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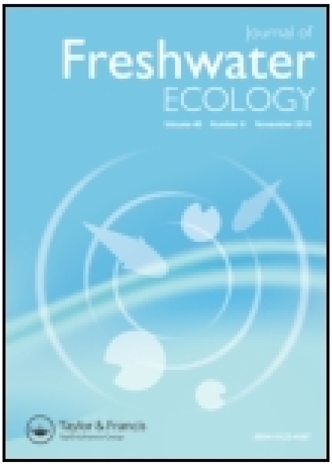

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Distribution, abundance, and vertical migrations of *Leptodora kindtii* in a mainstem Missouri River reservoir, Montana, USA

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Leptodora kindtii, a large, mobile, predaceous cladoceran zooplankter has been shown to make diel vertical migrations in some localities. *L. kindtii* were sampled in summer in the headwaters of Fort Peck Reservoir, Montana, USA, to assess and compare their day/night abundance in three habitat types (riverine, transitional, and reservoir), to determine if *L. kindtii* mean size and abundance differed vertically and horizontally, and to determine if their distribution differed under different turbidities and water temperatures. *L. kindtii* were sampled in six periods from 22 July to 10 September 2002 using a bongo net towed at set depths. Abundance displayed a patchy, highly variable distribution among periods and habitat types and among samples within periods and habitat types. Greatest abundances were found within the reservoir habitat type. Diurnal phase was not significantly related to *L. kindtii* abundance at depth. Highest daytime abundances were found at 1.25 m or deeper for five of six sample periods. Highest nighttime abundances were found at 1.25 m or deeper in three of the six sample periods. Significant interaction was found between diurnal phase and depth in five of six periods. In general, higher *L. kindtii* abundance was observed in association with higher water temperatures and lower turbidities.

Keywords: zooplankton; *Leptodora*; vertical migration; cladocera

Introduction

Diel vertical migration (DVM), a common and important migration pattern in many animal taxa (Bollens 1996; Wetzel 2001), has been observed in numerous zooplankton species in lakes and reservoirs (Levy 1991; Loose & Dawidowicz 1994; Ghan et al. 1998; De Robertis & Jaffe 2000). DVM is commonly undertaken to increase energy gain from feeding while decreasing the probability of death from predation (Gabriel & Thomas 1988; Bollens 1996; Ghan et al. 1998). In lakes, zooplankton DVM typically consists of ascent toward the surface at dusk and descent at dawn, although reversed DVM has also been reported (Levy 1990; Vijverberg 1991). Zooplankton may migrate to deeper, less productive waters during the day, avoiding visual predators, and ascend to food-rich surface waters to feed at night. The distance of zooplankton DVM can range from a few meters to more than 100 m (Levy 1991; Stewart & Sutherland 1993).

Leptodora kindtii (hereafter *Leptodora*), a large (6–12 mm), mobile predaceous cladoceran (Browman et al. 1989) has been shown to undertake modest DVM in lentic habitats (Costa & Cummins 1969; Vijverberg 1991; Stewart & Sutherland 1993; Liu et al. 2002). DVM ranges displayed by *Leptodora* are often less than 10 m (Stewart &

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Sutherland 1993; Liu & Hu 2001). *Leptodora* are voracious, tactile predators on other zooplankton, including *Diaphanosoma, Bosmina, Daphnia*, and *Ceriodaphnia* (Browman et al. 1989; Herzig & Auer 1990). Six pairs of legs anterior to the mouth enclose encountered prey like a basket and pull them towards the oral parts (Sebestyen 1931). *Leptodora* predation can significantly affect prey abundance and production. In Canyon Ferry Reservoir, Montana, for example, the average predation rate of *Leptodora* on *Daphnia* was 33% of the net *Daphnia* production (Wright 1965).

Leptodora is also an important food source for many reservoir fish species including yellow perch, *Perca flavescens*, crappie, *Pomoxis spp.*, and lake chub, *Couesius plumbeus* (Costa & Cummins 1969; Serns & Hoff 1984). Of particular interest is the relation between the abundance and distribution of *Leptodora* in Fort Peck Reservoir and the feeding ecology of paddlefish *Polyodon spathula*, a large, ancient zooplanktivorous Acipenseriform fish. *Leptodora* is the preferred food of age-0 paddlefish in Fort Peck Reservoir (Kozfkay & Scarnecchia 2002). The annual relative abundance of age-0 paddlefish (an index of reproductive success and year class strength) is based on visual counts of age-0 fish as they feed near the surface. DVM by their primary prey, *Leptodora*, would tend to bias these counts.

Several factors, including temperature and turbidity, may influence the abundance of *Leptodora* as well as its tendency to undertake DVM. Cummins et al. (1969) reported that *Leptodora* was temperature-limited at 14 °C and disappeared at lower temperatures. Garton et al. (1990) found *Leptodora* abundance to decline in western Lake Erie in water temperatures ranging from 5 to 15 °C in the fall of the year. Zettler and Carter (1986) found that zooplankton were displaced upward with increasing turbidity in a turbid Ontario lake. However, *Leptodora* were more abundant in higher turbidities whereas smaller cladocerans and copepods were more abundant in lower turbidities.

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

Methods

Fort Peck Reservoir, located in central Montana (USA), is the uppermost Pick-Sloan impoundment on the Missouri River. Completed in 1938, the reservoir stores 23.4 billion m^3 of water, inundates an area of 100,767 ha, and impounds the runoff of 149,000 km^2 of the Missouri River basin (US Army Corps of Engineers 1991).

The study was conducted near the reservoir headwaters from the river/reservoir interface at river kilometer (rkm) 2997 down reservoir to slightly above Mickus Bottom (rkm 2988) within the Charles M. Russell National Wildlife Refuge (Figure 1). The study area included the river–reservoir transitional zone as well as more lentic habitat. The study area was shallow (<1–7 m), turbid (Secchi depth <1 m), had negligible velocity (<1 m/s), and had a soft, fine sediment bottom. Average reservoir width was approximately 1 km.

The reservoir headwaters were classified into riverine, transitional, and reservoir habitat types. 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

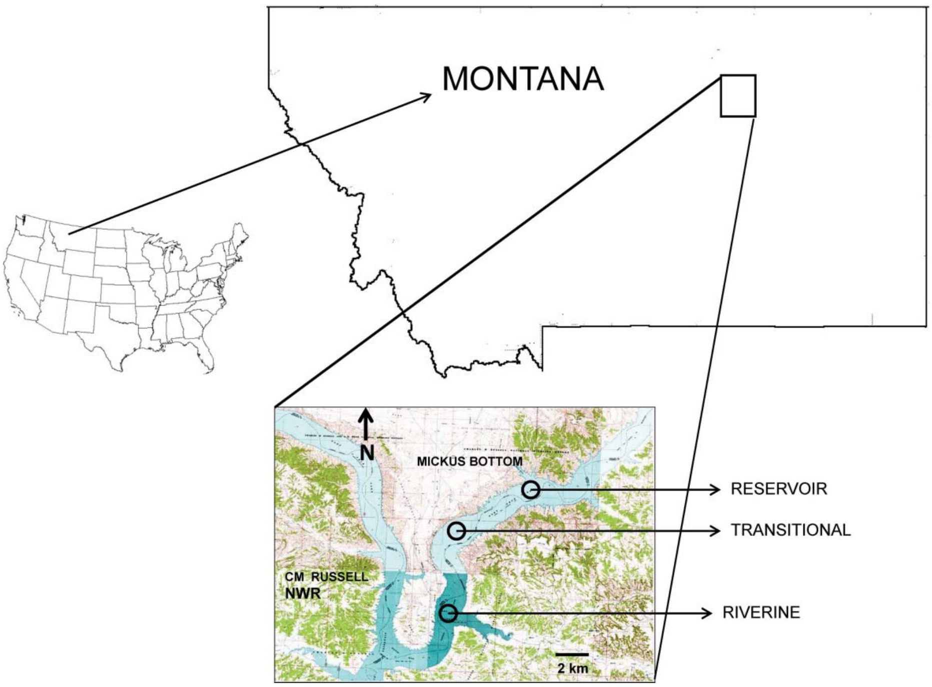

Figure 1. A map of the study area. Circular symbols represent locations of the sampling stations.

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 section of reservoir with 1 km separating each section longitudinally. Three waypoints spaced one-quarter, one-half, and three-quarters of the distance across the reservoir were established at the uppermost boundary of each habitat type. Two additional series of three waypoints were placed 0.75 and 1.5 km below the uppermost waypoints, resulting in nine waypoints per habitat type.

Sampling occurred during six periods from 22 July 2002 to 10 September 2002. For each of the six periods (P1, 22–29 July; P2, 1–3 August; P3, 11–15 August; P4, 21–22 August; P5, 2–4 September; P6, 9–10 September), three waypoints were chosen using a random numbers chart from the nine possible waypoints within each habitat type. At each waypoint, samples were taken both by day (1000–1700 h) and by night (2000–0100 h).

Fixed depth tows were conducted at waypoints using a 500-micron Bongo net (48.75 cm gape diameter) lowered into the water with a winch. In order to assess vertical distribution and abundance of *Leptodora*, tows were taken in 1 m increments from the surface of the water to within 1 m of the bottom. The net sampled 0.5 m of water at each depth, so the center of the gape was recorded as the sampled depth 0.25 (surface), 1.25 (1–1.5 m) and so on. Sampling always occurred from the surface to the bottom at these 1-m increments, although maximum depths for the riverine zone were typically 2.25 m, for the transitional zone 3.35 m, and for the reservoir zone 5.25 m. 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. After 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 was negligible. Three replicates were collected per depth. Zooplankton samples were preserved in labeled jars in 90% ethanol.

Zooplankton samples were analyzed to estimate the abundance and the average length of *Leptodora*. Contents of each sample jar were rinsed and diluted as necessary into a beaker and stirred with a Hensen-Stemple pipette. Three 2-ml samples were drawn with the pipette and placed into a counting tray. All *Leptodora* were counted from each tray with the aid of a dissecting microscope. This procedure was repeated three times per tow. The average *Leptodora* count of the three subsamples was used to obtain an overall mean count within the tow. Dilution volume of the sample in the beaker was divided by 6 ml to obtain 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:

$$V = (3.14 \times (N)^2 \times D)/4$$

and

$$D = (F \times R)/Q,$$

where $N =$ net diameter (48.75 cm), $D =$ distance of tow, $F =$ difference in flowmeter counts, $R =$ rotor constant (26,873), and $Q =$ set denominator (999999).

In order to compare lengths of *Leptodora* found at various depths, lengths of the first 10 individuals observed within each tow were measured using an ocular micrometer in the eyepiece of the dissecting microscope. The 10 lengths were recorded and averaged for each tow to obtain a mean length for each tow. In samples where only 10 or fewer individuals were found, all individuals present were recorded and measured to estimate abundance and mean length.

Total depth, water temperature, and turbidity were recorded at each waypoint during each 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 0.1 m with a sonar unit. Water temperature was recorded to the nearest 0.1 °C (YSI 30, YSI, Inc., http://ysi.com). Water samples for turbidity estimates were obtained with a Van Dorn water sampler. Turbidity (in Nephelometric Turbidity Units, NTU) was measured to the nearest 0.1 NTU (portable turbidimeter, Hach Corp., http://hach.com).

Analysis of Variance (ANOVA) was used to test for differences in day/night abundances of *Leptodora* and for length differences of *Leptodora* among sampling strata. Preliminary analysis indicated a positive correlation between the mean and standard deviation in *Leptodora* abundance for the six periods (Table 1). All abundance data were, therefore, transformed to natural logs and all statistical tests on abundance data were conducted on log-transformed data. 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 abundance. In addition to the overall model, separate models were run for each of the six sample periods because of variation among the periods.

Table 1. Mean *Leptodora* abundance (organisms/m^3), number of samples (N), standard deviation (SD), and standard error (SE) during each sample period in 2002. In the least significant (LS) means column, periods with the same letter were not significantly different.

Sample period	Mean	N	SD	SE	LS means
1 (22 July–29 July)	51.03	207	75.71	5.26	A
2 (1 August–3 August)	22.6	204	33.31	2.33	B
3 (11 August–15 August)	0.561	180	1.74	0.13	D
4 (21 August–22 August)	7.83	198	19.13	1.36	C
5 (2 September–4 September)	15.12	198	19.22	1.37	B
6 (9 September–10 September)	0.468	174	0.904	0.068	D

A least-squares means slice procedure in SAS was used to test for significant differences in mean abundance at different depths and different diurnal periods by habitat type (http://support.sas.com/documentation/; Version 9.2). The procedure specifies effects within which to test for differences between least squares and mean effects. The relations between abundance and turbidity and water temperature were also examined collectively over all six periods as well as during each 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 by day and night were investigated with ANOVA using means of the 10 recorded lengths for each of the tows. Length was the response variable and depth of tow, diurnal period, and habitat types were main effects. The least-squares means slice procedure was used to test for significant differences in mean lengths at different depths and diurnal periods within each habitat type (SAS Institute).

Temporal differences in water temperature, turbidity, and *Leptodora* abundance were plotted, and ANOVA used to test for differences in both water temperature and turbidity among habitat types. Results were used to determine if abundance varied longitudinally in the study area in relation to water temperature and turbidity.

Results

Leptodora abundance was patchy and highly variable by period, by habitat type, and by waypoint. Significant differences were found by period (ANOVA; $p < 0.0001$, Table 1 and 2). Significantly greater abundance was found during the first period (22–29 July) than in any later period (Table 1). No difference in abundance was found between the second period (1–3 August) and fifth period (2–4 September), nor between the third period (1–15 August) and sixth period (9–10 September, Table 1). Significant differences in abundance were also found by habitat type ($p < 0.0001$; Table 2). Overall abundance was highest within the reservoir habitat type (Figure 2). Abundance in five of six periods (1, 2, 4, 5, and 6) was higher within the reservoir habitat type than in the riverine and transitional habitat types. In addition, significant differences in abundance existed by waypoint within each of the separate periods ($p < 0.05$). Even the waypoints within a habitat type had highly significant overall differences in abundance (ANOVA; $p < 0.0001$, Table 2).

No consistent pattern of *Leptodora* abundance was found at depth by day and night. Abundance was not influenced by diurnal phase (day/night) within the overall model (ANOVA; $p = 0.9568$, Table 2). However, the interaction between diurnal phase and

Table 2. Overall ANOVA table of *Leptodora* abundances, 2002. Significant *p*-values are in bold.

Source	*df*	Mean square	*F*	*p*-value
Sample period	5	387.8	275.5	<**0.0001**
Habitat type	2	270.1	324.7	<**0.0001**
Depth	5	30.94	3.11	**0.0086**
Diurnal period	1	0.002	0.49	0.9568
Habitat type × depth	5	10.01	3.24	**0.0066**
Habitat type × diurnal	2	13.52	10.94	<**0.0001**
Depth × diurnal	5	11.3	3.67	**0.0027**
Habitat type × depth × diurnal	5	6.72	2.18	0.0544
Water temperature	1	4.65	7.53	**0.0062**
Turbidity	1	0.99	1.6	0.2058
Water temperature × turbidity	1	0.974	1.57	0.2109
Waypoint (Habitat type)	22	365.6	26.23	<**0.0001**
Error	1154	0.618		

depth was highly significant (ANOVA; $p = 0.0027$, Table 2). Significant interaction was found between diurnal phase and depth in five of the six periods.

No discernable difference in abundance at depth by diurnal phase was found within the transitional and reservoir habitat types. For example, within the transitional habitat type, three periods had significantly higher abundances of *Leptodora* at the surface by night than by day (Figure 3(a), 3(b) and 3(e)). Higher abundances were often found in deeper strata both by day and by night. For instance, during Periods 4, 5, and 6 higher abundances by night were found within deeper strata (3.25, 1.25, and 3.25 m) than at the surface (Figure 3(d)–(f)). In addition, by day, higher abundances were often observed at

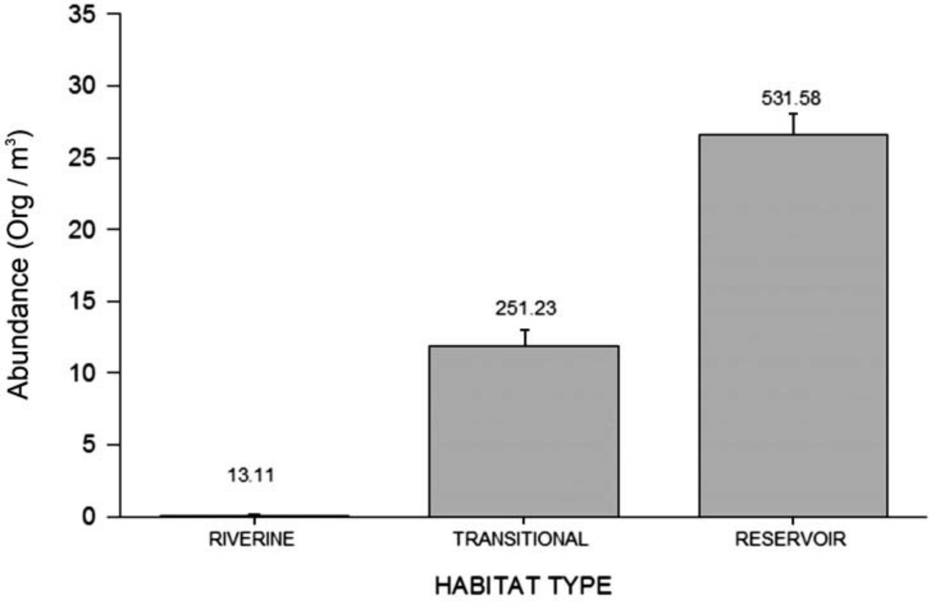

Figure 2. Mean *Leptodora* abundance within each habitat type of the headwaters of Fort Peck Reservoir, 22 July–10 September 2002.

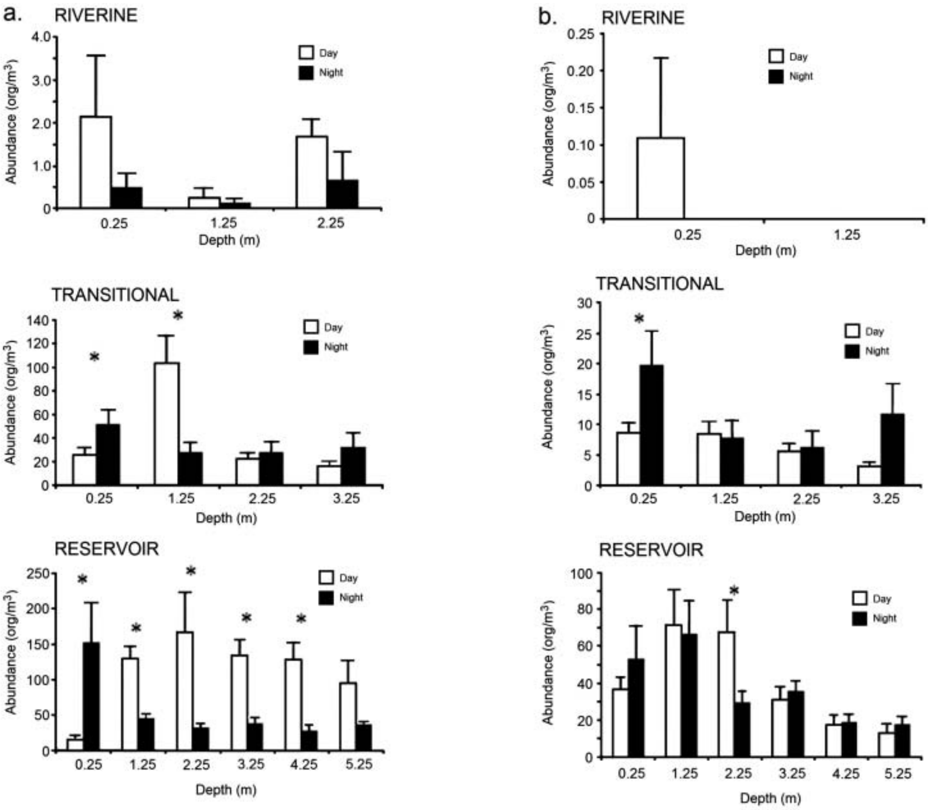

Figure 3. Mean and standard error of *Leptodora* abundance (not log transformed) at depths throughout the headwaters of Fort Peck Reservoir during (a) Period 1 (22–29 July), (b) Period 2 (1 August–3 August), (c) Period 3 (11 August–15 August), (d) Period 4 (21 August–22 August), (e) Period 5 (2 September–4 September), and (f) Period 6 (9 September–10 September), 2002. An asterisk (*) indicates a significant ($p \leq 0.05$) difference between day and night means at the specified depth.

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 by day (Figure 3(b) and 3(c)). 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 periods (Figure 3(a), 3(d) and 3(e)). However, during four periods (2, 3, 5, and 6) higher abundances by night were found in deeper strata rather than at the surface (Figure 3(b), 3(c), 3(e) and 3(f)). As with the transitional habitat type, higher abundances by day were found in deeper strata (1.25–4.25 m) except during Period 3 where higher abundances were found at the surface (Figure 3(c)).

Within the riverine habitat type, only 11% of tows contained *Leptodora* and abundance within those tows was low (<1 organisms m^3). No significant differences in abundance by diurnal phase or depth were detected in the riverine habitat type.

Within the transitional habitat type, mean lengths recorded by night were significantly higher than by day at all depths during the fifth period (Figure 4(e)). For all periods,

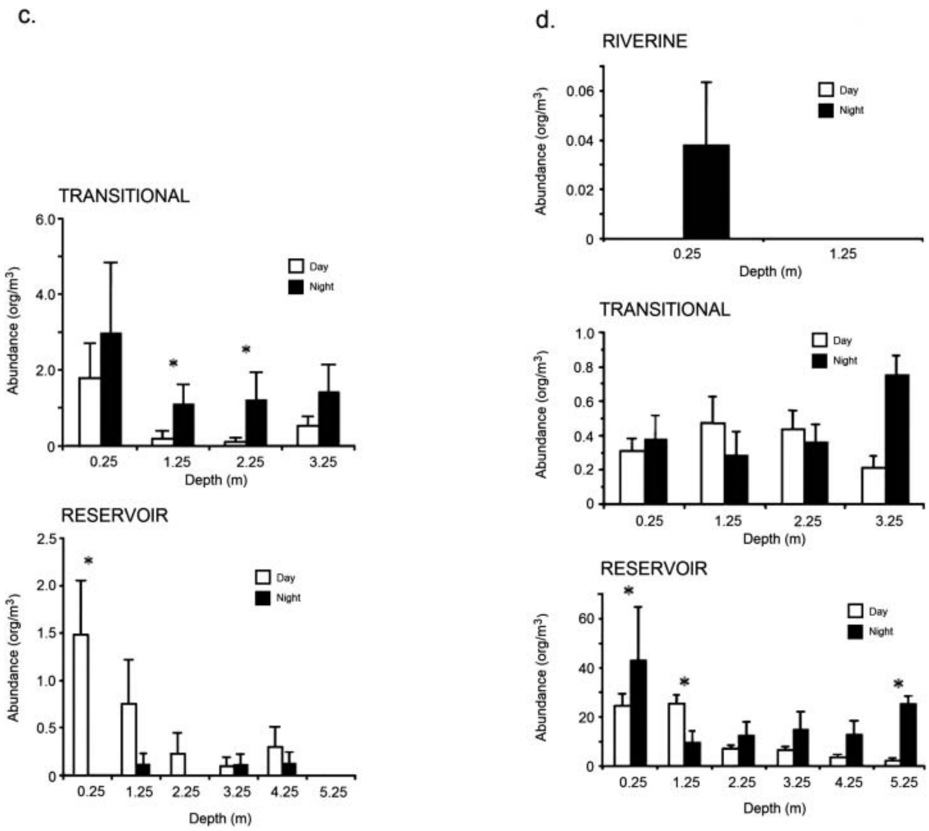

Figure 3. (*Continued*)

mean lengths by day were higher in the deeper strata (1.25–3.25 m) than at the surface (Figure 4).

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 at the surface by night for five of the six periods (Figure 4(a), 4(b), 4(d), 4(e) and 4(f)); however, in all but one instance, higher mean lengths by night were recorded in deeper strata during that period. During day and night sampling throughout the periods, maximum size of *Leptodora* was greater in deeper strata (Figure 4). Too few *Leptodora* were captured in the riverine habitat type for meaningful length comparisons to be made.

Water temperatures in all three habitat types exhibited substantial fluctuation throughout the study. Water temperature fluctuated and was positively related to abundance by sample period (Figure 5). Water temperature among habitat types was shown to differ significantly (ANOVA, $p < 0.0001$, Table 3). In addition, water temperature among habitat types was significantly different within periods (ANOVA, $p < 0.0001$, Table 3). When mean water temperatures within the three habitat types were examined, higher mean water temperatures were found within the reservoir habitat type during Periods 1, 2, 3, and 6 and the riverine habitat type during Periods 4 and 5.

Mean turbidity by sample period and mean *Leptodora* abundance fluctuated inversely (Figure 6). Overall turbidity for the entire study differed significantly among habitat types

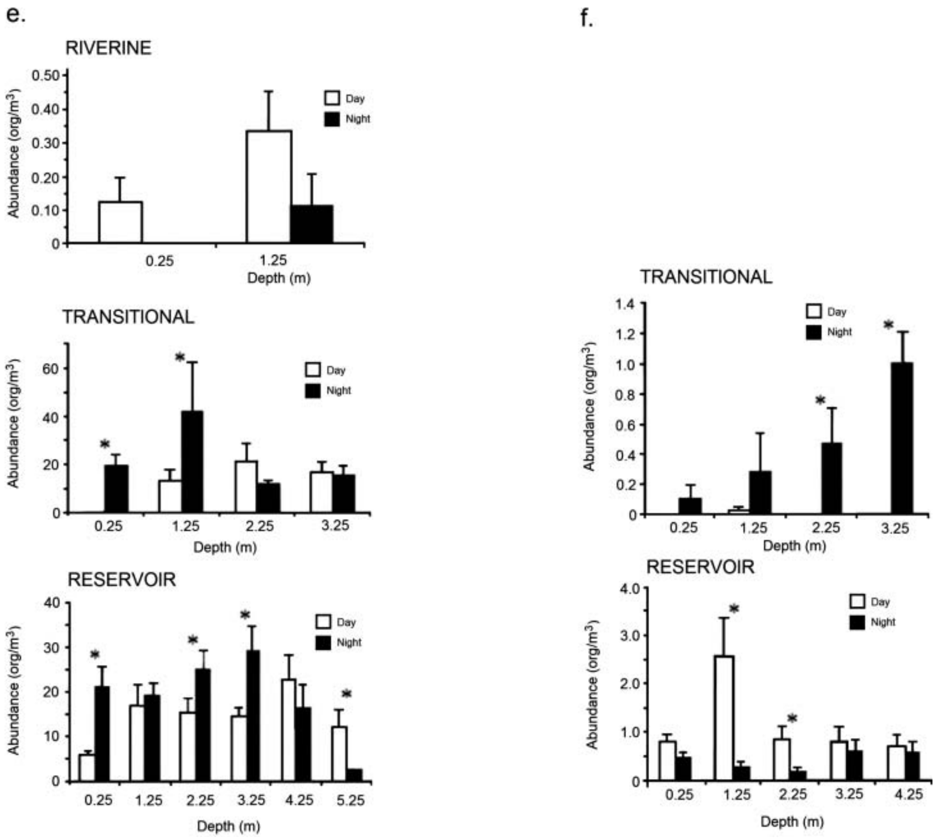

Figure 3. (*Continued*)

(ANOVA, $p < 0.0001$, Table 3). In addition, turbidity within habitat types was significantly different within periods (ANOVA, $p < 0.0001$, Table 3). Among habitat types, the reservoir habitat type consistently had the lowest mean turbidity for all periods. Greater abundance of *Leptodora* was, thus, typically associated with less turbid waters.

Discussion

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 periods within both the transitional and reservoir habitat types, even higher abundances were often found in deeper strata. The significantly 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, indicate 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 in any systematic way.

The absence or near lack of DVM in *Leptodora* in the Fort Peck Reservoir headwaters is consistent with several studies and contrary to several others. For example, Schindler

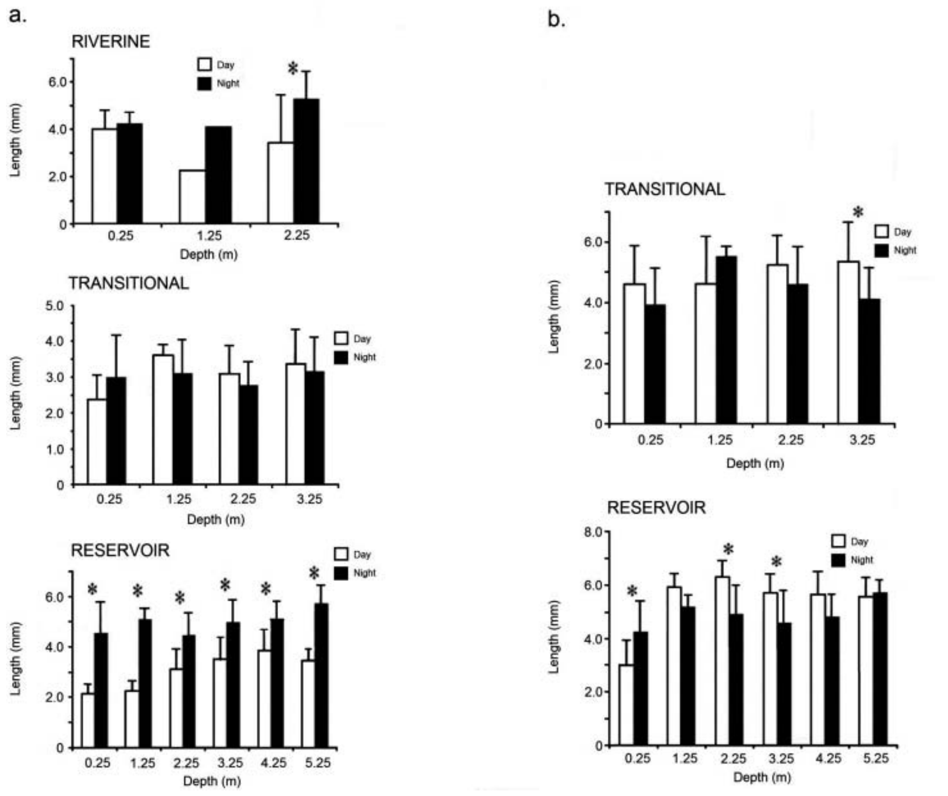

Figure 4. Mean and standard error of *Leptodora* length at depths throughout the headwaters of Fort Peck Reservoir during P1, 22–29 July; P2, 1–3 August; P3, 11–15 August; P4, 21–22 August; P5, 2–4 September; and P6, 9–10 September. An asterisk (*) indicates a significant difference between day and night means at the specified depth.

and Noven (1971) found that *Leptodora* underwent no DVM in an experimental lake in northwestern Ontario. Individuals remained at 4 m day and night. Similarly, Barbiero et al. (2000) found no discernable pattern of DVM in *Leptodora* in three of the Great Lakes. They speculated that the transparent body of *Leptodora* provided adequate protection from sight-feeding predators, making DVM unnecessary (Barbiero et al. 2000). Stewart and Sutherland (1993) found *Leptodora* to undergo a modest ascent towards the surface around sunset in a New York lake. However, as in this study, they found *Leptodora* abundances were often higher at greater depths than at the surface, even at night. In contrast, Vijverberg (1991) found a number of different DVM patterns in *Leptodora* in shallow (mean depth 1.5 m) Tjeukemeer Lake, Netherlands depending on size-class and time period. During some periods, some sizes displayed DVM or reversed DVM patterns. During other periods, however, he found no pattern of DVM regardless of size. He suggested that DVM within a *Leptodora* population was a dynamic rather than a fixed behavioral trait, mediated by predator avoidance.

Results of this study indicate that *Leptodora* abundance was patchy and highly variable throughout the headwaters of Fort Peck Reservoir. Although abundance increased in the downstream direction from the riverine to the reservoir habitat types, waypoints within a given habitat type often displayed significant differences in abundance,

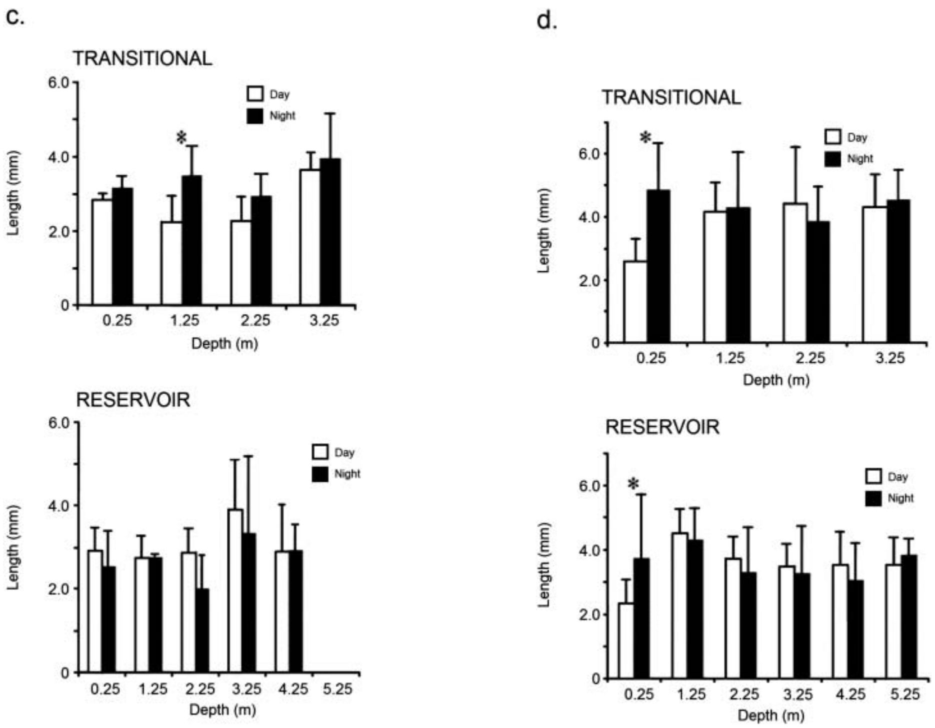

Figure 4. (*Continued*)

indicating an extremely patchy distribution at a small scale both spatially and temporally. Numerous studies on other waters have reported similar patches or swarms with other species of zooplankton (Colebrook 1960; Davies 1985; Verreth 1990; Kvam & Kleiven 1995). In his work on Windermere Lake, Scotland, Colebrook (1960) found swarms of the zooplankton *Daphnia* containing much higher abundances than the surrounding water. He cited wind driven turbulence or a social activity of some kind as the possible causes of the patchiness. Verreth (1990) found that *Daphnia* and *Bosmina* were concentrated heavily in the pelagic zone of a pond, and speculated that wind-induced currents within the pond may have displaced organisms on the down-wind side of the pond. Kvam and Kleiven (1995) found swarms of *Daphnia* with densities up to 4000 organisms/liter in Myravatn. They believed the formation of the swarms was a predator avoidance mechanism in response to the predaceous invertebrate *Chaoborus* (Kvam & 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 & 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).

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 found down-reservoir during the early part of the year. They attributed the higher densities to decreasing suspended sediment load as one moved down-reservoir. A similar gradient in suspended sediment, as indicated by turbidity, was

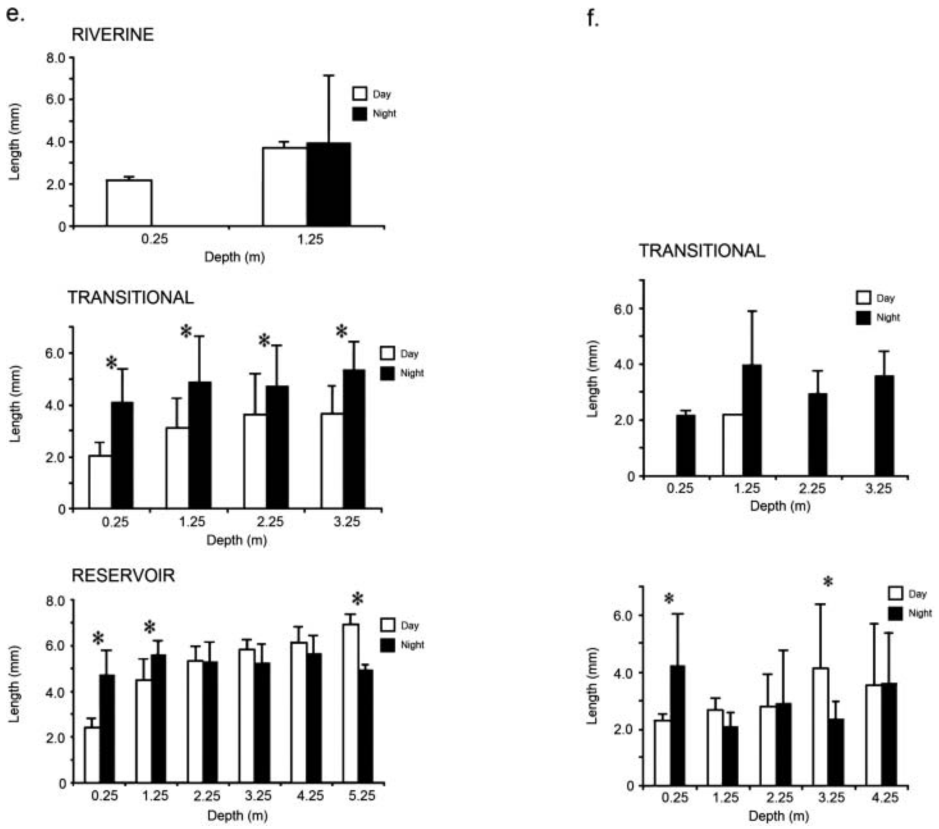

Figure 4. (*Continued*)

found in this study. Suspended sediment has been shown to interfere with *Daphnia* filter feeding, which in turn would affect *Leptodora* (Johnson et al. 1996). During periods of high suspended sediment (e.g. 11–14 August, Period 3) *Daphnia* may not be able to feed efficiently and forage for *Leptodora* may also be scarce.

The greater *Leptodora* abundance associated with lower turbidities in five of the six periods of this study is not, however, 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. Results from this 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 the reservoir. Perhaps in this study, moderate turbidities within the more lentic, reservoir habitat type provided *Leptodora* with adequate protection from sight-feeding predators and still allowed main prey items such as *Daphnia* to feed effectively (Johnson et al. 1996).

The peak *Leptodora* abundances observed during the first period occurred about a month after nutrients had been transported into the reservoir by high spring run-off. After the high inflows present during the third period, a secondary peak of *Leptodora*

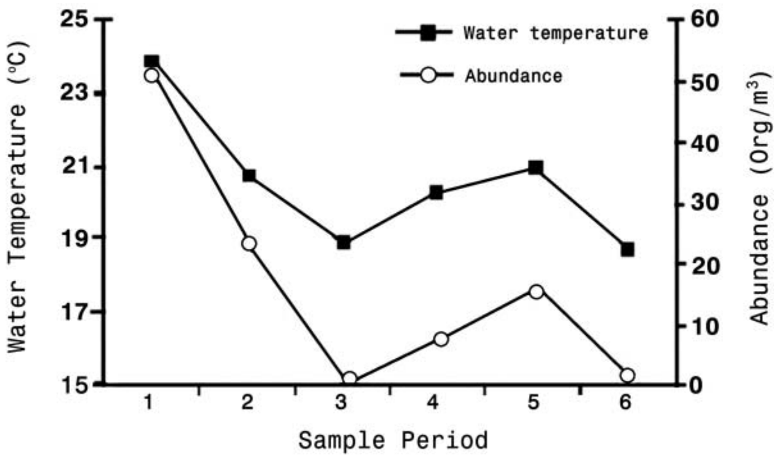

Figure 5. Mean water temperature and abundance of *Leptodora* within the headwaters of Fort Peck Reservoir, 22 July–10 September 2002.

abundance occurred in periods five and six. Abundances never reached those of the first sample period, however. The great 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 (Watson 1976; Wiedenheft 1984; Koapaha 1989; Clarke & Bennett 2003). When the suspended sediments begin to settle, the influx of nutrients associated with the inflow causes an increase in primary production which typically rapidly regenerates the abundance of consumers (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. To obtain a more complete description of fluctuations in the abundance of *Leptodora*, however, sampling should be conducted throughout the year.

The lowest water temperatures present in this study reached levels found to be a limiting factor for *Leptodora* in other studies. *Leptodora* was reported as being temperature-limited at 14 °C, by Cummins et al. (1969) and to have declined in abundance in water temperatures ranging from 5 to 15 °C in Western Lake Erie by Garton et al. (1990). Water temperatures in Fort Peck Reservoir were lowest during Periods 3 (15.9 °C) and 6 (15.7 °C), and were associated with the lowest overall abundances found. It is unknown

Table 3. ANOVA table for changes in water temperature and turbidity within habitat types and habitat types within sample periods. Significant *p*-values are in bold.

Variable	Source	*df*	Mean square	*F*	*p*-value
Water temperature	Habitat type	2	37.24	38.2	<**0.0001**
	Sample period	5	592.5	607.8	<**0.0001**
	Habitat type (Sample period)	10	63.98	65.64	<**0.0001**
Turbidity	Habitat type	2	427,924	15.08	<**0.0001**
	Sample period	5	750,269	26.44	<**0.0001**
	Habitat type (Sample period)	10	286,810	10.11	<**0.0001**

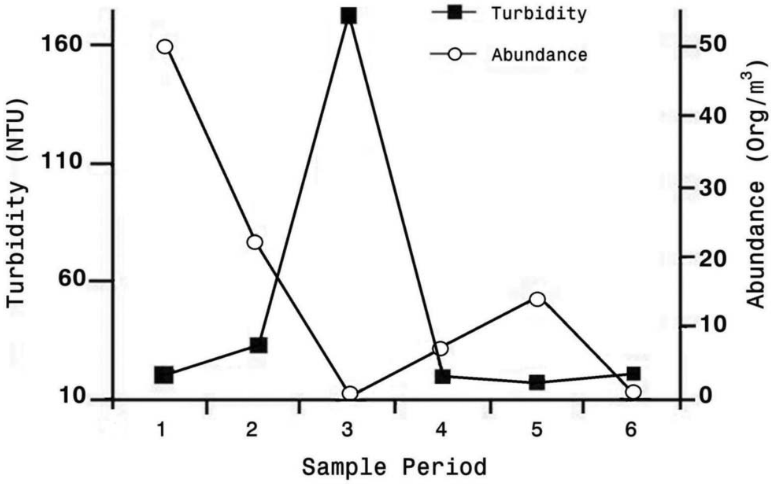

Figure 6. Mean turbidity and abundance of *Leptodora* in the headwaters of Fort Peck Reservoir, 22 July–10 September 2002.

if individuals may have migrated to warmer water temperatures down-reservoir or became increasingly dormant in colder water.

To fully understand *Leptodora* ecology in the headwaters of Fort Peck Reservoir, it will be necessary to extend this sampling protocol throughout different seasons and years under different reservoir conditions, including depth, temperature, and turbidity. *Leptodora* abundance and movements may differ according to water levels, spring runoff inflows, presence, absence or relative abundance of species zooplanktivorous fish, and other environmental changes not observed or quantified in this study.

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