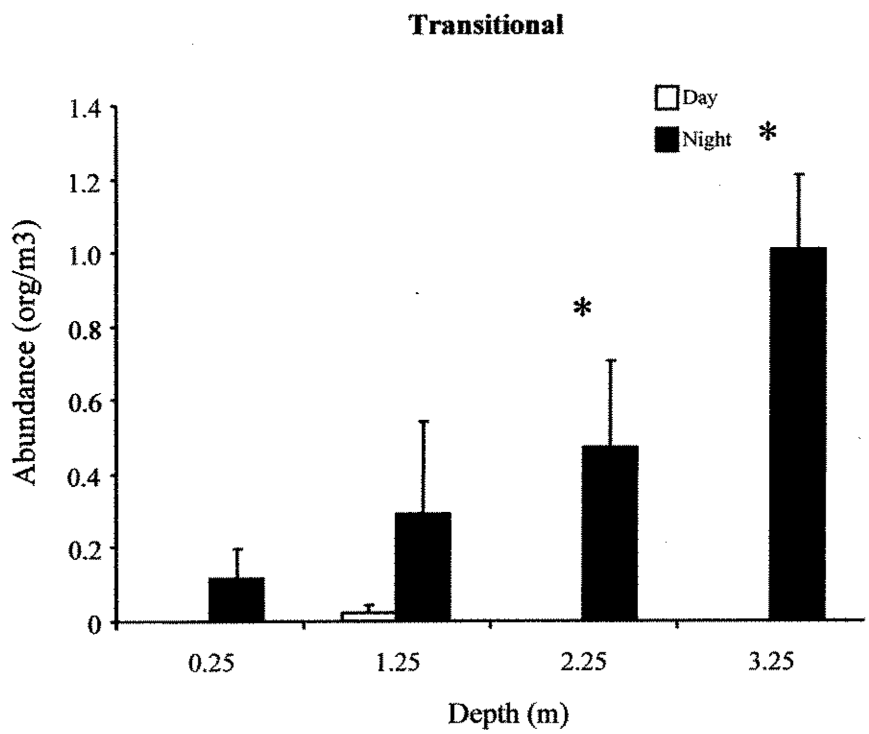



Figure 10. Mean and standard error of *Leptodora* abundance at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 5 (September 2 – September 4). An asterisk (*) indicates a significant ($p <= 0.05$) difference between day and night means at the specified depth.



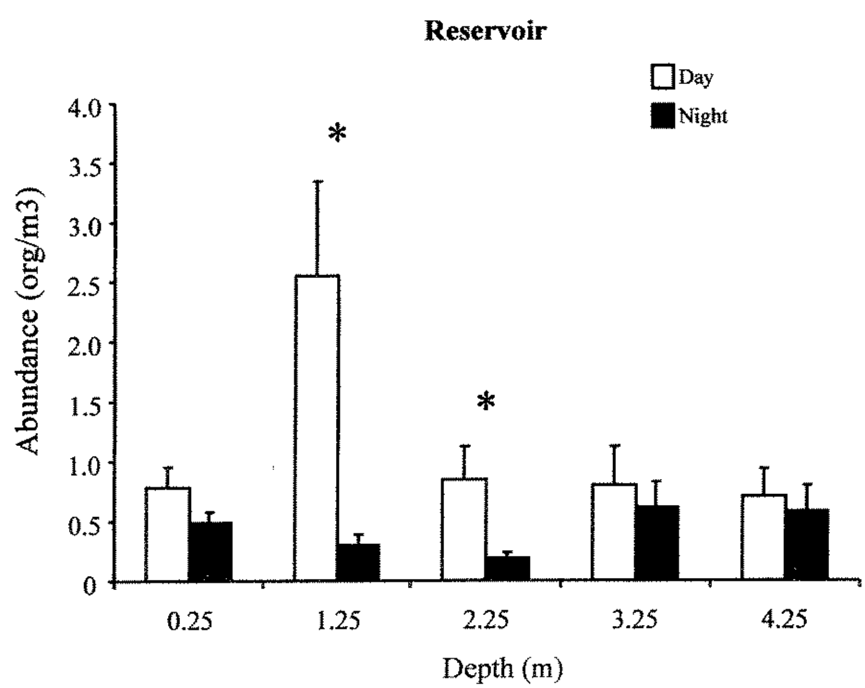




Figure 11. Mean and standard error of *Leptodora* abundance at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 6 (September 9 – September 10). An asterisk (*) indicates a significant ($p <= 0.05$) difference between day and night means at the specified depth.

*Leptodora* Length Distribution

There was no consistent pattern of *Leptodora* length distribution according to depth or diurnal period (day/night). Although higher mean length was often observed at the surface by night, larger individuals were found in deeper strata both by day and by night within the transitional and reservoir habitat types (Figures 9-14).

Within the transitional habitat type, no consistent significant changes in *Leptodora* length distribution were found. During the fifth sample period, mean lengths recorded by night were significantly higher than by day at all depths sampled (Figure 13). For all sample periods, mean lengths by day were higher in the deeper strata of 1.25 to 3.25 m than at the surface (Figures 9-14). Although significant changes in mean *Leptodora* length by day and by night were observed during the second, third and fourth sample periods, no consistent pattern was found.

Within the reservoir habitat type, lower mean lengths were observed at the surface than in deeper strata both by day and by night. There was a significant increase in mean lengths of *Leptodora* at the surface by night for five of the six sample periods (Figures 9, 10, 12, 13, and 14); however, in all but one of these instances, higher mean lengths by night were recorded in deeper strata during that sample period. During day and night sampling, an overall pattern of larger *Leptodora* present in deeper strata was observed throughout this study (Figures 9-14).

A small number of *Leptodora* were captured in the riverine habitat type; therefore few length measurements were taken and no patterns were able to be determined.

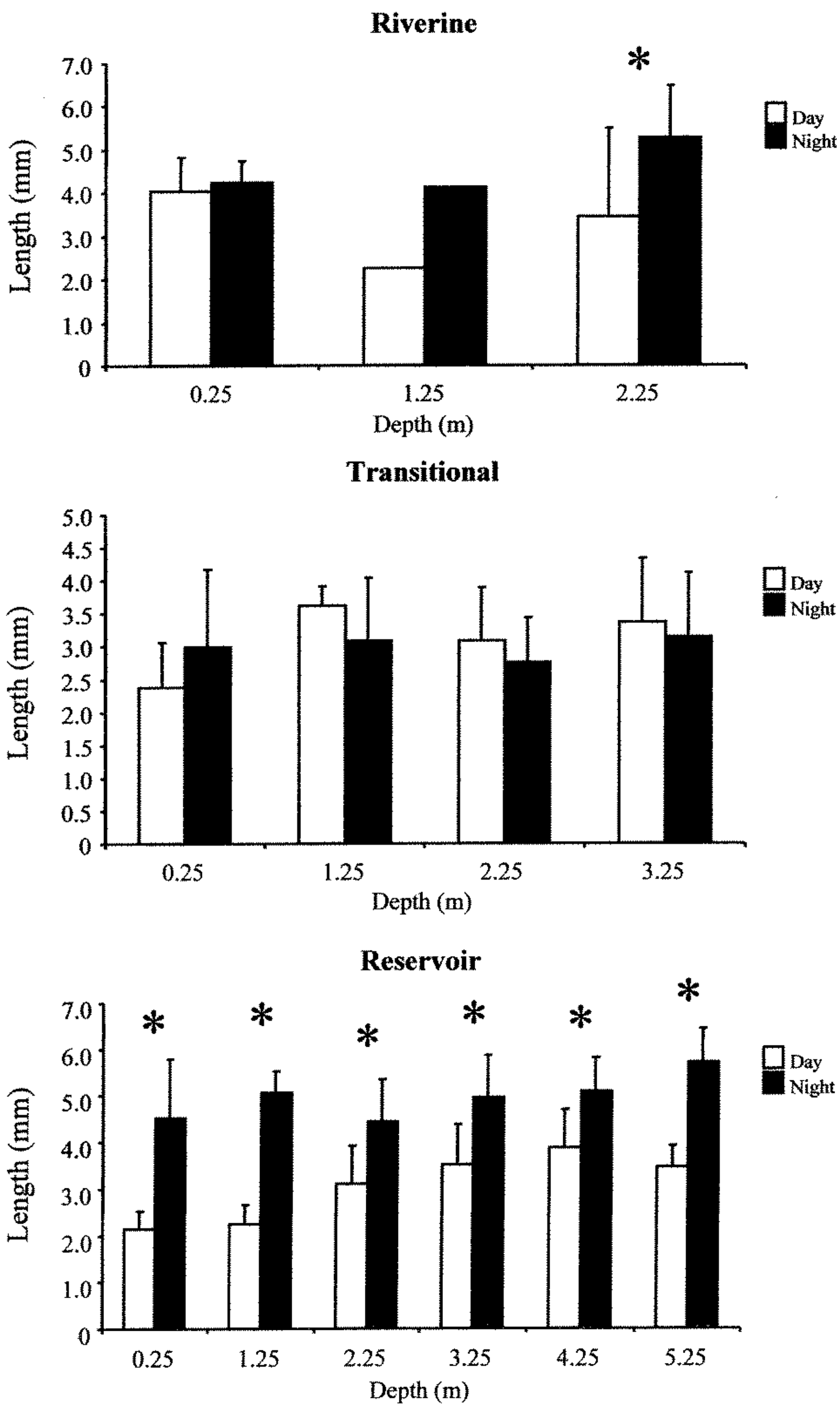



Figure 12. Mean and standard error of *Leptodora* length at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 1 (July 22 – July 29). An asterisk (*) indicates a significant difference between day and night means at the specified depth.

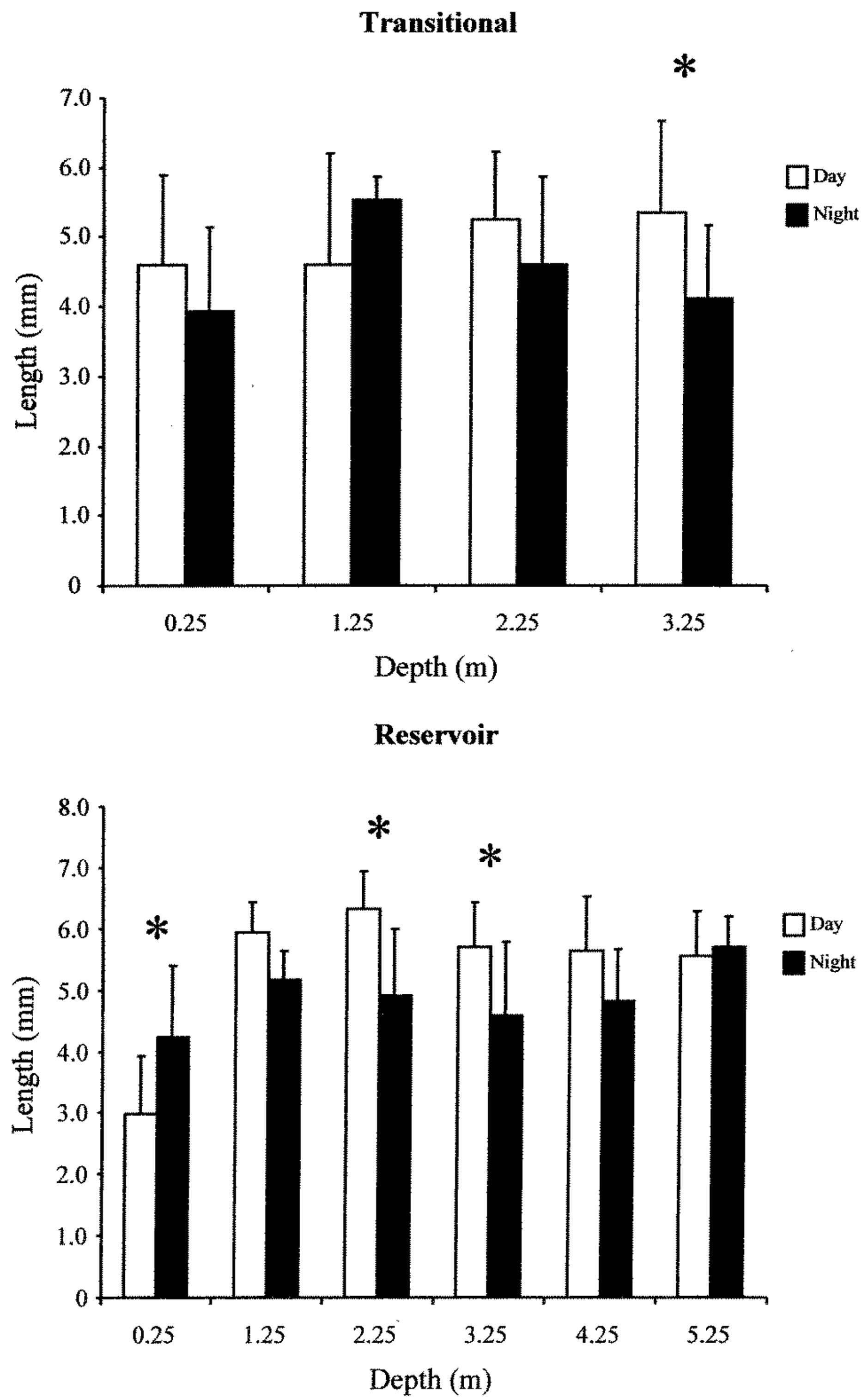



Figure 13. Mean and standard error of *Leptodora* length at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 2 (Aug. 1 – Aug. 3). An asterisk (*) indicates a significant difference between day and night means at the specified depth.

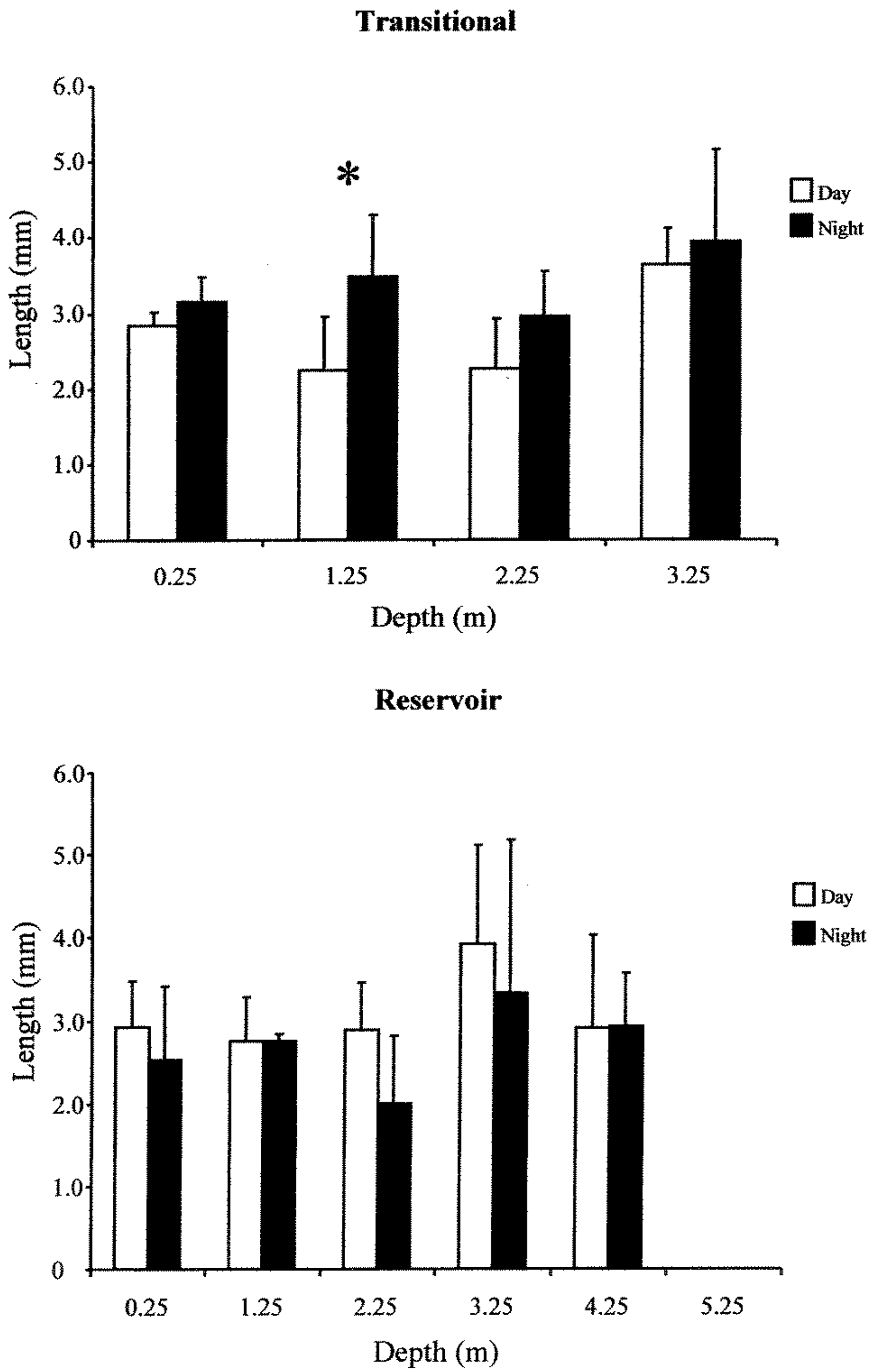



Figure 14. Mean and standard error of *Leptodora* length at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 3 (Aug. 11 – Aug. 15). An asterisk (*) indicates a significant difference between day and night means at the specified depth.

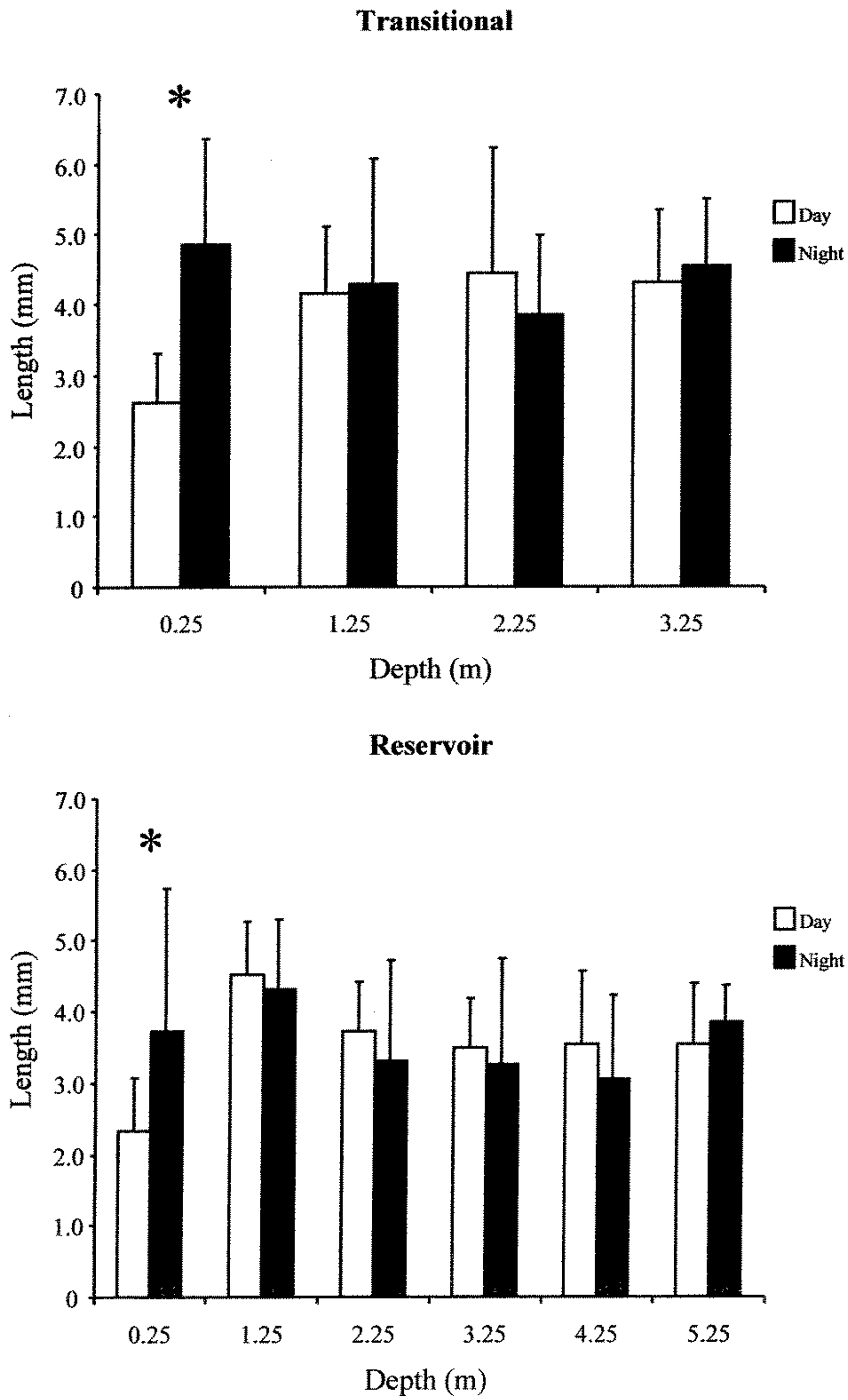



Figure 15. Mean and standard error of *Leptodora* length at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 4 (Aug. 21 – Aug. 22). An asterisk (*) indicates a significant difference between day and night means at the specified depth.

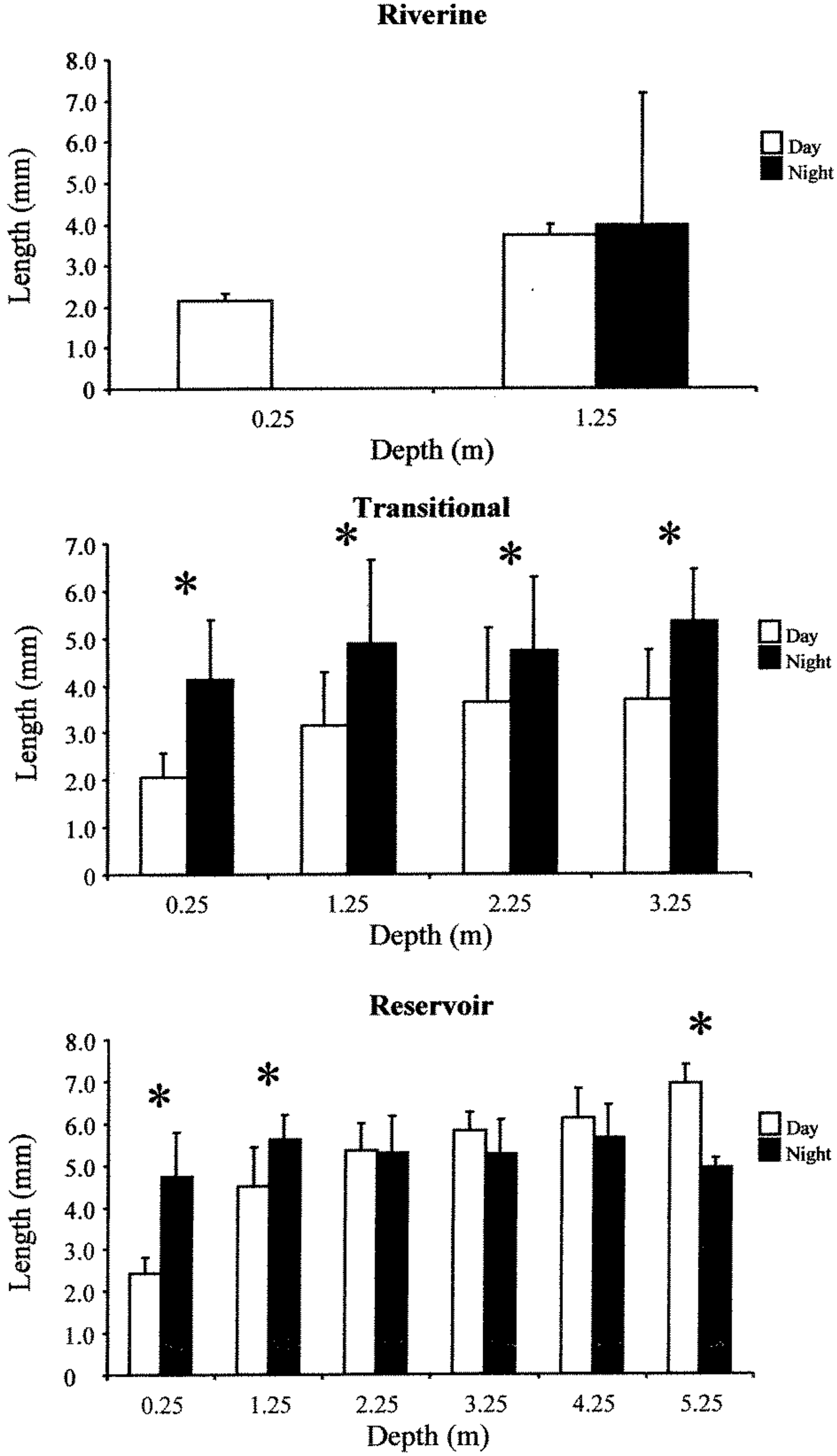



Figure 16. Mean and standard error of *Leptodora* length at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 5 (Sept. 2 – Sept. 4). An asterisk (*) indicates a significant difference between day and night means at the specified depth.

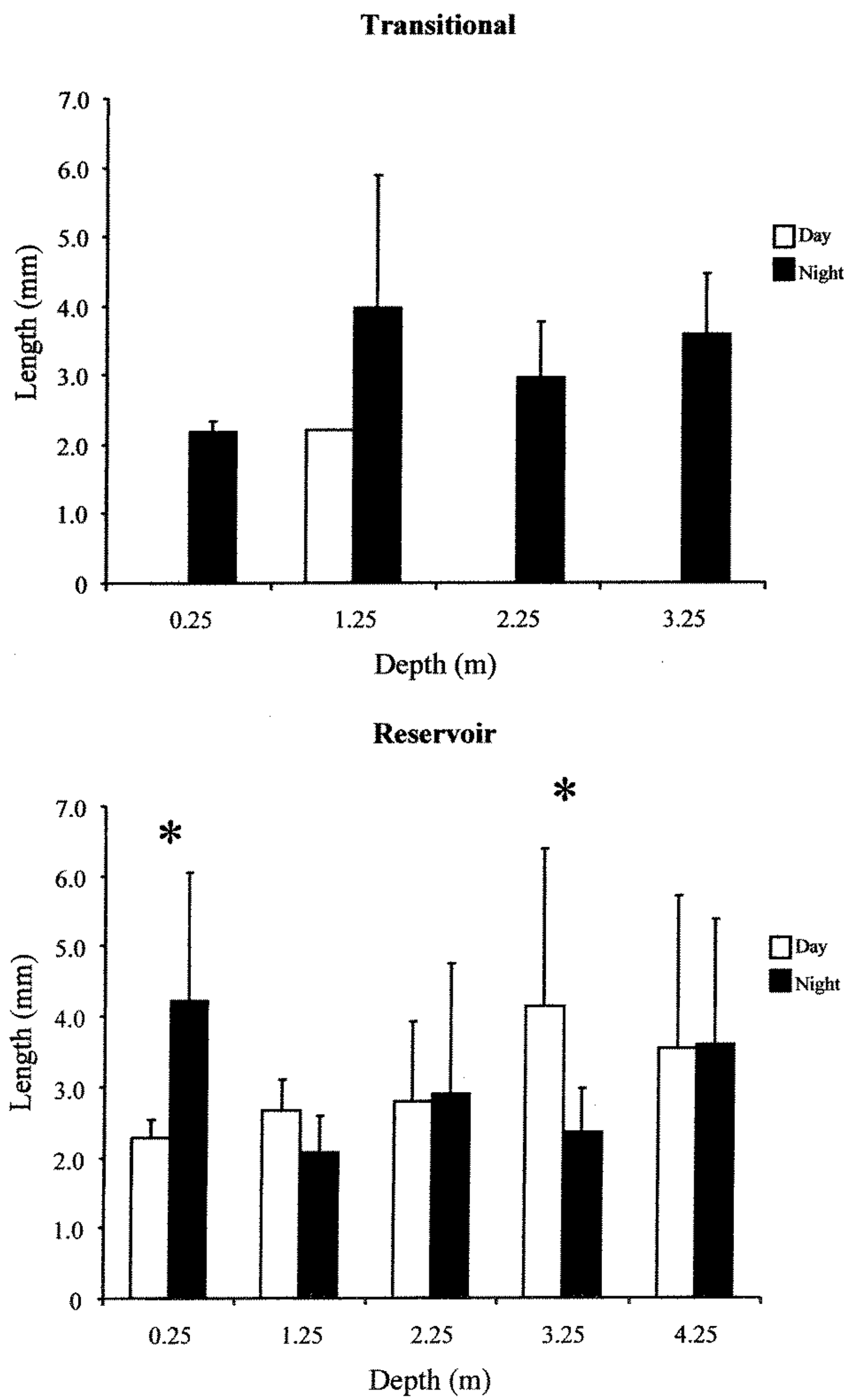



Figure 17. Mean and standard error of *Leptodora* length at sampled depths throughout the headwaters of Fort Peck Reservoir during sample period 6 (Sept. 9 – Sept. 10). An asterisk (*) indicates a significant difference between day and night means at the specified depth.

Environmental Effects on *Leptodora* Abundance

Water temperatures within the headwaters exhibited substantial fluctuations throughout the study (Figure 18). When mean water temperature and mean *Leptodora* abundance data for the entire study area were grouped into sample periods, water temperature was positively correlated with *Leptodora* abundance (Figure 18).

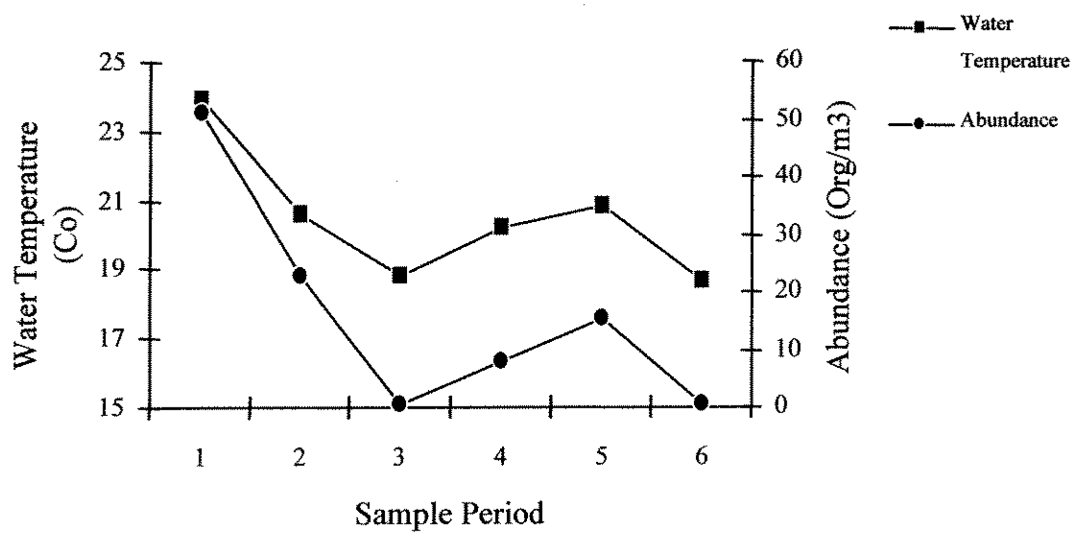



Figure 18. Mean water temperature and abundance trends of *Leptodora* within the headwaters of Fort Peck Reservoir, July 22 – September 10, 2002.

Water temperature among habitat types was shown to differ significantly (ANOVA, p<0.0001) (Appendix, Table 16). In addition, water temperature among habitat types was significantly different within sample periods (ANOVA, p <0.0001) (Appendix, Table 16). When mean water temperatures within the three habitat types were examined, higher mean water temperatures were found within the reservoir habitat type during sample periods 1, 2, 3, and 6 and the riverine habitat type during sample periods 4 and 5 (Figure 19).

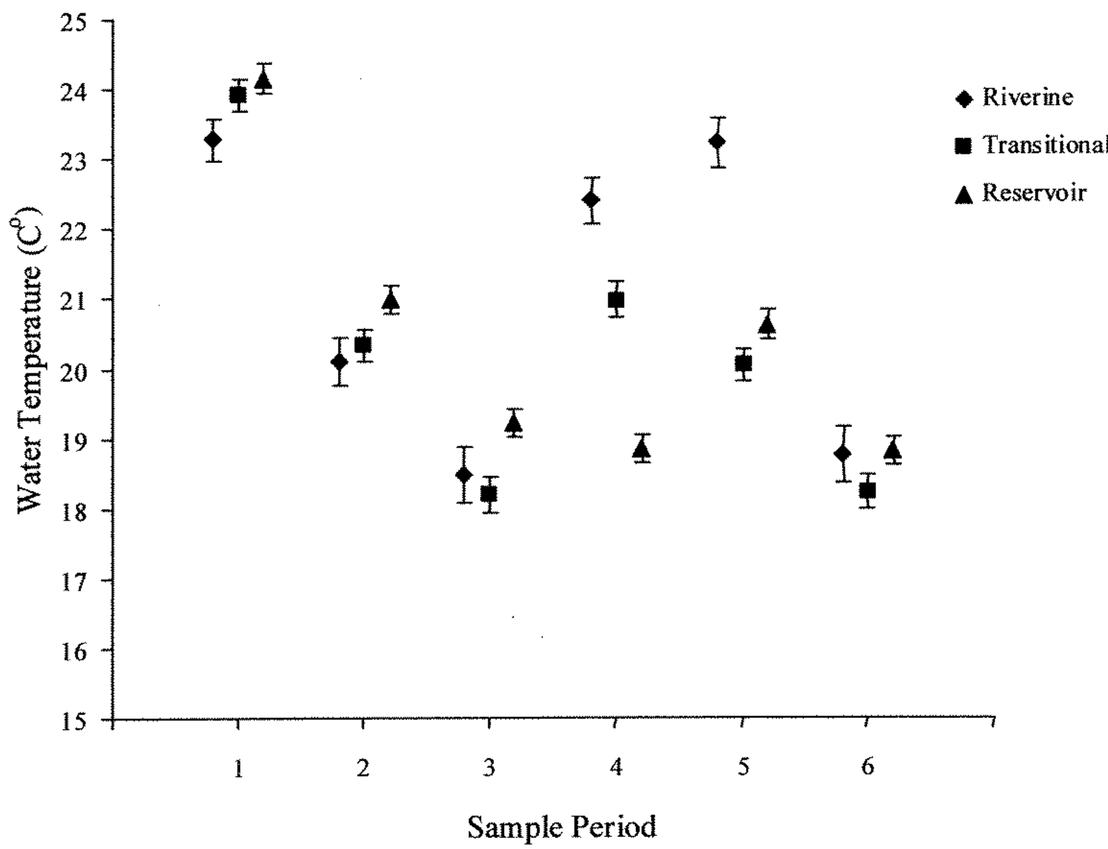



Figure 19. Mean water temperature within each habitat type of the headwaters of Fort Peck Reservoir, July 22 – September 10, 2002.

*Leptodora* abundance was consistently highest in the reservoir habitat type during all sample periods, except for sample period three (Figure 20). Water temperature and *Leptodora* abundance displayed different patterns, indicating that water temperature is not a consistent predictor of *Leptodora* abundance longitudinally within the study site.

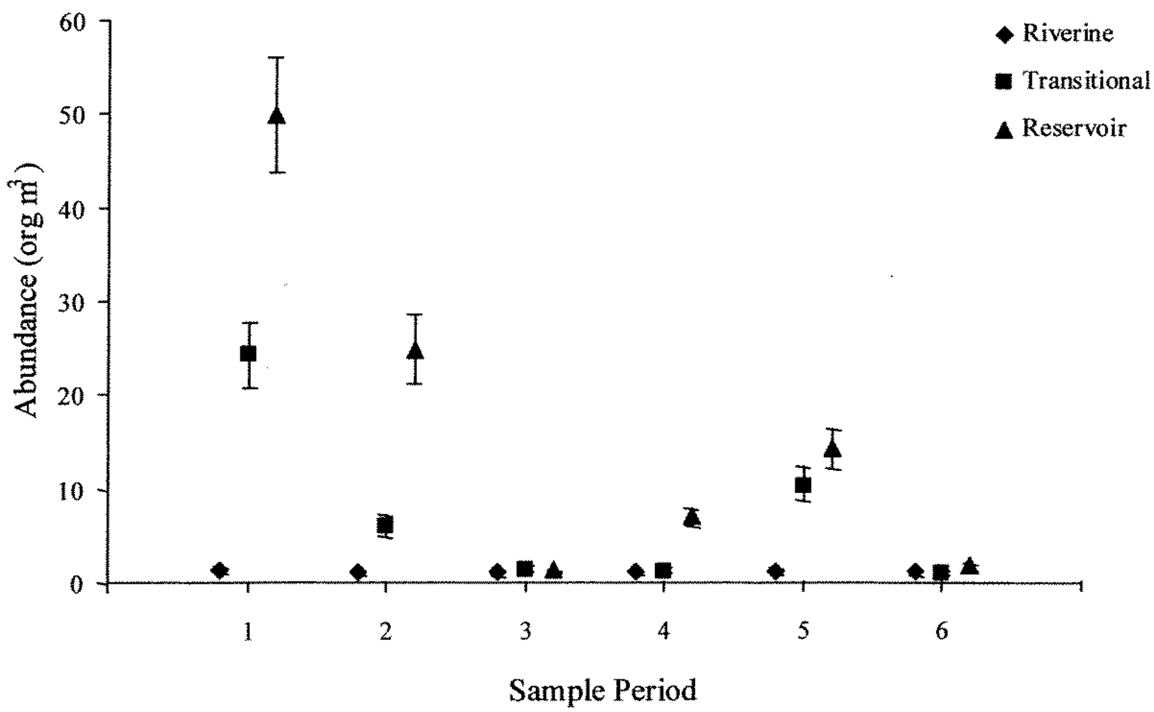



Figure 20. Mean *Leptodora* abundance within each habitat type of the headwaters of Fort Peck Reservoir, July 22 – September 10, 2002.

In contrast to water temperature, when mean turbidity and mean *Leptodora* abundance data were grouped into sample periods, the variables displayed opposite fluctuations (Figure 21).

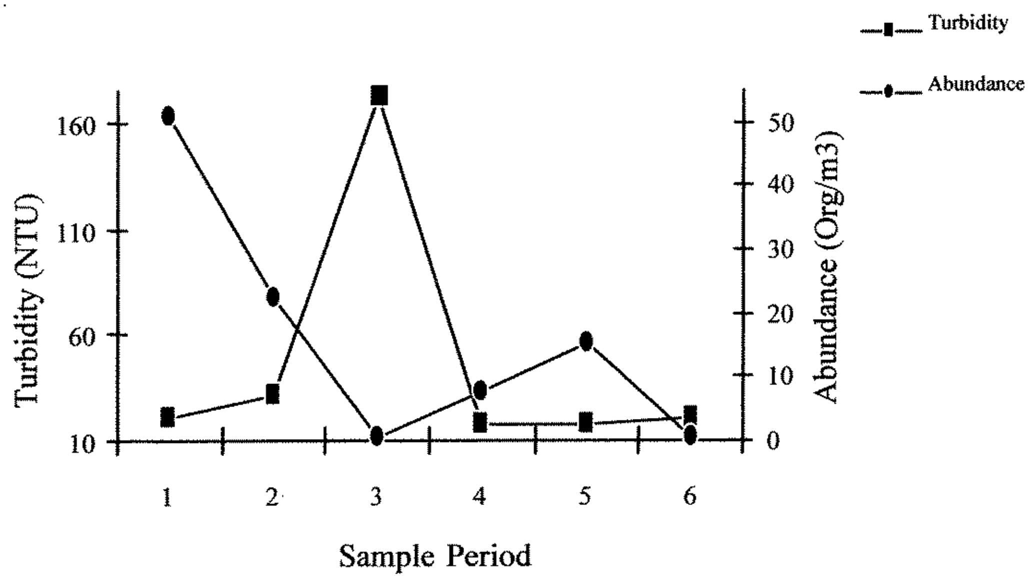



Figure 21. Mean turbidity and abundance trends of *Leptodora* in the headwaters of Fort Peck Reservoir, July 22 – September 10, 2002.

The grouped turbidity data for the entire study, was shown to differ significantly among habitat types (ANOVA, p<0.0001) (Appendix, Table 16). In addition, turbidity within habitat types was significantly different within sample periods (ANOVA, p <0.0001) (Appendix, Table 16). When mean turbidities within the three habitat types were examined, the reservoir habitat consistently had the lowest average turbidities for all six sample periods (Figure 22). The high turbidities present during sample period 3 were caused by runoff from a storm event up-river that flushed large amounts of sediment and debris into the headwaters a few days before the sample period. Lower turbidities were still located within the reservoir habitat type, even during this event. More *Leptodora* were thus associated with less turbid waters.

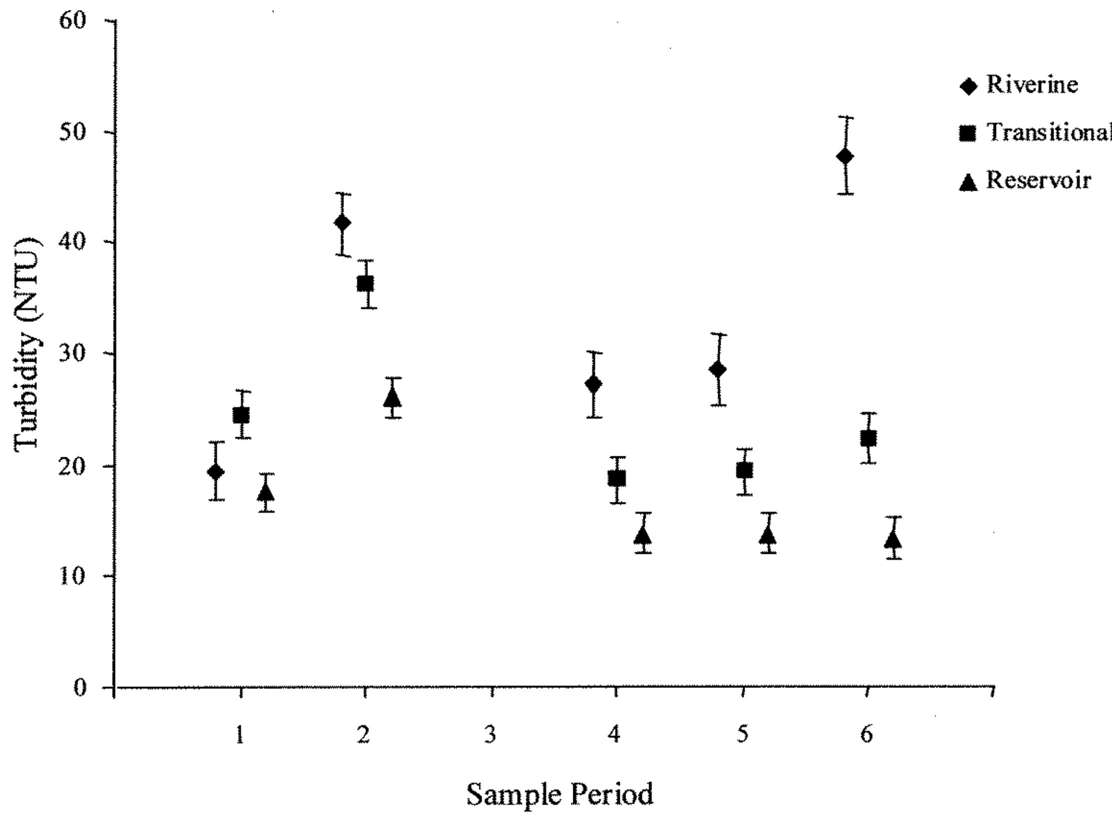



Figure 22. Mean *Leptodora* turbidity within each habitat type of the headwaters of Fort Peck Reservoir, July 22 – September 10, 2002. Due to abnormally high values, sample period three is not displayed. However, the reservoir habitat type had significantly lower turbidities within this sample period.

# DISCUSSION

Data from this study indicate that *Leptodora* abundance was highly variable throughout the headwaters of Fort Peck Reservoir. The habitat types had significant differences in densities of *Leptodora,* with highest abundances in the reservoir habitat. However, the waypoints within a given habitat type often displayed significant differences in abundance as well, indicating an extremely patchy distribution at a small scale both spatially and temporally. Previous studies on other water bodies have found similar patches or swarms with other species of zooplankton (Colebrook 1960, Davies 1985, Verreth 1990, Kvam and Kleiven 1995). In his work on Windermere Lake, Scotland, Colebrook (1960) found swarms of the zooplankton *Daphnia* with much higher abundances than the surrounding water. He cited wind driven turbulence or a social activity of some kind as the possible factors for such a phenomenon (Colebrook 1960). Verreth (1990) found that *Daphnia* and *Bosmina* were concentrated heavily in the pelagic zone of a pond. In addition, he found that wind induced currents within the pond may have displaced organisms on the down-wind side of the water body (Verreth 1990). Kvam and Kleiven (1995) found swarms of *Daphnia* with densities up to 4,000 org/l in Myravatn. They believed the formation of the swarms was a predator avoidance mechanism to the predaceous invertebrate *Chaoborus* (Kvam and Kleiven 1995). *Chaoborus* and *Leptodora* are similar in that both are voracious tactile predators and have been shown to have significant effects on *Daphnia* populations (Wright 1965, Kvam and Kleiven 1995). A plains reservoir such as Fort Peck is often subject to extended periods of strong winds, which may concentrate zooplankton and result in patchy distributions. Langmuir circulation patterns may form aggregations of both *Leptodora* and *Daphnia*

(Wetzel 2001). If this is the case, age-0 paddlefish may key in on these patches and thereby exhibit a patchy distribution themselves. Such patches in age-0 paddlefish have frequently been observed in Lake Sakakawea, North Dakota, a plains reservoir with similar dimensions as Fort Peck Reservoir (Dennis Scarnecchia, University of Idaho, personal communication).

Despite patchiness on a small scale within a given habitat type, overall *Leptodora* abundance increased down-reservoir. In a study conducted by Johnson et al. (1996) higher densities of *Daphnia* were located down-reservoir during the early part of the year. They attributed the higher densities to decreasing suspended sediment load as one moved down-reservoir (Johnson et al. 1996). A similar gradient in sediment was present in the headwaters of Fort Peck Reservoir throughout the entire period of my study. Suspended sediments have been shown to interfere with *Daphnia* filter feeding, which in turn would affect *Leptodora* (Johnson et al. 1996). During periods of increased suspended sediment (i.e. August 11-14; Sample Period 3) *Daphnia* may not be able to feed efficiently, and forage for *Leptodora* may also be scarce.

The peak *Leptodora* abundances observed during the first sample period in this study occurred a month after nutrients were brought into the reservoir by spring run-off. After the high inflows present during sample period 3, a secondary peak of *Leptodora* abundance occurred in sample periods 5 and 6. Abundances never reached those of the first sample period, however. The high temporal variation in *Leptodora* abundance during the study was consistent with numerous studies indicating that zooplankton populations fluctuate widely over the course of a growing season (Clarke and Bennett 2003, Watson 1976, Koapaha 1989, Wiedenheft 1984). When the suspended sediments begin to settle, the influx of nutrients associated with the inflow, causes an explosion of primary production which should rapidly regenerate consumer abundances (Wetzel 2001). The direct cause of variation in *Leptodora* was not studied; it is possible that the inflow of nutrients associated with spring run-off increased zooplankton production during late June and July. Sampling for this study was concentrated during late summer because previous work has shown late July and August to be the months when age-0 paddlefish enter the reservoir (Wiedenheft 1992, Kozfkay and Scarnecchia 2002). To obtain a more complete description of fluctuations in the abundance of *Leptodora*, however, sampling would need to be conducted throughout the year.

The lowest water temperatures present in this study reached levels near water temperatures found to be a limiting factor of *Leptodora* abundance in other studies. *Leptodora* was reported as being temperature-limited at 14 C°, by Cummins et al. (1969) and declining in water temperatures ranging from 5-15 C° in Western Lake Erie by Garton et al. (1990). Water temperatures in Fort Peck Reservoir were lowest during sample periods 3 and 6 corresponding to the lowest overall abundances found in the study. Temperatures fell to as low as 15.9 and 15.7 °C during sample period 3 and 6 respectively. It is unknown if individuals may have migrated to warmer water temperatures down-reservoir or became increasingly dormant during these colder conditions. However, decreases in *Leptodora* abundance were associated with these low temperatures.

The greater *Leptodora* abundance associated with lower turbidities in five of the six sample periods of this study is not consistent with some other studies. Zettler and Carter (1986) for example, found higher densities *Leptodora* at sample sites with higher turbidities in Lake Temiskaming, Canada. In addition, they found an upward displacement of zooplankton corresponded to an increase in turbidity (Zettler and Carter 1986). Results from my study were the opposite; low densities of *Leptodora* were found in the high turbidities of the riverine habitat type. In his work on Fort Peck Reservoir, Wiedenheft (1984) found lower zooplankton abundance within the higher turbidities associated with the Missouri River compared to sample sites within in the reservoir. Perhaps in my study, turbidities within the more lentic, reservoir habitat type provided *Leptodora* with adequate protection from sight-feeding predators and still allowed the main prey item, *Daphnia*, to feed effectively (Johnson et al. 1996).

Throughout this study, *Leptodora* were found at the surface both day and night within the transitional and reservoir habitat types. While there were increases in nighttime surface abundances found in three of six sample periods within both the transitional and reservoir habitat types, often, even higher abundances were found in deeper strata. The statistically greater mean lengths found in five of the six sample periods during nighttime surface tows suggest that some larger *Leptodora* are undergoing a migration towards the surface. However, the greater mean lengths present at depths, even by night in most sample periods, indicates that many individuals were staying at depths both by day and by night. This study thus found no predictable migrations in *Leptodora*, and little evidence that DVM is undertaken.

Absence of DVM in *Leptodora*, or at most low levels of it, are well documented. For example, Schindler and Noven (1971) found that *Leptodora* underwent no DVM in an experimental lake in northwestern Ontario. Individuals remained at 4 m during both day and night sample periods (Schindler and Noven 1971). Similarly, Barberio et al.

(2000) found no discernable pattern of DVM in *Leptodora* in three of the Great Lakes, United States, sampled during their study. They speculated that the transparent body of *Leptodora* provided adequate protection from sight-feeding predators, making DVM unnecessary (Barberio et al. 2000). Vijverberg (1991) suggested that *Leptodora* DVM was a dynamic behavior trait within the population of Tjeukemeer Lake, Netherlands, finding a number of different DVM patterns in *Leptodora* depending on size-class and time period. During some periods, Vijverberg (1991) found no DVM pattern displayed in *Leptodora* irregardless of size class. During other periods, however, some size-classes did display DVM or reversed DVM patterns. Stewart and Sutherland (1993) found *Leptodora* to undergo a modest ascent towards the surface around sunset in a New York lake. However, as in my study, Stewart and Sutherland (1993) found *Leptodora* abundances were often higher in deeper strata when compared to the surface, even during nighttime sampling.

The patchy distribution of *Leptodora* and their lack of a strong consistent pattern of DVM in the headwaters of Fort Peck Reservoir have implications for the assessment of age-0 paddlefish recruitment. Visual transect counts are conducted in the headwaters of Fort Peck to estimate yearly age-0 paddlefish recruitment (Kozfkay and Scarnecchia 2002). The method has been shown to be effective in locating large numbers of age-0 paddlefish in Fort Peck Reservoir as well as in Lake Sakakawea, North Dakota (Scarnecchia et al. 1997, Kozfkay and Scarnecchia 2002). The possibility of bias in the method has been a concern, however, because of the dominance of *Leptodora* as prey (Fredericks and Scarnecchia 1997, Kozfkay and Scarnecchia 2002) and because of the documented DVM of *Leptodora* in other waters (Liu et al. 2002). . If age-0 paddlefish occupy deeper strata during the day to feed on higher abundances of *Leptodora*, low counts may result. Based upon the sporadic distribution of *Leptodora* found in this study and the large surface area that can be covered using visual counts, this method appears to be a favorable measure of age-0 paddlefish recruitment in Fort Peck Reservoir. Highest daytime abundances of *Leptodora* were found at 1.25 m or greater depths for five of six sample periods. If the visual counts are biased by *Leptodora* distribution during the day, they are biased somewhat conservatively. A conservative estimate of recruitment may be in the best interest of this unique stock.

A longer term study is necessary to better understand *Leptodora* ecology in the headwaters of Fort Peck Reservoir. In future studies, it may be necessary to extend this sampling protocol throughout the entire growing season and over the course of some years under different reservoir conditions. During the 2002 field season persistent drought resulted in low spring inflows into the reservoir from the Missouri River, as well as low water levels throughout the summer. *Leptodora* abundance and movements may differ under higher water levels and higher spring runoff inflows. Responses from the *Leptodora* population may vary and need to be examined as this dynamic system undergoes changes not observed in this study.

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# CHAPTER 2. LONG-TERM CHANGES IN THE GROWTH RATES OF THE PADDLEFISH, *POLYODON SPATHULA*, IN FORT PECK RESERVOIR, MONTANA

## ABSTRACT

The Missouri River above Fort Peck Reservoir has supported a recreational fishery for the past 30-40 years. Although the catch of adult paddlefish has remained relatively constant, large individuals (< 42 kg) have become increasingly rare. The objectives of this study are to examine changes in paddlefish weight and body length distributions and early growth during three different reservoir time periods (1977-1978, 1992-1993, and 2000, 2002).

Weight and body length frequency histograms were constructed based on samples collected from the fishery during three time periods (1977-1978, 1992-1993, and 2000, 2002). Histograms were examined to compare the frequency of large fish (>21 kg males, >42 kg females) within each of the three time periods. In addition, a 2-way ANOVA was run on two age groups (< 15and 16-20 for males, 16-20 and 21-25 for females) to determine if mean weight achieved for these age groups changed between the three time periods. The analysis indicated that the number of large fish in the population and early growth of both male and female paddlefish have decreased over time.

The exact cause of the decrease is not known, however it is hypothesized that a contributing factor is reduced reservoir productivity associated with reservoir aging.

# INTRODUCTION

The construction of reservoirs in the United States was widespread throughout twentieth century. By 1980, 1,608 reservoirs of at least 202 ha each and having a total surface area of 4 million ha of water were present (Benson 1982). These water bodies were built for a variety of reasons and uses including flood control, municipal water supplies, hydropower, recreation and irrigation; ecological considerations were often not adequately considered prior to construction (Kimmel and Groeger 1986).

Several studies have been conducted to look at ecological changes within a reservoir after impoundment (Eschmeyer and Jones 1941, Abell and Fisher 1953, Chamberlain 1972, Benson 1982, Popp and Hoagland 1995, Popp et al. 1996, Holz et al. 1997). Research has shown reservoirs to undergo a substantial increase in primary productivity shortly after impoundment (Benson 1982) a period often referred to as "trophic upsurge" (Baranov 1961). Chamberlain (1972) found that primary productivity was still increasing in Merle Collins Reservoir, CA three years after impoundment. Internal nutrient loading from organic matter present results in higher production of organisms at all trophic levels, resulting in increased growth and higher biomass of organisms including fish.

The upsurge is a short-term event, and productivity typically declines after the initial peak following reservoir filling (Kimmel and Groeger 1986). In Pawnee Reservoir, Nebraska, for example, Holz et al. (1997) found that total phosphorus and nitrate concentrations were significantly higher three years after impoundment (1968-1969) than later sample periods (1970-1973 and 1990-1992). A second study on the ecological status of Pawnee Reservoir showed a reduction in benthic macroinvertebrate taxa from 23 to 15 and a decrease in mean total benthic macroinvertebrate biomass from 2.0 g/m $^2$ to 0.2 g/m $^2$ between 1968-1979 and 1991-1992 (Popp and Hoagland 1995). The subsequent decline in productivity at various trophic levels following initial filling is believed to be associated with reservoir aging. (Popp and Hoagland 1995, Popp et al. 1996, and Holz et al. 1997). Reservoirs fill up with sediments from the surrounding watershed at a much faster rate than most natural lakes because the drainage area associated with reservoir is generally much larger (Benson 1982 and Kimmel and Groeger 1986).

The pattern of an initial trophic upsurge after impoundment followed by declining productivity as the reservoir ages had been observed through its effects on fish production (Eschmeyer and Jones 1941, Abell and Fisher 1953, Chamberlain 1972, and Benson 1982). The effects have often been most noticeable to the public in fish populations because of the high economic and recreational value of fisheries. Although the effects of trophic upsurge and subsequent declines can manifest themselves as rapid increases in abundance and size of short-lived species such as centrachids, (Abell and Fischer 1953) the effects can be more protracted in long-lived residents of reservoirs such as the paddlefish, *Polyodon spathula*.

Paddlefish are native to Montana and support an important recreational fishery on the Missouri River above the headwaters of Fort Peck Reservoir (Scarnecchia and Stewart 1996). Fort Peck Reservoir, completed in 1940, is the uppermost major main stem Missouri River impoundment and is 216 km long and 100,767 ha in area at full pool (U.S. Army Corps of Engineers, 1991). Spawning habitat located on the Missouri River above the reservoir allows the Fort Peck paddlefish stock to be one of the few wild stocks capable of supporting a recreational fishery (Scarnecchia and Stewart 1996).

Paddlefish rear in the reservoir until mature individuals gather in the headwaters of the reservoir during the early spring of the year (Wiedenheft 1992). Fish move out of the reservoir and into the Missouri River to spawn in the spring. It is during these annual spawning runs when most fishing occurs. The fishery, which is open year-round, is concentrated in the river above the reservoir. In the past decade, harvest has been approximately 500 fish per year (Gilge and Liebelt 1997). The fishing is based on snagging of migrating adults, which rarely take conventional baits.

Creel census surveys conducted during these spring migrations have provided information on age, growth, and size of adult paddlefish and tagging of adult paddlefish in the river has provided information on movements and harvest rates (Gilge and Liebelt 1997). In addition, dentaries (lower jawbones) taken from harvested individuals provide information on age of fish. Although catches have remained relatively constant over time, a decrease in the number of large paddlefish as well as the maximum size attained has been suspected during the creel surveys (Gilge 2003). Because paddlefish are a long-lived species, at least (35-55 yrs) (Scarnecchia et al. 1996); fish that reared during the trophic upsurge of the reservoir could have been present in the population until at least the late 1970s and early 1980s (Russell 1986).

If paddlefish growth rates and maximum size attained have declined as the reservoir has aged, it should be detectable by comparing frequency of large fish (females > 42 kg and males > 21 kg) and size at age of fish rearing in successive decades within the reservoir. In particular, paddlefish are strongly sexually size dimorphic; with mature females usually being much larger than mature males (Scarnecchia et al. 1996). It is the largest fish, all of which are females, that are most sought by anglers, and the most noticeable when absent.

The objectives of the study were to 1) compare weight and body length distributions within the paddlefish population of Fort Peck Reservoir from successive decades (1977-1978, 1992-1993, and 2000, 2002) to determine if the frequency of large individuals has decreased and 2) compare mean weight and body length of two age classes of male (<15 and 16-20) and female (16-20 and 21-25) paddlefish from the three decades (1977-1978, 1992-1993, and 2000, 2002) to determine if any changes in growth rates have occurred.

## STUDY AREA

Fort Peck Reservoir is located in Central Montana and is the uppermost main stem impoundment on the Missouri River system. The Fort Peck Project was placed in operation in 1938 and when it was finished, it was the largest earthfill hydraulic dam in the world (U.S. Army Corps of Engineers 1991).

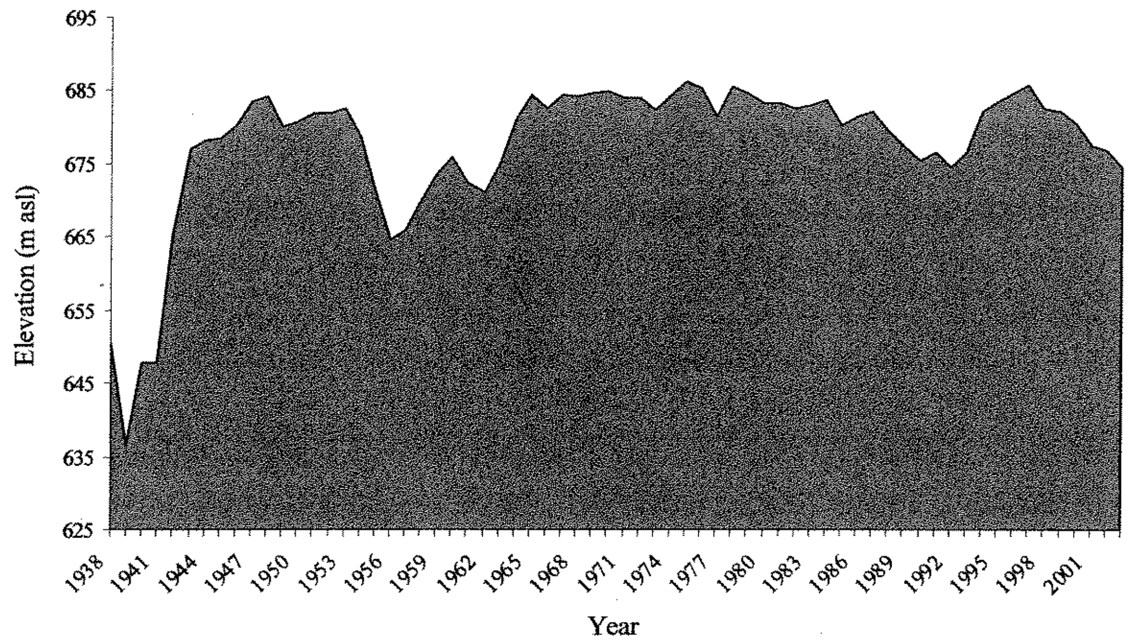


Figure 23. Mean July elevation of Fort Peck Reservoir, MT, from 1938 thru 2003

At full-pool, the reservoir stores approximately 23.4 billion cubic meters of water (U.S. Army Corps of Engineers 1991). The lake impounds the runoff of approximately 149,000 square kilometers of the Missouri River drainage basin (U.S. Army Corps of Engineers 1991). Upon closure of the dam, the reservoir took approximately 10 years to fill (Figure 23). After reaching full-pool, the reservoir experienced a rapid decline in level in the late 1950s (Figure 23). Since then, the reservoir has fluctuated between 680 m asl and 686 m asl (Figure 23). However, significant declines in water levels occurred in the periods of 1990-1993 and 2002-2003 as well.

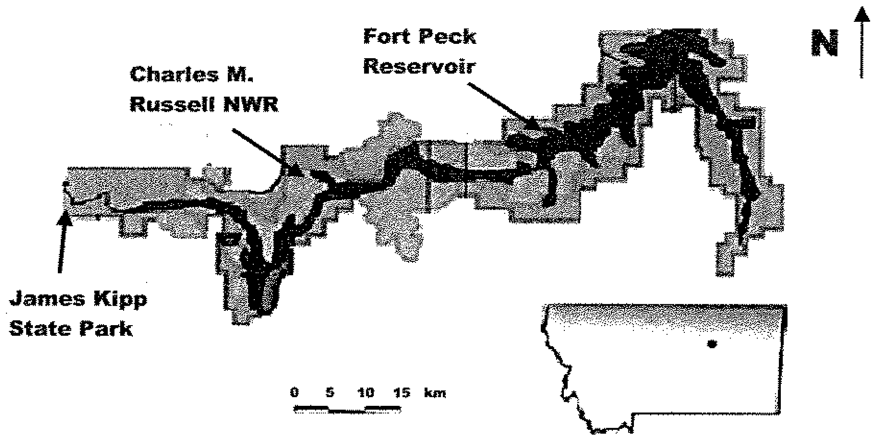


Figure 24. Area of paddlefish creel censuses on the Missouri River above Fort Peck Reservoir.

The study area was located within the Charles M. Russell Wildlife Refuge. Samples were collected along the Missouri River encompassing an area approximately 42 km below James Kipp State Park to the headwaters of the reservoir (Figure 24). Creel census data was collected along the river close to popular fishing access sites. Samples were taken above the reservoir in the spring of each sample year during the paddlefish spawning migration up the Missouri River.

## METHODS

Ages of paddlefish were estimated using dentary bone samples from the population (Adams 1942). Dentaries were collected from three periods 1977-1978, 1992-1993, and 2000 and 2002, and grouped into three treatments (early, middle, and late) in order to examine changes in growth over time. Dentaries were obtained in the field from creeled fish by making a cut at the anterior tip of the lower jaw and two other cuts along both the distal sides of the jaw near the back of the mouth. Dentaries were then stripped of attached flesh, put in envelopes marked with an identification number, date, and location of catch. Additional data collected from the harvested fish included total length or body length (anterior of eye to fork of caudal fin; (Ruelle and Hudson 1977) weight, and sex.

In the laboratory, dentaries were cleaned in a dilute detergent solution for 13-14 hrs at 41-43 °C, then cleaned of all flesh and cartilage material before being soaked in a 50% ammonia solution for an additional 6 hrs. Dentaries were rinsed and then soaked in a 50% ethanol solution for 24 hrs before being dried and stored.

Dentaries were sectioned using a Buehler Low-speed saw to a thickness of 0.3 mm. Three sections were cut. Sections were then placed on a depression slide filled with glycerin to be read. A BioSonics Inc. Optical Pattern Recognition System (OPRS) unit was used to view the cross-sections. Annual rings were counted and results recorded onto datasheets.

Weight and body length frequency histograms were created using creel census data collected from the three time periods. Histograms were examined visually for changes in weight and body length distribution as well as changes in the number of fish classified as large (>21 kg males, >42 kg females) within the population during each time period.

Changes in paddlefish weight and body length for all three time periods were examined using a two-way analysis of variance (ANOVA). Fish were separated into two age categories depending, on sex (<=15 and 16-20 for males, 16-20 and 21-25 for females). Only early ages were used to insure an independent sample was tested from each time period. A least-squares means procedure was run (PROC GLM, lsmeans option, SAS Institute 1989) to determine if significant differences were present in mean weight and body length for the three periods.

# RESULTS

Weight Frequency Histograms

Weight frequency histograms for both male and female paddlefish showed a decline in large fish (> 21 kg male and > 42 kg female) from the late 1970's to the early 2000's. In the early period, 24.7 % of the females sampled from the population were over 42 kg (Figure 25). That frequency had declined to 7.4 % in the middle period and 1.4 % in the late period (Figure 25). Proportions of females in the larger weight classes were found to be significantly different between the three periods (Chi-square test; $p < 0.05$) (Appendix, Figure 15). Much of the variation was caused by the higher proportion of females found within the larger weight classes in the early period. The pattern was similar in males, with 18.9 % of the population weighing over 21 kg in the early period but only 6.6 % in the middle period and 4.0 % in the late period (Figure 26). Again, proportions of males in the larger weight classes were found to be significantly different between the three periods (Chi-square test; $p < 0.05$) (Appendix, Figure 15). Much of the variation in males was also caused by the higher proportion of males found within the larger weight classes in the early period.

Body Length Frequency Histograms

Body length frequency histograms also showed a decline in large males and females (>108 cm male and > 126 cm female) (Figures 27 and 28). In the early and middle periods, 27.5 % and 28.8 % of females were found within the longer body length classes, respectively (Figure 27). In the late period, 14.5 % of females were found within the longer body length classes (Figure 27). The proportions of females within the longer body length classes were found to be significantly different between the three periods (Chi-square; $p< 0.05$) (Appendix, Figure 15). Much of the variation in females was caused by the low proportion of females found within the longer body length classes in the late period. Although a similar trend was observed in the males, proportions of males in the longer body length classes were not found to be significantly different between the three periods (Chi-square test; $p < 0.05$) (Figure 15). Overall, as the paddlefish matured and aged most size was gained in girth rather than length.

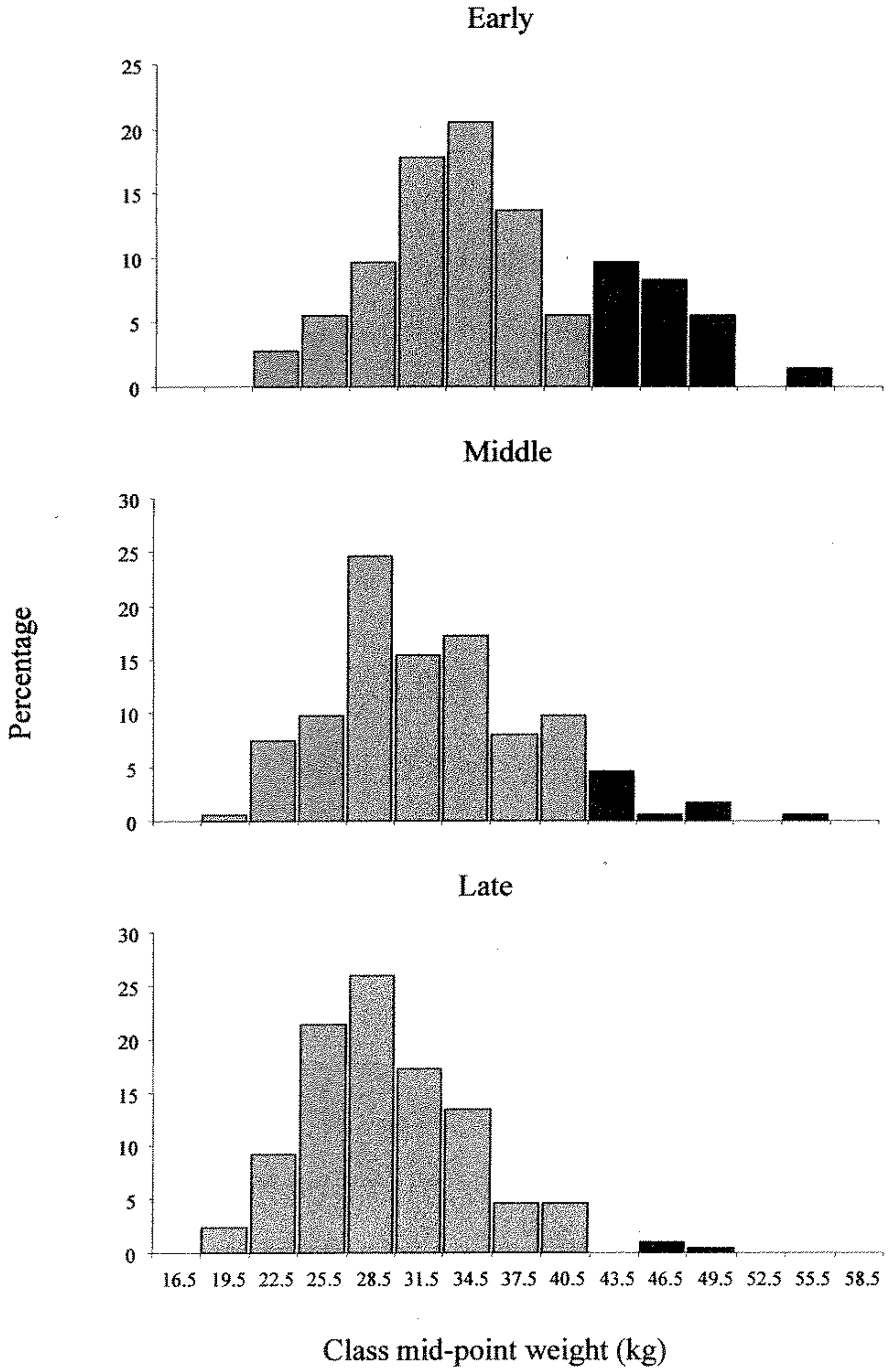


Figure 25. Weight class frequency plot of female paddlefish from the three sampled time periods. N= 73, 175, and 216 for early (1977-1978), middle (1992-1993), and late (2000,2002) periods respectively. Darker bars indicate fish in large weight classes (> 42 kg).

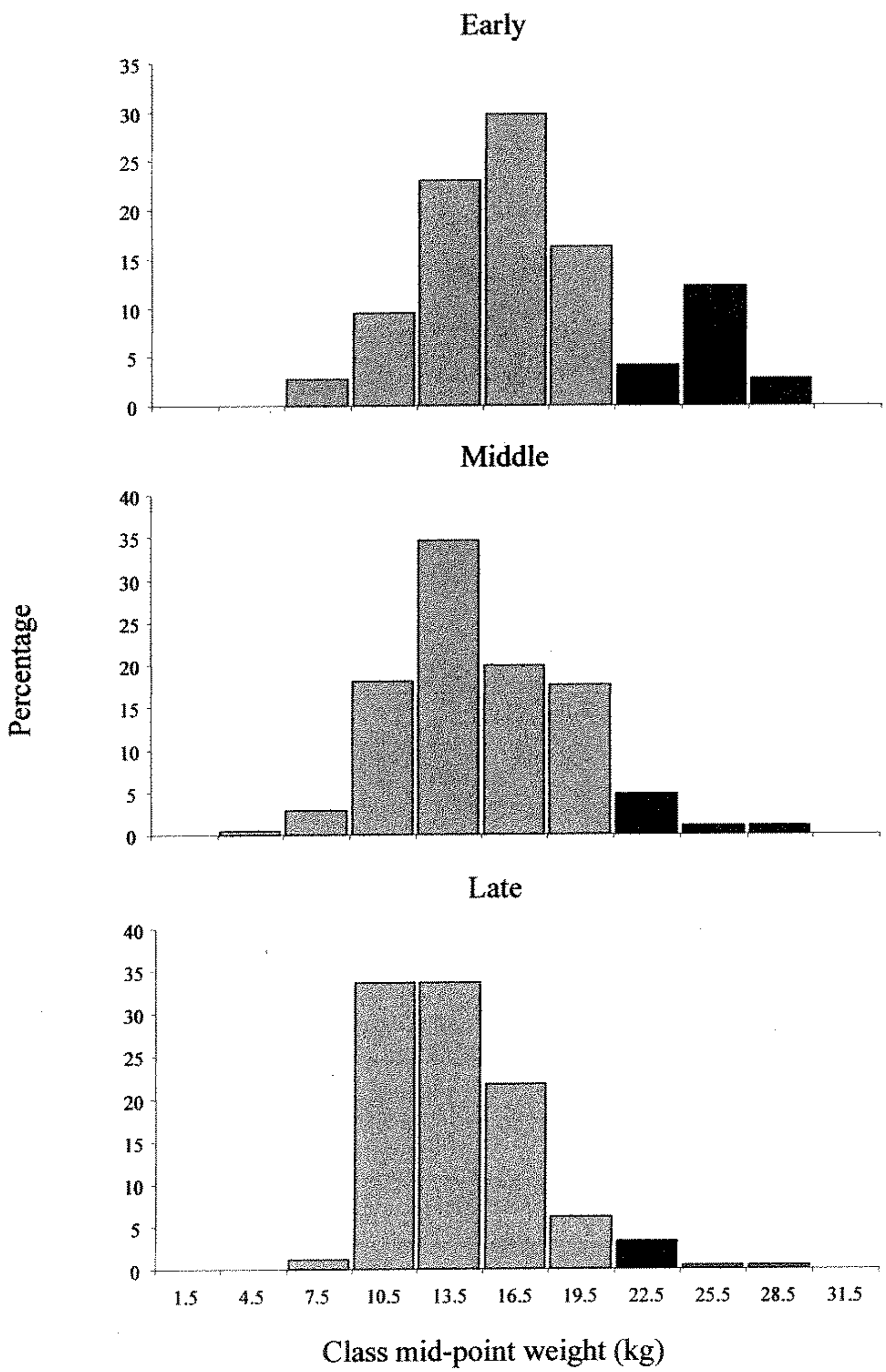


Figure 26. Weight class frequency plot of male paddlefish from the three sampled time periods. N= 74, 211, and 277 for early (1977-1978), middle (1992-1993), and late (2000,2002) periods respectively. Darker bars indicate fish in large weight classes (> 21 kg).

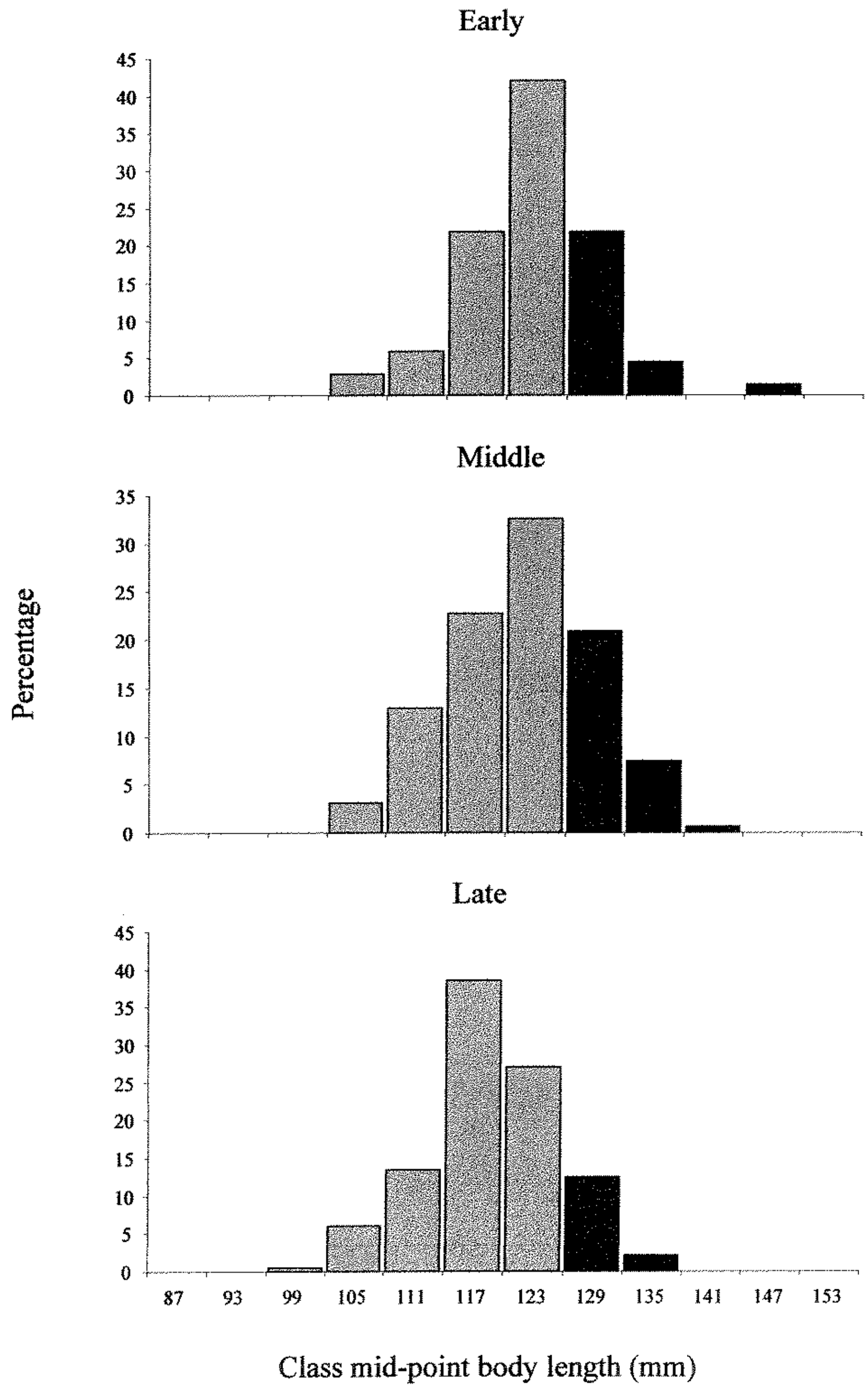


Figure 27. Body length class frequency plot of female paddlefish from the three sampled time periods. N= 69, 163, and 200 for early (1977-1978), middle (1992-1993), and late (2000,2002) periods respectively. Darker bars indicate fish in large body length classes (> 126 cm).

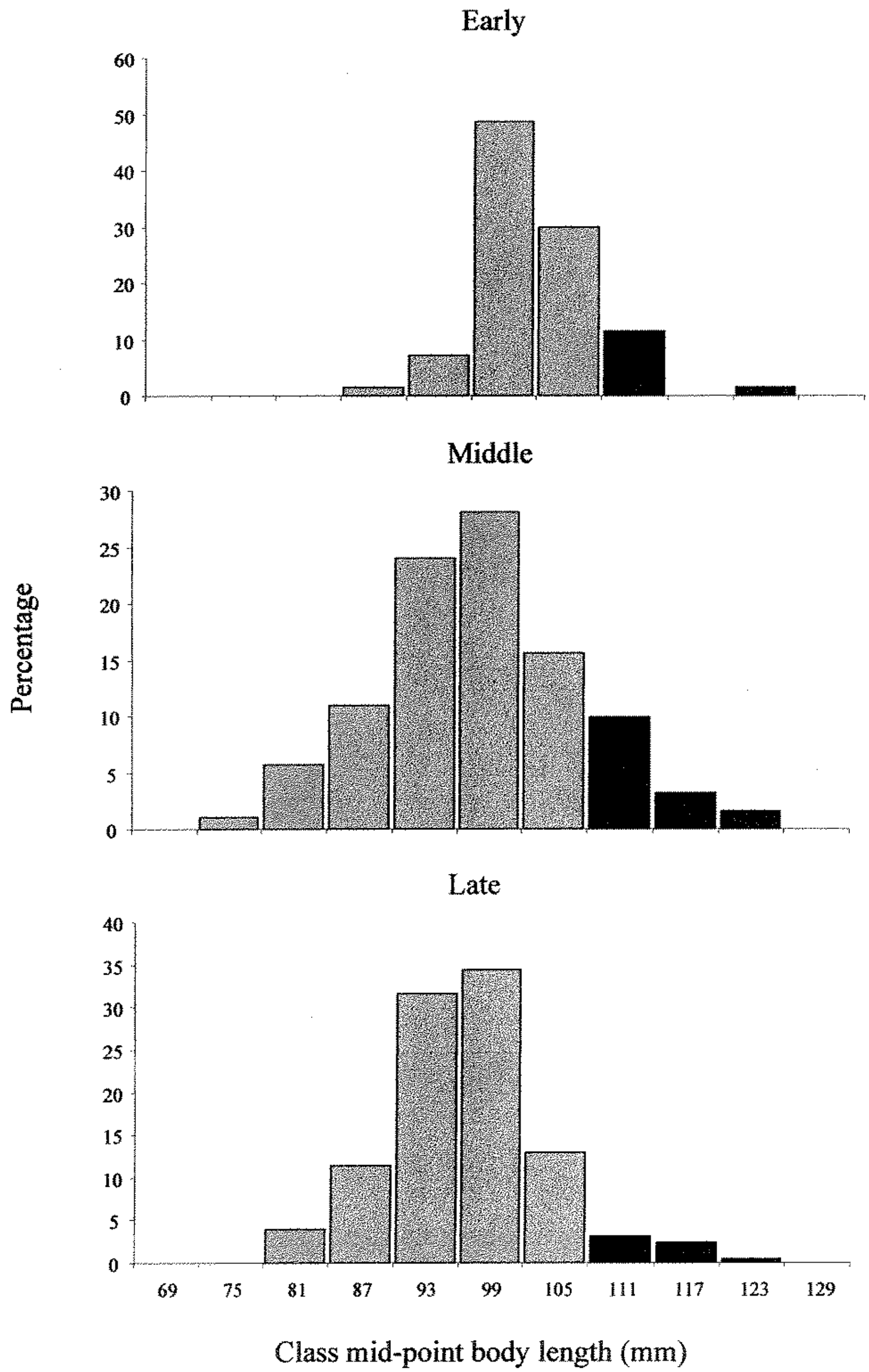


Figure 28. Body length class frequency plot of male paddlefish from the three sampled time periods. N = 70, 192, and 256 for early (1977-1978), middle (1992-1993), and late (2000,2002) periods respectively. Darker bars indicate fish in large body length classes (> 108 cm).

Female Weight

The highest mean weights for female paddlefish in both age categories (ages 16-20 and 20-25) occurred in the early period (Figure 29). Female paddlefish weight in the first age category (ages 16-20) was significantly higher in the early period than either the middle (p = 0.0015) or the late period (p = 0.0007) (Table 3).

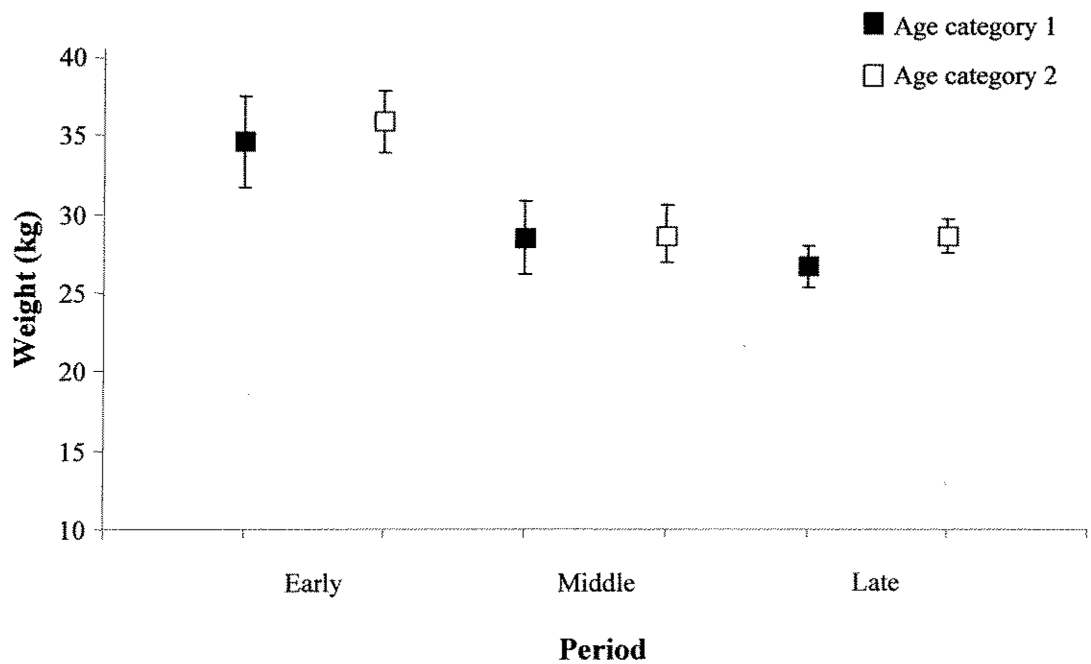


Figure 29. Mean weight and 95% confidence limit of female paddlefish sampled by spring creel census in the early (1977-1978), middle (1992-1993), and late (2000, 2002) periods in the Missouri River above Fort Peck Reservoir.

For the second age category (ages 21-25), the early period had significantly higher weights than both the middle and late periods (p<.0001) (Table 3). No significant differences were found between the middle and late periods for either of the two age

Table 3. Least-squares means for the effect of period (early, middle, and late) * age category (1 and 2) versus female weight (dependant variable).

| | | Early | | Middle | | Late | |
|---|---|---|---|---|---|---|---|
| | **i/j** | **1** | **2** | **1** | **2** | **1** | **2** |
| **Early** | **1** | | | | | | |
| | **2** | 0.4966 | | | | | |
| **Middle** | **1** | **0.0015** | <.000 | | | | |
| | **2** | 0.0023 | **<.0001** | 0.7854 | | | |
| **Late** | **1** | **<.0001** | <.000 | 0.0959 | 0.039 | | |
| | **2** | 0.0007 | **<.0001** | 0.8389 | 0.9005 | 0.0126 | |

Male Weight

As with the females, male weights in both age categories (ages <=15 and 16-20) were highest during the early period (Figure 30).

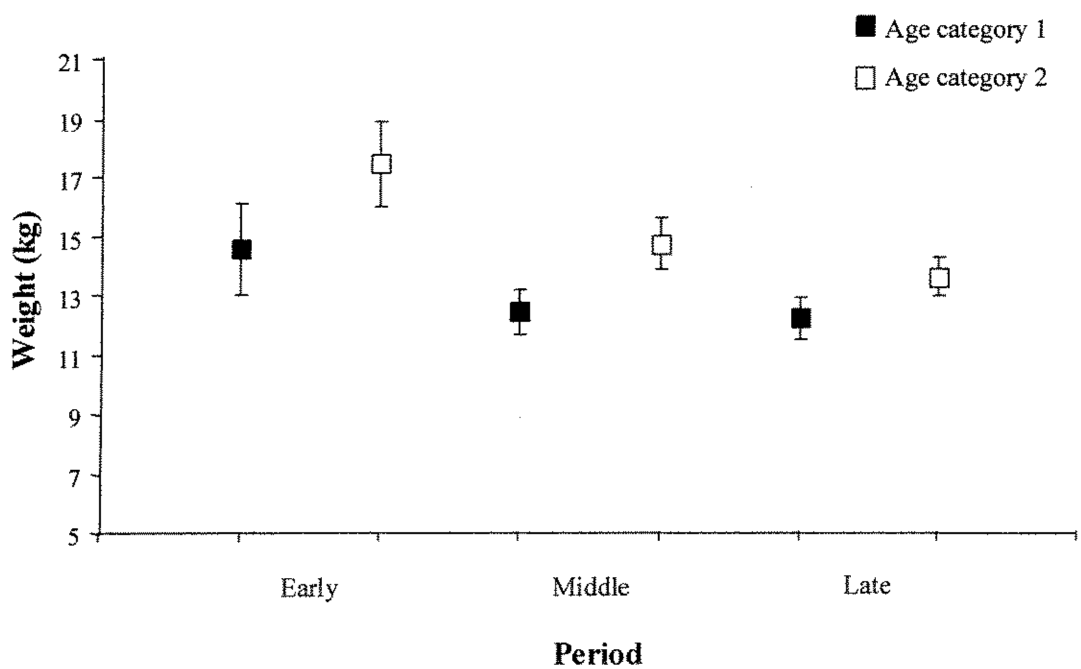


Figure 30. Mean weight and 95% confidence limit of male paddlefish sampled by spring creel census in the early (1977-1978), middle (1992-1993), and late (2000, 2002) periods in the Missouri River above Fort Peck Reservoir.

Mean weights for males from the early period in age category one (ages <=15) were significantly greater than mean weights from the middle period (p = 0.0211) and late period (p = 0.0125) (Table 4). Mean male weight from age category one in the middle period was not significantly different than mean weight found in the late period (p= 0.7885) (Table 4). In the second age category (ages 16-20), mean weight in the early period was significantly greater than weight during the middle period (p = 0.0058) and late period (p = <.0001) (Table 4). Mean weight of males in the second age category in the middle period was significantly greater than mean weight in the late period (p = 0.0251) (Table 4).

Table 4. Least-squares means for the effect of period (early, middle, and late) * age category (1 and 2) versus male weight (dependant variable).

| | | **Early** | | **Middle** | | **Late** | |
|---|---|---|---|---|---|---|---|
| | i/j | **1** | **2** | **1** | **2** | **1** | **2** |
| **Early** | **1** | | | | | | |
| | **2** | 0.0068 | | | | | |
| **Middle** | **1** | **0.0211** | <.0001 | | | | |
| | **2** | 0.5395 | **0.0058** | <.0001 | | | |
| **Late** | **1** | **0.0125** | <.0001 | 0.7885 | <.0001 | | |
| | **2** | 0.4252 | **<.0001** | 0.0075 | **0.0251** | 0.0022 | |

Female Body Length

Highest mean body lengths for females for both age categories (ages 16-20 and 21-25) were found in the early period (Figure 31). For the first age category (ages 16-20), mean lengths between the early and middle periods were not statistically different (p= 0.2056) (Table 5). Mean female body length in the first age category was significantly greater in early period than the late period (p= 0.004) (Table 5). Within the second age category, mean length in the early period was significantly greater than in the middle period (p= 0.0019) and the late period (<.0001) (Table 5).

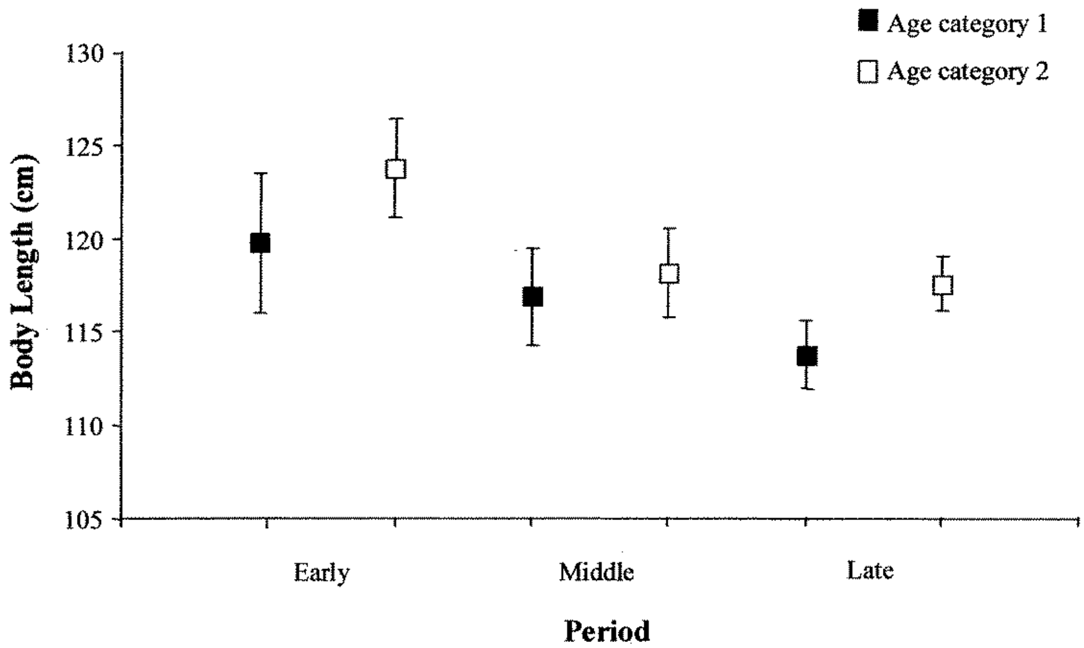


Figure 31. Mean female paddlefish body length and 95% confidence limit for each age category from samples collected during creel censuses in early (1977-1978), middle (1992-1993), and late (2000, 2002) periods on the Missouri River above Fort Peck Reservoir.

Table 5. Least-square means for the effect of period (early, middle, and late) * age category (1 and 2) versus female body length (dependant variable).

| | | **Early** | | **Middle** | | **Late** | |
|---|---|---|---|---|---|---|---|
| | **i/j** | **1** | **2** | **1** | **2** | **1** | **2** |
| **Early** | **1** | | | | | | |
| | **2** | 0.095 | | | | | |
| **Middle** | **1** | 0.205 | 0.0003 | | | | |
| | **2** | 0.424 | **0.0019** | 0.4764 | | | |
| **Late** | **1** | **0.004** | <.0001 | 0.0542 | 0.0039 | | |
| | **2** | 0.269 | **<.0001** | 0.6539 | 0.6749 | 0.0014 | |

Male Body Length

Mean body lengths for males in the first age category (ages <=15) were significantly greater in the early period than in the middle period ($p = 0.0299$) and the late period ($p = 0.0063$) (Figure 32) (Table 6). Within the second age category (ages 16-20), body lengths were also significantly greater in the early period than in the middle period ($p = 0.0344$) and the late period ($p = 0.0044$) (Table 6). There were no significant differences in mean lengths between the middle and late periods (Table 6).

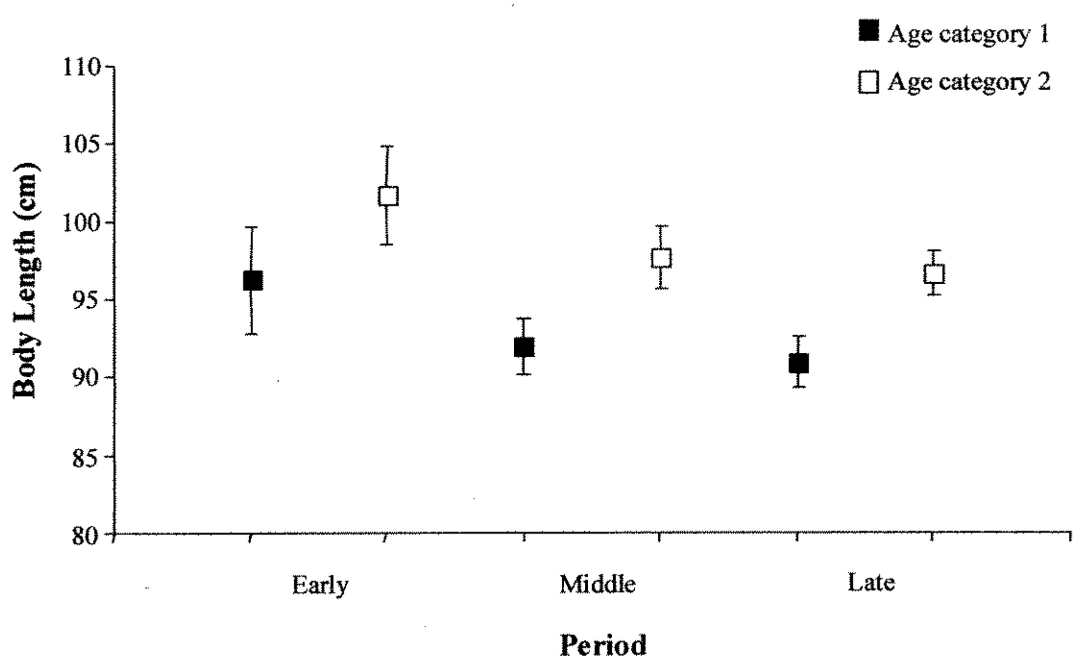


Figure 32. Mean male paddlefish body length and 95% confidence limit for each age category from samples collected during creel censuses in early (1977-1978), middle (1992-1993), and late (2000, 2002) periods on the Missouri River above Fort Peck Reservoir.

Table 6. Least-squares means for the effect of period (early, middle, and late) * age category (1 and 2) versus male body length (dependant variable).

| | | **Early** | | **Middle** | | **Late** | |
|---|---|---|---|---|---|---|---|
| | **i/j** | **1** | **2** | **1** | **2** | **1** | **2** |
| **Early** | **1** | | | | | | |
| | **2** | 0.0233 | | | | | |
| **Middle** | **1** | **0.0299** | <.0001 | | | | |
| | **2** | 0.4989 | **0.0344** | <.0001 | | | |
| **Late** | **1** | **0.0063** | <.0001 | 0.4201 | <.0001 | | |
| | **2** | 0.8532 | **0.0044** | <.0001 | 0.4167 | <.0001 | |

# DISCUSSION

Results of this study indicate a significant decline in both large paddlefish and in paddlefish growth from the early period (1977-1978) to the late period (2000, 2002). These declines have been coincident with the aging of Fort Peck Reservoir. Previous studies on other water bodies have shown similar trends with regards to fish production and reservoir aging. Abell and Fisher (1953) found high catch rates bluegill, *Lepomis macrochirus*, (six fish per angler day) in Millerton Lake, California in 1946, two years after impoundment. Two years later catch per angler day had declined sharply (0.33 bluegill per angler day). They also found that the average weight of largemouth bass *Micropterus salmoides*, declined from 0.32 kg in 1949 to 0.26 kg in 1952. Eschmeyer and Jones (1941) found similar results in Norris Reservoir, Tennessee, with the growth rates of six game fish species declining in the fourth and fifth years after impoundment, from higher growth rates during the first three years.

Similar instances of reservoir productivity affecting population and individual growth have also been reported in paddlefish. For example, Scarnecchia et al. (1996) found that soon after closure of Garrison Dam, North Dakota, in 1953 and the filling of the reservoir (1953 – 1966), the paddlefish population in the reservoir increased substantially. However, the number of the paddlefish in the population has since declined as the reservoir has aged. Paukert and Fisher (2001) found that initial paddlefish growth in productive lentic systems was significantly higher than in less productive lotic systems. In addition, they suggested that mean length-at-age of paddlefish in these populations was largely attributed to first-year growth (Paukert and Fisher 2001). A primary difference in a long-lived species such as paddlefish is that the effects on the population may become more obvious much farther into the future, many years after the early productivity associated with trophic upsurge. Although it is unclear if other habitat changes have occurred to exacerbate the declines in paddlefish growth, reservoir aging is probably a contributing factor.

The decrease in large paddlefish and declining growth rates may have a number of negative effects on the Fort Peck Reservoir population. First, decreased fecundity of females may result. Many studies have shown a positive correlation between fish size and fish fecundity (Trippel 1993, Michaletz 1998, Morita and Takashima 1998, Coward and Bromage 1999). Some studies have also shown that an increase in growth rates has resulted in an increased fecundity (Scott 1962, McFadden and Cooper 1962, Trippel 1993). Scott (1962) found in a laboratory study that the number of mature eggs within females was directly related to the level of starvation to which the fish was subjected. Faster growth rates produced larger fish and higher fecundities. Similarly, Trippel (1993) found that lake trout, *Salvelinus namaycush*, in the higher conductivity lakes had substantially higher growth rates and fecundities than those in lower conductivity lakes. Reed et al. (1992) found lower fecundities in female paddlefish in Louisiana with a mean weight of 11.3 kg than more northerly populations with larger individuals. As both size-at-age and growth rates have declined, the reproductive potential of the Fort Peck paddlefish will decline both in individuals and in the population as a whole.

In addition to decreased fecundity, lower growth rates of paddlefish in Fort Peck Reservoir may result in maturation at older ages and at smaller sizes. Studies have shown earlier maturation in fish of the same species with more favorable environmental conditions (McFadden et al. 1965, Bagenal 1969, Duston and Saunders 1999, Morita and

Morita 2002). Both McFadden et al. (1965) and Bagenal (1969) found a higher proportion of mature brown trout, *Salmo trutta*, in populations from more productive waters than those from less productive waters. Morita and Morita (2002) found that slow growing white-spotted char, *Salvelinus leucomaenis*, not only matured later than fast growing individuals; but that they also matured at a smaller size than the fast growing individuals. For paddlefish, Reed et al. (1992) attributed the lower age-at-maturity of Louisiana paddlefish when compared with to other populations to their high growth rates. If paddlefish in the Fort Peck Reservoir population are maturing later and at smaller sizes, overall stock productivity can also be expected to decrease.

A possible factor for the decreased proportions of large fish, specifically females, in the Fort Peck paddlefish stock is fishing pressure. Fishing pressure during the paddlefish spring spawning migration has increased from approximately 2000-2500 angler days in 1977-1978 to 3500-4700 angler days in 2000 and 2002 respectively (Gilge and Perszyk 2002). Immediate high-grading is also allowed within the fishery, whereby an angler can release a fish immediately upon capture until a fish of desirable size is caught. Although high-grading is preferred by anglers, the loss of large fish to harvest, all of which would be females, is probably a contributing factor in the decrease in size. High-grading would not be expected to influence the observed changes in growth rates, because there is no fishing pressure present in the reservoir while the fish are rearing to young adulthood. The observed differences in early paddlefish growth displayed between periods can therefore not be attributed to the effects of fishing pressure. Other unidentified factors could influence growth rates, such as increases in the number of competitors, which warrant further investigation.

The results of this study indicate that both early growth and maximum size of paddlefish in Fort Peck Reservoir have declined over the past 30 years. In view of the documented effects of reservoir aging on fish production in many locations, as well as the tendency of snaggers to harvest the largest females, it can be anticipated that without some change in regulations and habitat conditions, the large paddlefish harvested in the 1970's and 1980's will be less common in the future.

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# APPENDIX

Table 1. ANOVA table of log transformed *Leptodora* abundance for sample period 1.

| Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|
| Habitat Type | 2 | 73.2342 | 196.75 | <.0001 |
| Depth | 5 | 1.8638 | 5.01 | 0.0003 |
| Diurnal Period | 1 | 5.09232 | 13.68 | 0.0003 |
| Habitat Type x Depth | 5 | 2.18881 | 5.88 | <.0001 |
| Habitat Type x Diurnal | 2 | 3.7948 | 10.19 | <.0001 |
| Depth x Diurnal | 5 | 2.40257 | 6.45 | <.0001 |
| Habitat Type x Depth x Diurnal | 5 | 4.7566 | 12.78 | <.0001 |
| Water Temperature | 1 | 8.62697 | 23.18 | <.0001 |
| Turbidty | 1 | 0.44649 | 1.2 | 0.2749 |
| Waypoint (Habitat Type) | 6 | 7.25038 | 19.48 | <.0001 |
| Error | 206 | 0.37222 | | |

Table 2. ANOVA table of log transformed *Leptodora* abundance for sample period 2.

| Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|
| Habitat Type | 2 | 24.5125 | 83.72 | <.0001 |
| Depth | 5 | 1.15255 | 3.94 | 0.0021 |
| Diurnal Period | 1 | 0.08869 | 0.3 | 0.5828 |
| Habitat Type x Depth | 4 | 1.86343 | 6.36 | <.0001 |
| Habitat Type x Diurnal | 2 | 0.22069 | 0.75 | 0.4721 |
| Depth x Diurnal | 5 | 1.5803 | 5.4 | <.0001 |
| Habitat Type x Depth x Diurnal | 4 | 0.43884 | 1.5 | 0.2046 |
| Water Temperature | 1 | 0.12086 | 0.41 | 0.5214 |
| Turbidty | 1 | 1.58173 | 5.4 | 0.0213 |
| Waypoint (Habitat Type) | 6 | 8.11233 | 27.71 | <.0001 |
| Error | 203 | 0.29278 | | |

Table 3. ANOVA table of log transformed *Leptodora* abundance for sample period 3.

| Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|
| Habitat Type | 2 | 0.91193 | 6.22 | 0.0026 |
| Depth | 4 | 0.48728 | 3.32 | 0.0123 |
| Diurnal Period | 1 | 0.12065 | 0.82 | 0.3659 |
| Habitat Type x Depth | 4 | 0.30513 | 2.08 | 0.0864 |
| Habitat Type x Diurnal | 2 | 1.26044 | 8.59 | 0.0003 |
| Depth x Diurnal | 4 | 0.19305 | 1.32 | 0.2667 |
| Habitat Type x Depth x Diurnal | 4 | 0.07306 | 0.5 | 0.7371 |
| Water Temperature | 1 | 0.01565 | 0.11 | 0.7443 |
| Turbidty | 1 | 0.02529 | 0.17 | 0.6785 |
| Waypoint (Habitat Type) | 6 | 2.4173 | 16.48 | <.0001 |
| Error | 173 | 0.14667 | | |

Table 4. ANOVA table of log transformed *Leptodora* abundance for sample period 4.

| Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|
| Habitat Type | 2 | 14.9326 | 34.55 | <.0001 |
| Depth | 5 | 1.09379 | 2.53 | 0.0309 |
| Diurnal Period | 1 | 0.55614 | 1.29 | 0.2583 |
| Habitat Type x Depth | 4 | 1.37413 | 3.18 | 0.0151 |
| Habitat Type x Diurnal | 2 | 8.09338 | 18.72 | <.0001 |
| Depth x Diurnal | 5 | 5.25237 | 12.15 | <.0001 |
| Habitat Type x Depth x Diurnal | 4 | 0.39291 | 0.91 | 0.4601 |
| Water Temperature | 1 | 1.74388 | 4.03 | 0.0462 |
| Turbidty | 1 | 0.76378 | 1.77 | 0.1856 |
| Waypoint (Habitat Type) | 6 | 10.8521 | 25.11 | <.0001 |
| Error | 197 | 0.43224 | | |

Table 5. ANOVA table of log transformed *Leptodora* abundance for sample period 5.

| Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|
| Habitat Type | 2 | 23.6155 | 68.39 | <.0001 |
| Depth | 5 | 2.74457 | 7.95 | <.0001 |
| Diurnal Period | 1 | 0.11078 | 0.32 | 0.5719 |
| Habitat Type x Depth | 4 | 0.77286 | 2.24 | 0.0671 |
| Habitat Type x Diurnal | 2 | 5.57791 | 16.15 | <.0001 |
| Depth x Diurnal | 5 | 2.81322 | 8.15 | <.0001 |
| Habitat Type x Depth x Diurnal | 4 | 1.77093 | 5.13 | 0.0006 |
| Water Temperature | 1 | 2.40562 | 6.97 | 0.0091 |
| Turbidty | 1 | 0.13525 | 0.39 | 0.5323 |
| Waypoint (Habitat Type) | 6 | 5.5154 | 15.97 | <.0001 |
| Error | 197 | 0.34532 | | |

Table 6. ANOVA table of log transformed *Leptodora* abundance for sample period 6.

| Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|
| Habitat Type | 2 | 0.71993 | 10.69 | <.0001 |
| Depth | 4 | 0.07098 | 1.05 | 0.3814 |
| Diurnal Period | 1 | 0.016617 | 0.25 | 0.6201 |
| Habitat Type x Depth | 4 | 0.21684 | 3.22 | 0.0145 |
| Habitat Type x Diurnal | 2 | 1.16363 | 17.29 | <.0001 |
| Depth x Diurnal | 4 | 0.38093 | 5.66 | 0.0003 |
| Habitat Type x Depth x Diurnal | 4 | 0.14978 | 2.23 | 0.0692 |
| Water Temperature | 1 | 0.00012 | 0 | 0.9685 |
| Turbidty | 1 | 0.12936 | 1.92 | 0.1678 |
| Waypoint (Habitat Type) | 6 | 0.64301 | 9.55 | <.0001 |
| Error | 173 | 0.06731 | | |

Table 7. Test results investigating changes in mean *Leptodora* abundance between day and night samples within each sample period, habitat type, and depth using the least-squares means slice procedure in SAS. Level of significance p<=0.05, significant values in bold.

| SP | Habitat Type | Depth of Tow | DF | Mean Square | F-value | Pr > F |
|---|---|---|---|---|---|---|
| 1 | Riverine | 0.25 | 202 | 0.536 | 1.28 | 0.259 |
| | | 1.25 | 202 | 0.009 | 0.02 | 0.879 |
| | | 2.25 | 202 | 0.536 | 1.28 | 0.259 |
| | Transitional | 0.25 | 202 | 3.4 | 8.13 | **0.005** |
| | | 1.25 | 202 | 7.709 | 18.44 | **<.0001** |
| | | 2.25 | 202 | 0.003 | 0.01 | 0.925 |
| | | 3.25 | 202 | 0.197 | 0.47 | 0.492 |
| | Reservoir | 0.25 | 202 | 14.534 | 34.76 | **<.0001** |
| | | 1.25 | 202 | 5.085 | 12.16 | **0.0006** |
| | | 2.25 | 202 | 9.497 | 22.72 | **<.0001** |
| | | 3.25 | 202 | 7.34 | 17.56 | **<.0001** |
| | | 4.25 | 202 | 11.821 | 28.28 | **<.0001** |
| | | 5.25 | 202 | 1.043 | 2.5 | 0.116 |
| 2 | Riverine | 0.25 | 199 | 0.026 | 0.09 | 0.77 |
| | | 1.25 | 199 | 3.46 E-31 | 0 | 1 |
| | Transitional | 0.25 | 199 | 1.893 | 6.27 | **0.01** |
| | | 1.25 | 199 | 0.302 | 1 | 0.318 |
| | | 2.25 | 199 | 0.125 | 0.41 | 0.521 |
| | | 3.25 | 199 | 0.521 | 1.73 | 0.191 |
| | Reservoir | 0.25 | 199 | 0.344 | 1.14 | 0.287 |
| | | 1.25 | 199 | 0.062 | 0.21 | 0.65 |
| | | 2.25 | 199 | 1.21 | 4.02 | **0.046** |
| | | 3.25 | 199 | 0.767 | 2.54 | 0.112 |
| | | 4.25 | 199 | 0.336 | 1.11 | 0.292 |
| | | 5.25 | 199 | 2.757 | 9.14 | **0.003** |
| 3 | Riverine | 0.25 | 169 | 2.844 E-31 | 0 | 1 |
| | | 1.25 | 169 | 9.482 E-32 | 0 | 1 |
| | Transitional | 0.25 | 169 | 0.118 | 0.84 | 0.361 |
| | | 1.25 | 169 | 0.616 | 4.37 | **0.038** |
| | | 2.25 | 169 | 0.694 | 4.92 | **0.028** |
| | | 3.25 | 169 | 0.199 | 1.42 | 0.235 |
| | Reservoir | 0.25 | 169 | 2.097 | 14.86 | **0.0002** |
| | | 1.25 | 169 | 0.387 | 2.74 | 0.099 |
| | | 2.25 | 169 | 0.067 | 0.48 | 0.492 |
| | | 3.25 | 169 | 0.0002 | 0 | 0.965 |
| | | 4.25 | 169 | 0.047 | 0.33 | 0.565 |
| | | 5.25 | 169 | [illegible] E-30 | 0 | 1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | 4.25 | 169 | 0.047 | 0.33 | 0.565 |
| | | 5.25 | 169 | 2.299 E-29 | 0 | 1 |
| 4 | Riverine | 0.25 | 193 | 0.005 | 0.01 | 0.911 |
| | | 1.25 | 193 | 3.549 E-30 | 0 | 1 |
| | Transitional | 0.25 | 193 | 0.002 | 0 | 0.947 |
| | | 1.25 | 193 | 0.075 | 0.17 | 0.679 |
| | | 2.25 | 193 | 0.014 | 0.03 | 0.861 |
| | | 3.25 | 193 | 0.408 | 0.93 | 0.337 |
| | Reservoir | 0.25 | 193 | 8.37 | 18.99 | **<.0001** |
| | | 1.25 | 193 | 16.59 | 37.63 | **<.0001** |
| | | 2.25 | 193 | 1.468 | 3.33 | 0.069 |
| | | 3.25 | 193 | 0.322 | 0.73 | 0.394 |
| | | 4.25 | 193 | 0.567 | 1.29 | 0.258 |
| | | 5.25 | 193 | 7.046 | 15.98 | **<.0001** |
| 5 | Riverine | 0.25 | 193 | 0.058 | 0.01 | 0.911 |
| | | 1.25 | 193 | 0.089 | 0 | 1 |
| | Transitional | 0.25 | 193 | 26.11 | 0 | 0.947 |
| | | 1.25 | 193 | 3.122 | 0.17 | 0.679 |
| | | 2.25 | 193 | ,015 | 0.03 | 0.861 |
| | | 3.25 | 193 | 0.009 | 0.93 | 0.337 |
| | Reservoir | 0.25 | 193 | 5.039 | 18.99 | **<.0001** |
| | | 1.25 | 193 | 0.406 | 37.63 | **<.0001** |
| | | 2.25 | 193 | 1.553 | 3.33 | 0.069 |
| | | 3.25 | 193 | 1.861 | 0.73 | 0.394 |
| | | 4.25 | 193 | 0.676 | 1.29 | 0.258 |
| | | 5.25 | 193 | 2.246 | 15.98 | **<.0001** |
| 6 | Riverine | 0.25 | 169 | 4.194 E-31 | 0 | 1 |
| | | 1.25 | 169 | 5.662 E-30 | 0 | 1 |
| | Transitional | 0.25 | 169 | 0.037 | 0.56 | 0.457 |
| | | 1.25 | 169 | 0.095 | 1.41 | 0.236 |
| | | 2.25 | 169 | 0.398 | 5.9 | **0.016** |
| | | 3.25 | 169 | 0.702 | 10.41 | **0.0015** |
| | Reservoir | 0.25 | 169 | 0.116 | 1.72 | 0.192 |
| | | 1.25 | 169 | 3.418 | 50.69 | **<.0001** |
| | | 2.25 | 169 | 0.579 | 8.59 | **0.004** |
| | | 3.25 | 169 | 0.026 | 0.38 | 0.536 |
| | | 4.25 | 169 | 0.027 | 0.4 | 0.527 |

Table 8. Test results investigating changes in mean *Leptodora* length between day and night samples within each sample period, habitat type, and depth using the least-squares means slice procedure in SAS. Level of significance p<=0.05, significant values in bold.

| SP | Habitat Type | Depth of Tow | DF | Mean Square | F-value | Pr > F |
|---|---|---|---|---|---|---|
| 1 | Riverine | 0.25 | 159 | 0.07 | 0.1 | 0.749 |
| | | 1.25 | 159 | 1.767 | 2.59 | 0.11 |
| | | 2.25 | 159 | 5.005 | 7.32 | **0.0076** |
| | Transitional | 0.25 | 159 | 1.705 | 2.49 | 0.1164 |
| | | 1.25 | 159 | 1.264 | 1.85 | 0.1759 |
| | | 2.25 | 159 | 0.483 | 0.71 | 0.4017 |
| | | 3.25 | 159 | 0.209 | 0.31 | 0.581 |
| | Reservoir | 0.25 | 159 | 25.08 | 36.7 | **<.0001** |
| | | 1.25 | 159 | 35.47 | 51.9 | **<.0001** |
| | | 2.25 | 159 | 7.508 | 10.99 | **0.0012** |
| | | 3.25 | 159 | 7.745 | 11.33 | **0.001** |
| | | 4.25 | 159 | 6.734 | 9.85 | **0.002** |
| | | 5.25 | 159 | 7.504 | 10.98 | **0.0012** |
| 2 | Riverine | 0.25 | 159 | . | . | . |
| | Transitional | 0.25 | 159 | 2.081 | 2.14 | 0.145 |
| | | 1.25 | 159 | 3.726 | 3.84 | 0.0521 |
| | | 2.25 | 159 | 1.732 | 1.78 | 0.184 |
| | | 3.25 | 159 | 4.477 | 4.61 | **0.034** |
| | Reservoir | 0.25 | 159 | 5.229 | 5.38 | **0.022** |
| | | 1.25 | 159 | 2.8 | 2.88 | 0.092 |
| | | 2.25 | 159 | 8.287 | 8.53 | **0.004** |
| | | 3.25 | 159 | 5.882 | 6.06 | **0.015** |
| | | 4.25 | 159 | 3.05 | 3.14 | 0.076 |
| | | 5.25 | 159 | 0.161 | 0.17 | 0.684 |
| 3 | Riverine | 0.25 | 69 | . | . | . |
| | Transitional | 0.25 | 69 | 0.002 | 0 | 0.954 |
| | | 1.25 | 69 | 2.666 | 4.19 | **0.046** |
| | | 2.25 | 69 | 0.398 | 0.63 | 0.432 |
| | | 3.25 | 69 | 0.096 | 0.15 | 0.699 |
| | Reservoir | 0.25 | 69 | 0.403 | 0.63 | 0.429 |
| | | 1.25 | 69 | 0.002 | 0 | 0.96 |
| | | 2.25 | 69 | 1.567 | 2.46 | 0.123 |
| | | 3.25 | 69 | 0.379 | 0.6 | 0.444 |
| | | 4.25 | 69 | 0.001 | 0 | 0.968 |

| | | | | | | |
|---|---|---|---|---|---|---|
| 4 | Riverine | 0.25 | 134 | . | . | . |
| | Transitional | 0.25 | 134 | 11.95 | 9.87 | **0.002** |
| | | 1.25 | 134 | 0.025 | 0.02 | 0.885 |
| | | 2.25 | 134 | 1.93 | 1.59 | 0.209 |
| | | 3.25 | 134 | 0.147 | 0.12 | 0.727 |
| | Reservoir | 0.25 | 134 | 6.46 | 5.33 | **0.022** |
| | | 1.25 | 134 | 0.081 | 0.07 | 0.796 |
| | | 2.25 | 134 | 0.453 | 0.37 | 0.542 |
| | | 3.25 | 134 | 0.203 | 0.17 | 0.683 |
| | | 4.25 | 134 | 1.09 | 0.9 | 0.345 |
| | | 5.25 | 134 | 0.129 | 0.11 | 0.745 |
| 5 | Riverine | 0.25 | 170 | . | . | . |
| | | 1.25 | 170 | 0.184 | 0.24 | 0.623 |
| | Transitional | 0.25 | 170 | 17.81 | 23.47 | **<.0001** |
| | | 1.25 | 170 | 13.14 | 17.32 | **<.0001** |
| | | 2.25 | 170 | 5.335 | 7.03 | **0.0089** |
| | | 3.25 | 170 | 12.4 | 16.34 | **<.0001** |
| | Reservoir | 0.25 | 170 | 24.1 | 31.76 | **<.0001** |
| | | 1.25 | 170 | 5.689 | 7.5 | **0.007** |
| | | 2.25 | 170 | 0.031 | 0.04 | 0.8395 |
| | | 3.25 | 170 | 1.473 | 1.94 | 0.166 |
| | | 4.25 | 170 | 1.051 | 1.39 | 0.241 |
| | | 5.25 | 170 | 5.98 | 7.88 | **0.006** |
| 6 | Transitional | 0.25 | 82 | . | . | . |
| | | 1.25 | 82 | . | . | . |
| | | 2.25 | 82 | . | . | . |
| | | 3.25 | 82 | . | . | . |
| | Reservoir | 0.25 | 82 | 13.94 | 7.45 | **0.008** |
| | | 1.25 | 82 | 0.658 | 0.35 | 0.555 |
| | | 2.25 | 82 | 0.002 | 0 | 0.974 |
| | | 3.25 | 82 | 11.4 | 6.1 | **0.016** |
| | | 4.25 | 82 | 0.016 | 0.01 | 0.928 |

Table 9. Log transformed least-squares means of *Leptodora* abundance within each habitat type, depth, and diurnal period for sample period 1.

| Habitat type | Depth | Diurnal period | log LSMean |
|---|---|---|---|
| Riverine | 0.25 | 1 | 0.6019 |
| | | 2 | 0.2568 |
| | 1.25 | 1 | 0.1301 |
| | | 2 | 0.0836 |
| | 2.25 | 1 | 0.4274 |
| | | 2 | 0.1704 |
| Transitional | 0.25 | 1 | 2.8688 |
| | | 2 | 3.7381 |
| | 1.25 | 1 | 4.4407 |
| | | 2 | 3.1318 |
| | 2.25 | 1 | 2.9633 |
| | | 2 | 2.9921 |
| | 3.25 | 1 | 2.5996 |
| | | 2 | 2.8094 |
| Reservoir | 0.25 | 1 | 2.5892 |
| | | 2 | 4.3864 |
| | 1.25 | 1 | 4.8012 |
| | | 2 | 3.7381 |
| | 2.25 | 1 | 4.7351 |
| | | 2 | 3.2364 |
| | 3.25 | 1 | 4.7381 |
| | | 2 | 3.3674 |
| | 4.25 | 1 | 4.7016 |
| | | 2 | 3.0808 |
| | 5.25 | 1 | 4.4706 |
| | | 2 | 3.6366 |

Table 10. Log transformed least-squares means of *Leptodora* abundance within each habitat type, depth, and diurnal period for sample period 2.

| Habitat type | Depth | Diurnal period | log LSMean |
|---|---|---|---|
| Riverine | 0.25 | 1 | 0.0758 |
| | | 2 | 0.0000 |
| | 1.25 | 1 | 0.0000 |
| | | 2 | 0.0000 |
| Transitional | 0.25 | 1 | 2.0398 |
| | | 2 | 2.6876 |
| | 1.25 | 1 | 1.9061 |
| | | 2 | 1.6472 |
| | 2.25 | 1 | 1.5613 |
| | | 2 | 1.3945 |
| | 3.25 | 1 | 0.8686 |
| | | 2 | 1.2853 |
| Reservoir | 0.25 | 1 | 3.4625 |
| | | 2 | 3.1859 |
| | 1.25 | 1 | 4.0351 |
| | | 2 | 3.9173 |
| | 2.25 | 1 | 3.7468 |
| | | 2 | 3.2275 |
| | 3.25 | 1 | 3.0527 |
| | | 2 | 3.4655 |
| | 4.25 | 1 | 2.5051 |
| | | 2 | 2.7784 |
| | 5.25 | 1 | 1.9902 |
| | | 2 | 2.9488 |

Table 11. Log transformed least-squares means of *Leptodora* abundance within each habitat type, depth, and diurnal period for sample period 3.

| Habitat type | Depth | Diurnal period | log LSMean |
|---|---|---|---|
| Riverine | 0.25 | 1 | 0.0000 |
| | | 2 | 0.0000 |
| | 1.25 | 1 | 0.0000 |
| | | 2 | 0.0000 |
| Transitional | 0.25 | 1 | 0.6907 |
| | | 2 | 0.7721 |
| | 1.25 | 1 | 0.1129 |
| | | 2 | 0.4830 |
| | 2.25 | 1 | 0.0736 |
| | | 2 | 0.4663 |
| | 3.25 | 1 | 0.3590 |
| | | 2 | 0.0061 |
| Reservoir | 0.25 | 1 | 0.6827 |
| | | 2 | 0.0000 |
| | 1.25 | 1 | 0.3724 |
| | | 2 | 0.0793 |
| | 2.25 | 1 | 0.1221 |
| | | 2 | 0.0000 |
| | 3.25 | 1 | 0.0695 |
| | | 2 | 0.0773 |
| | 4.25 | 1 | 0.1871 |
| | | 2 | 0.0850 |
| | 5.25 | 1 | 0.0939 |
| | | 2 | 0.0939 |

Table 12. Log transformed least-squares means of *Leptodora* abundance within each habitat type, depth, and diurnal period for sample period 4.

| Habitat type | Depth | Diurnal period | log LSMean |
|---|---|---|---|
| Riverine | 0.25 | 1 | 0.0000 |
| | | 2 | 0.0352 |
| | 1.25 | 1 | 0.0000 |
| | | 2 | 0.0000 |
| Transitional | 0.25 | 1 | 0.2581 |
| | | 2 | 0.2789 |
| | 1.25 | 1 | 0.3404 |
| | | 2 | 0.2107 |
| | 2.25 | 1 | 0.3392 |
| | | 2 | 0.2842 |
| | 3.25 | 1 | 0.0831 |
| | | 2 | 0.4519 |
| Reservoir | 0.25 | 1 | 3.1362 |
| | | 2 | 1.7720 |
| | 1.25 | 1 | 3.1558 |
| | | 2 | 1.2357 |
| | 2.25 | 1 | 2.0093 |
| | | 2 | 1.4381 |
| | 3.25 | 1 | 1.8073 |
| | | 2 | 1.5399 |
| | 4.25 | 1 | 1.3912 |
| | | 2 | 1.7462 |
| | 5.25 | 1 | 0.1112 |
| | | 2 | 2.0562 |

Table 13. Log transformed least-squares means of *Leptodora* abundance within each habitat type, depth, and diurnal period for sample period 5.

| Habitat type | Depth | Diurnal period | log LSMean |
|---|---|---|---|
| Riverine | 0.25 | 1 | 0.1132 |
| | | 2 | 0.0000 |
| | 1.25 | 1 | 0.2465 |
| | | 2 | 0.0739 |
| Transitional | 0.25 | 1 | 0.3865 |
| | | 2 | 2.7954 |
| | 1.25 | 1 | 2.3314 |
| | | 2 | 3.1649 |
| | 2.25 | 1 | 2.4446 |
| | | 2 | 2.5017 |
| | 3.25 | 1 | 2.5408 |
| | | 2 | 2.5860 |
| Reservoir | 0.25 | 1 | 1.8610 |
| | | 2 | 2.9192 |
| | 1.25 | 1 | 2.5896 |
| | | 2 | 2.8900 |
| | 2.25 | 1 | 2.5746 |
| | | 2 | 3.1620 |
| | 3.25 | 1 | 2.6118 |
| | | 2 | 3.2548 |
| | 4.25 | 1 | 2.8027 |
| | | 2 | 2.4150 |
| | 5.25 | 1 | 2.9563 |
| | | 2 | 1.7326 |

Table 14. Log transformed least-squares means of *Leptodora* abundance within each habitat type, depth, and diurnal period for sample period 6.

| Habitat type | Depth | Diurnal period | log LSMean |
|---|---|---|---|
| Riverine | 0.25 | 1 | 0.0000 |
| | | 2 | 0.0000 |
| | 1.25 | 1 | 0.0000 |
| | | 2 | 0.0000 |
| Transitional | 0.25 | 1 | 0.0000 |
| | | 2 | 0.0913 |
| | 1.25 | 1 | 0.0203 |
| | | 2 | 0.1658 |
| | 2.25 | 1 | 0.0000 |
| | | 2 | 0.2975 |
| | 3.25 | 1 | 0.1728 |
| | | 2 | 0.5114 |
| Reservoir | 0.25 | 1 | 0.5379 |
| | | 2 | 0.3775 |
| | 1.25 | 1 | 1.1067 |
| | | 2 | 0.2351 |
| | 2.25 | 1 | 0.5205 |
| | | 2 | 0.1617 |
| | 3.25 | 1 | 0.4753 |
| | | 2 | 0.3995 |
| | 4.25 | 1 | 0.4767 |
| | | 2 | 0.3991 |

Figure 15. Chi-square contingency table for observed and expected weight and body length values for male and female paddlefish.

| | Large Classes | | Smaller Classes | | |
|---|---|---|---|---|---|
| **Female Weight** | **Observed** | **Expected** | **Observed** | **Expected** | **Total** |
| 77-78 | 18 | 5.3 | 55 | 67.7 | 73 |
| 92-93 | 13 | 12.8 | 162 | 162.2 | 175 |
| 00,02 | 3 | 15.8 | 213 | 200.1 | 216 |
| **Total** | 34 | 33.9 | 430 | 430 | 464 |

| **Male Weight** | **Observed** | **Expected** | **Observed** | **Expected** | **Total** |
|---|---|---|---|---|---|
| 77-78 | 14 | 5.14 | 60 | 68.8 | 74 |
| 92-93 | 14 | 14.6 | 197 | 196.4 | 211 |
| 00,02 | 11 | 19.2 | 266 | 257.7 | 277 |
| **Total** | 39 | 38.94 | 523 | 522.9 | 562 |

| **Female Body Length** | **Observed** | **Expected** | **Observed** | **Expected** | **Total** |
|---|---|---|---|---|---|
| 77-78 | 19 | 15.1 | 50 | 53.8 | 69 |
| 92-93 | 47 | 35.8 | 116 | 127.2 | 163 |
| 00,02 | 29 | 43.9 | 171 | 156 | 200 |
| **Total** | 95 | 94.8 | 337 | 337 | 432 |

| **Male Body Length** | **Observed** | **Expected** | **Observed** | **Expected** | **Total** |
|---|---|---|---|---|---|
| 77-78 | 9 | 7 | 61 | 62.9 | 70 |
| 92-93 | 28 | 19.3 | 164 | 172.7 | 192 |
| 00,02 | 15 | 25.6 | 241 | 230.3 | 256 |
| **Total** | 52 | 51.9 | 466 | 465.9 | 518 |

**Final Chi-square value:**

| | |
|---|---|
| Female Weight | 41.6 |
| Male Weight | 20.2 |
| Female Body Length | 12.3 |
| Male Body Length | 8.9 |

Chi-square $p < 0.05$ value = 11.07

Table 16. ANOVA table for changes in water temperature and turbidity within habitat types and habitat types within sample periods.

| Variable | Source | *df* | Mean Square | *F* | Pr < *F* |
|---|---|---|---|---|---|
| Water temperature | Habitat type | 2 | 37.243 | 38.2 | <.0001 |
| | Sample Period | 5 | 592.499 | 607.8 | <.0001 |
| | Habitat type (Sample Period) | 10 | 63.985 | 65.64 | <.0001 |
| Turbidity | Habitat type | 2 | 427924.6 | 15.08 | <.0001 |
| | Sample Period | 5 | 750269.3 | 26.44 | <.0001 |
| | Habitat type (Sample Period) | 10 | 286810.3 | 10.11 | <.0001 |