Food web consequences of size-based predation and vertical migration of an invertebrate predator (*Leptodora kindtii*)

R. J. Vogt, a B. Matthews, a T. P. Cobb, b M. D. Graham, c and P. R. Leavitt

Limnology Laboratory, Department of Biology, University of Regina, Regina, Saskatchewan, Canada

Abstract

In an intensive study of the vertical and horizontal distribution of zooplankton in a eutrophic lake (Katepwa Lake), we found that only adult *Leptodora kindtii* (> 5 mm in body size) exhibited diel vertical migration (DVM), whereas juvenile *Leptodora* (< 5 mm) and other zooplankton species did not. Even though a longitudinal survey of five lakes (1994–2004) indicated that variation in *Leptodora* density was correlated with several indicators of habitat use (e.g., water temperature) and resource availability (e.g., zooplankton abundance), feeding experiments performed in both lit and unlit conditions demonstrated that a vertebrate predator (perch) strongly reduced *Leptodora* abundances under all conditions and always preferentially selected large-bodied individuals. Collectively, this evidence suggests that the migratory behavior of large *Leptodora* is consistent with an antipredator defense strategy. To estimate the ecological significance of *Leptodora* DVM behavior, we modeled how predation rates on different zooplankton taxa differed between day and night in Katepwa Lake. We found that *Leptodora* had as much as five-fold higher prey-specific predation rates at night, particularly for intermediate-sized prey. We conclude that ignoring the habitat use, size-structure, and vertical migration behavior of *Leptodora* could considerably underestimate the significance of invertebrate predation in lake food webs, particularly in eutrophic lakes where *Leptodora* can coexist at high densities with planktivorous fish.

*Leptodora kindtii* (hereafter, *Leptodora*) is a large invertebrate predator (2–14 mm) that is widely distributed among lakes of the Northern Hemisphere, including North America, Europe, and Asia (Andrews 1948; Carter et al. 1980; McNaught 1993a). In a survey of 696 glaciated lakes in eastern North America it was among the 10 most common species (*N*species = 48), occurring in 45% of lakes (Carter et al. 1980). *Leptodora* is a voracious predator of small- to medium-sized zooplankton (Andrews 1948; Herzig and Auer 1990) and is thought to have strong effects on the abundance (Hall 1964; Herzig 1995; Uusitalo et al. 2003), seasonality (Costa and Cummins 1969; Herzig 1995), and composition of zooplankton communities (Lane 1979; Yan et al. 2002; McNaught et al. 2004). Although *Leptodora* densities are influenced by macro-invertebrate predators such as *Bythotrephes* in boreal lakes (Weisz and Yan 2011), this taxon remains an important predator in productive European and North American lakes (Enz et al. 2001; Palmer et al. 2001) where *Bythotrephes* abundance has declined because of eutrophication (Therriault et al. 2001). Despite *Leptodora*’s wide distribution and potentially strong effects on lake food webs, very little is known about what factors explain variation in *Leptodora* density, habitat use, feeding behavior, and size structure.

The overall effect of *Leptodora* predation on lake zooplankton communities depends partly on its ability to avoid predation by planktivorous fish. *Leptodora* is common prey for many planktivorous fish (Herzig 1995) and there is some evidence for positive size-selectivity of fish on *Leptodora* (Liu and Herzig 1996; Branstrator and Holl 2000). Compared with other cladocerans, *Leptodora* have exceptionally high body transparency (Nilsson et al. 1983) and low ratios of eye area to body size (Liu and Herzig 1996; Branstrator and Holl 2000), both of which are plausible adaptations to predation by planktivorous fish (Liu and Herzig 1996; Branstrator and Holl 2000). Previous studies have also suggested that *Leptodora* exhibits diel vertical migration (DVM), presumably in response to planktivorous fish predation (Vijverberg 1991). DVM behavior may be a critical defensive strategy for large-bodied *Leptodora* (adult > 5 mm in body size) to avoid planktivorous fish that forage visually during the day (Branstrator and Holl 2000) or that use mechanoreception to forage in turbid or low-light conditions (Hairston et al. 1982; Liu and Uiblein 1996). Alternatively, *Leptodora* could migrate to track the migratory movements of their zooplankton prey or to optimize digestive processes through regulation of thermal habitat (Enright 1977). At present, it is unclear how *Leptodora* respond to variation in predation risk, food availability, and temperature regime, and, as a result, both the underlying causes and the ecological consequences of this vertical migration behavior remain uncertain.

In previous studies, the importance of *Leptodora* predation has been estimated by daytime surveys of its abundance, size structure, and spatial distribution in surface layers of lakes (Lunte and Luecke 1990; Branstrator and Lehman 1991). Because of the low biomass of *Leptodora* in surface waters during the day (typically < 1 m⁻³), the
importance of predation by *Leptodora* on zooplankton communities is often thought to be trivial relative to that of vertebrate planktivores (Lunte and Luecke 1990). Such conclusions are misleading, however, because mass- and metabolism-specific predation rates are often much higher for invertebrates than vertebrates (Yodzis and Innis 1992; Shurin and Seabloom 2005), meaning that small underestimates of the abundance and size structure of invertebrate predators could lead to considerable underestimates of their ecological importance (Blumenshine and Hambright 2003). Indeed, nighttime sampling of other invertebrate predators, such as *Chaoborus*, has revealed strong effects of invertebrate predation on zooplankton biomass (Ramcharan et al. 2001).

In this study, we used a mix of comparative, experimental, and modeling approaches to investigate factors influencing variation in the abundance and size structure of *Leptodora* populations, and the ecological effects of *Leptodora* predation on lake zooplankton communities. We tested which environmental conditions best explained variation in *Leptodora* density by using an 11 yr survey of five lakes of the Northern Great Plains (Leavitt et al. 2006). We further quantified the vertical and horizontal distribution of *Leptodora* in the water column of eutrophic Katepwa Lake in order to examine variation in the dynamics of *Leptodora* DVM behavior in relation to the migration behavior of other zooplankton species. In addition, we conducted a laboratory feeding experiment to test whether DVM behavior is a plausible response to vertebrate predation, and specifically whether fish predation pressure is greater in the light or dark and whether it is size-selective. Comparing our experimental results with our observations of DVM, we could ascertain whether *Leptodora* DVM is more likely driven by predation risk as opposed to vertical structure in food availability or lake characteristics. Finally, we developed a simple model of size-specific *Leptodora* predation rates to estimate the net effect of the observed DVM behavior on zooplankton community composition of Katepwa Lake in particular, and to investigate the potential effects of *Leptodora* predation on aquatic food webs in general.

**Methods**

*Site description and limnological monitoring*—Five study lakes are situated within the Qu’Appelle River catchment, a system that drains ~ 52,000 km² of mixed grassland in southern Saskatchewan, Canada. Lakes range from meso-eutrophic upstream reservoirs (Diefenbaker, Buffalo Pound), through sub-saline Last Mountain Lake, to hyper-eutrophic downstream lakes (Katepwa, Crooked) and vary 10-fold in morphometric and limnological parameters that could affect *Leptodora* density (Table 1). The lakes are generally polymictic; although Katepwa and Diefenbaker lakes can exhibit thermal stratification during some summers because of basin depth and orientation relative to prevailing and storm-related winds. Zooplankton composition is similar among Qu’Appelle lakes with cyclopoid copepods (*Diacylops thomasi*) numerically dominant in all basins and densities of calanoid copepods...
(Leptodiaptomus siciloides) increasing from west to east (Table 1). Regional fish communities include walleye (Sander vitreus), northern pike (Esox lucius), yellow perch (Perca flavescens), cisco (Coregonus artedii), bigmouth buffalo (Ictiobus cyprinellus), and white sucker (Catostomus commersoni), although community composition is not known precisely for the years of study.

All study lakes were sampled biweekly during May–August (1994–2004) to quantify seasonal changes in total dissolved phosphorus (TDP), dissolved organic carbon (DOC), water temperature, chlorophyll a (Chl a) concentration, and Secchi depth, as well as densities of other zooplankton species (details in Leavitt et al. 2006; Patoine et al. 2006). TDP, DOC, and Chl a were measured from an integrated water sample, collected at 0.5 m intervals for the entire water column (1 m intervals in lakes > 10 m depth) using a 2 liter Van Dorn bottle. Zooplankton densities were estimated from either duplicate or triplicate vertical tows of a 20 cm diameter Wisconsin net (243 μm mesh) at the deepest point in the lake. A 50 cm diameter Wisconsin net (750 μm mesh) was used to estimate Leptodora abundance, and was also cast in either duplicate or triplicate at the deepest point in the lake. In this catchment, Leptodora overwinter in the sediments as diapausing eggs, move into the water column during day and night to evaluate whether Leptodora was tracking DVM by potential prey species. Diel changes in the mean depth of each prey species were calculated as the log ratio of a depth-weighted density (DWD = \( \sum n_i d_i \times \sum n_i^{-1} \)) during night and day (night : day), where \( n_i \) is density of a given species \( i \) at depth \( d \). In this calculation, negative log ratios indicate a normal vertical migration (down by day, up by night); whereas, values near zero represent a non-migratory population, and positive ratios indicate a reverse DVM (up by day, down by night). One-sample t-test was used to test for significant differences from zero in log ratios of zooplankton and Leptodora communities during night and day, and two-sample t-test was used compare abundances of adult and juvenile Leptodora in the water column during day and night.

Horizontal variation in vertical distribution of Leptodora—In 1996 alone (DOY = 233), we investigated the midday (12:00–14:00 h) vertical distribution of Leptodora in Katepwa Lake at three stations of differing depth (12 m, 15.5 m, 20 m) along a 2.5 km transect from the lakeshore to the center of the lake. The purpose of this survey was to determine whether Leptodora were found in greater densities in deep waters at all three sampling stations, and whether deep-water densities were greatest at the central station relative to shallower habitats closer to shore. The bottom 3 m at each station were sampled at 1 m intervals using a 12 liter Schindler–Patalas trap (63 μm mesh), while triplicate tows of a 50 cm diameter Wisconsin net (750 μm mesh) were used to determine adult densities in the uppermost 5 m of the water column. Finally, surface sediments (0–15 cm depth) were collected using an Ekman grab sampler, and 1 liter of sediment slurry was enumerated under a dissecting microscope to estimate the presence of benthic Leptodora populations.

Fish predation experiment—We performed feeding experiments in summer 1996 to assess both the susceptibility of Leptodora to predation by yellow perch in illuminated and dark treatments, and the degree to which this common predator fed size-selectively in these different light environments. Fifty adult Leptodora from Katepwa Lake were transferred into nine opaque containers filled with 75 liters of lake water screened through a 10 μm Nitex® mesh, and were allowed to acclimatize for 24 h prior to each experiment. One fingerling perch was added to each of six containers and allowed to feed unobserved for 2 h in either overhead light (300 μE m⁻² s⁻¹; \( n = 3 \)) or darkness (0 μE m⁻² s⁻¹; \( n = 3 \)). Three reference containers received no fish. Lids were removed from the three containers of the illuminated treatments, while the dark and control treatments were sealed and completely darkened. All nine containers were housed in environmentally controlled
chambers equipped with Grow-Lux cool-white bulbs. Light levels were measured with a LiCor LI 185B meter equipped with a LI-1905B quantum sensor. An additional reference container with fish was maintained outside of the environmental chambers to determine when ~50% of *Leptodora* had been consumed, at which time all treatments were stopped by removing perch by hand-net. At the end of the experiment the remaining *Leptodora* were concentrated on a 243 μm mesh and preserved in sugared ethanol. Each sample was counted for total remaining *Leptodora*, which were sexed and measured for body length. We used one-way ANOVA with post-hoc Tukey Honestly Significant Difference to determine whether average tank body length differed significantly among treatments (control, illuminated, dark). We further used two-sample *t*-tests to compare *Leptodora* abundances between tanks of illuminated and dark treatments. All analyses were conducted for both the pooled *Leptodora* population and for males and females separately.

*Models of Leptodora predation*—We modeled potential predation rates (PR) of *Leptodora* based on observed density of each prey (*N*<sub>prey</sub>; individual [ind.] L<sup>-1</sup>) using the Type II functional response equation of Pichlova and Vijverberg (2001; see also Holling 1959):

\[
PR = \frac{(a \times N_{\text{prey}})}{(1 + a \times h \times N_{\text{prey}})}^{-1}
\]

In this formulation, the predation rate of individual *Leptodora* (PR: *N*<sub>prey</sub> min<sup>-1</sup>) depends on handling time (*h*, min prey<sup>-1</sup>) by *Leptodora* and attack rate (*a*, prey captured min<sup>-1</sup>). Further, we modeled handling time of *Leptodora* following Branstrator (1998) as

\[
h = 1 / \left[ 0.067 \times (\text{basket size/prey size} - 1)^{0.436} \right]
\]

Here the size of *Leptodora*'s feeding basket (mm) was estimated from its body size following the equation of Manca and Comoli (1995), where

\[
\text{Basket length} = 0.145 \times (\text{body length}) + 0.152
\]

Using parameter estimates and their standard error from previous studies, we performed a sensitivity analysis of our model (Eqs. 1–3) to assess how uncertainty in each parameter (i.e., ± two standard errors) influenced our estimates of predation rate (Table 2). Unfortunately, no previous study has reported a variance in prey capture rate (*a*), because it has only been estimated from a single study that reports a maximum capture rate by adult *Leptodora* of 0.6 *Daphnia pulex* prey (size range ~1–1.5 mm) h<sup>-1</sup>, at a density of about 80–100 individuals L<sup>-1</sup> (Browman et al. 1989). In order to estimate a variance in the attack rate for our sensitivity analysis, we used Eq. 2 to calculate a likely range of handling times of 4.2–115 min prey<sup>-1</sup> (from Eq. 2: Branstrator 1998), based on a *Leptodora* size range of 1–12.5 mm and a prey size range from 0.1 mm to 2.1 mm, which amounts to a range of maximum predation rates that varies from about 0.5 prey h<sup>-1</sup> to 14.4 prey h<sup>-1</sup>. Using this range of maximum predation rates and the single capture rate estimate from Browman et al. (1989), we linearized Eq. 1 and calculated a range of plausible attack rates from 0.55 prey h<sup>-1</sup> to 0.63 prey h<sup>-1</sup>. We acknowledge there is considerable uncertainty in this estimate and therefore we used a very broad range of attack rates in our sensitivity analysis (from 0.2 to 1.0 prey h<sup>-1</sup>).

We calculated log ratios (night:day) of total predation rates (TPR: prey L<sup>-1</sup> d<sup>-1</sup>) to evaluate how DVM by *Leptodora* might affect in situ predation rates on zooplankton. Here, we split the observed *Leptodora* population into seven size categories (mean length = 1, 3, 5, 7, 9, 11, 13 mm), calculated the predation rate of each size class, multiplied by the density of the size class, and summed over the entire population of *Leptodora*. Using our parameter estimates in Table 2, this model allowed us to determine how changes in the size distribution of *Leptodora* population from day to night might affect predation on the resident zooplankton community.

**Results**

*Leptodora density*—Analysis of mean summer *Leptodora* densities (May–August: 1994–2004) revealed a wide range of abundances, from 0.03 ind. L<sup>-1</sup> to 0.15 ind. L<sup>-1</sup>, with maximum date-specific densities of 0.24 ind. L<sup>-1</sup> in Diefenbaker to 1.6 ind. L<sup>-1</sup> in Buffalo Pound (Table 1; seasonal patterns in Fig. 1A). Overall, mean *Leptodora* density was correlated significantly with several important environmental parameters, including average water temperature (*r* = 0.37, *p* = 0.007), Chl *a* concentration (*r* = 0.46, *p* = 0.003), and Secchi depth (*r* = −0.48, *p* < 0.001), as well as the density of *Diacyclops thomasi* (*r* = 0.55, *p* = 0.0001), *Daphnia* spp. (*r* = 0.48, *p* = 0.002), and...
accounted for ~57% of the variation in Leptodora density, but had a much lower AIC score ($R^2_{adj} = 0.57, p < 0.001$, AIC = −170.926). Other candidate models, including those composed of subsets of the variables included in this best model, were rejected on the basis of their higher AIC scores (see Table 3). Even the best of this latter subset of models (including one with Secchi disk transparency) was only 0.37 times as probable as the best model according to multi-model inference calculation (Johnson and Omland 2004). Together, these models confirm that Leptodora abundance increases mainly as a function of prey availability and increases in water temperature.

Diurnal vertical migration—Statistical analysis of Leptodora distribution revealed significantly more adults (>5 mm) in the upper 20 m of Katepwa Lake at night than during the day ($t$-test, $t = −2.689, df = 6, p = 0.036$). Conversely, juveniles (<5 mm) exhibited no substantive differences in abundance between day and night sampling periods ($t$-test, $t = −0.158, df = 6, p = 0.831$). When Leptodora were categorized according to size intervals (0–2 mm, 2–3 mm, 3–5 mm, 5–7 mm, 7–10 mm, >1 mm), diel differences in densities were most pronounced for the largest size adults (>5 mm) and non-significant for the smallest individuals. Collectively, these patterns are consistent with size-specific DVM (Fig. 2).

Analysis of log ratios (night:day) of DWD confirmed that adult Leptodora exhibited DVM ($t$-test, $t = −0.262, df = 3, p = 0.39$), but that other zooplankton species did not undergo typical vertical migration through the water column (Fig. 3A). Specifically, the confidence intervals of log ratios were not significantly less than zero for Diaphanosoma birgei ($t$-test, $t = 0.378, df = 3, p = 0.635$), Bosmina longirostris ($t$-test, $t = 1.987, df = 3, p = 0.092$), Daphnia galeata mendotae ($t$-test, $t = 0.246, df = 3, p = 0.840$), Diacyclops thomasi ($t$-test, $t = 0.111, df = 1, p = 0.281$), Leptodiaptimus siciloides ($t$-test, $t = −0.534, df = 3, p = 0.315$), and juvenile Leptodora ($t$-test, $t = 0.180, df = 3, p = 0.566$). Daphnia retrocurva, however, displayed a significant inverse DVM with log ratios significantly greater than zero ($t$-test, $t = 2.875, df = 3, p = 0.032$; Fig. 3A). For each zooplankton taxon, the depth of the maximum DWD changed <2 m between day and night.

When averaged over four sampling dates, mean night-time densities of adult Leptodora increased by a factor of 4.4 (Standard error of mean [SEM] = 0.4, n = 4) relative to values during the day (Fig. 3B). In all cases, daytime densities of adults were <0.10 ind. L$^{-1}$, whereas mean water-column densities at night varied from 0.10 ind. L$^{-1}$ to 0.31 ind. L$^{-1}$ (Fig. 4B). Although the density of juvenile Leptodora did not increase significantly at night ($t_3 = −0.35, p = 0.75$; Figs. 3B, 4B), the overall density of the entire Leptodora population increased by 2.5-fold after sunset (SEM = 0.65, n = 4; Fig. 3B). As a consequence of selective nighttime migration of adult Leptodora, average body size increased by 1.9 mm relative to daytime values (SEM = 0.38, n = 4; $t_3 = 5.1, p = 0.015$; Fig. 4A). During the day, Leptodora always made up <8% of the total zooplankton biomass (Fig. 4C), but at night this proportion increased up to 31%.

**Fig. 1.** (A) Summarized seasonal patterns (±1 SEM) of Leptodora density from 1994 to 2004. (B) Bottom water temperature (±1 SEM) for the depth indicated from 1994 to 2004.

*Leptodiaptomus siciloides* ($r = 0.39, p = 0.005$). In contrast, *Leptodora* density was uncorrelated with water column concentrations of TDP, DOC, or other water column parameters ($p > 0.05$). Limnological variables significantly correlated with *Leptodora* density were combined in a multiple regression model ($R^2 = 0.58, p < 0.001$, AIC = 147.599), but only water temperature ($p = 0.025$) and densities of *L. siciloides* ($p = 0.001$) and *Daphnia* spp. ($p < 0.001$) exhibited significant regression coefficients (Chl $a$ [$p = 0.401$], Secchi depth [$p = 0.436$], and *D. thomasi* [$p = 0.425$]). The resulting multiple regression based on water temperature, and densities of *L. siciloides* and *Daphnia* spp.
Table 3. Multiple regression models presenting potential drivers of *Leptodora* density in a longitudinal survey of five lakes (1994–2004). Models are composed of predictor variables shown to be significantly correlated to *Leptodora* density, and include water temperature (Temp), Secchi depth (Secchi), concentration of chlorophyll a (Chl a), and densities of *Diacyclops thomasi* (*D. thomasi*), *Leptodiaptomus siciloides* (*L. siciloides*), and *Daphnia* spp. (*Daphnia*). Model A1 includes all variables, while models B1–B4 include only those variables that had significant partial coefficients ($p < 0.05$) from model A. Models C1–C3 show consequences for re-adding variables excluded from models B1. Number of parameters, model fit and significance ($R^2$, $p$), Akaike Information Criterion (AIC), delta-AIC ($\Delta$AIC), and Akaike weights are provided.

<table>
<thead>
<tr>
<th>Model</th>
<th>Variables included in model</th>
<th>No. parameters</th>
<th>$R^2$</th>
<th>$p$</th>
<th>AIC</th>
<th>$\Delta$AIC</th>
<th>Akaike weight</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1</td>
<td>Temp, Secchi, Chl a, <em>D. thomasi</em>, <em>L. siciloides</em>, <em>Daphnia</em></td>
<td>6</td>
<td>0.58</td>
<td>&lt;0.001</td>
<td>−147.60</td>
<td>23.33</td>
<td>0</td>
</tr>
<tr>
<td>B1</td>
<td>Temp, <em>L. siciloides</em>, <em>Daphnia</em></td>
<td>3</td>
<td>0.57</td>
<td>&lt;0.001</td>
<td>−170.93</td>
<td>0.00</td>
<td>1</td>
</tr>
<tr>
<td>B2</td>
<td>Temp, <em>Daphnia</em></td>
<td>2</td>
<td>0.43</td>
<td>&lt;0.001</td>
<td>−156.58</td>
<td>14.35</td>
<td>0</td>
</tr>
<tr>
<td>B3</td>
<td>Temp, <em>L. siciloides</em></td>
<td>2</td>
<td>0.31</td>
<td>&lt;0.001</td>
<td>−146.37</td>
<td>24.56</td>
<td>0</td>
</tr>
<tr>
<td>B4</td>
<td><em>L. siciloides</em>, <em>Daphnia</em></td>
<td>2</td>
<td>0.52</td>
<td>&lt;0.001</td>
<td>−166.61</td>
<td>4.31</td>
<td>0.12</td>
</tr>
<tr>
<td>C1</td>
<td>Temp, <em>L. siciloides</em>, <em>Daphnia</em>, Secchi</td>
<td>4</td>
<td>0.57</td>
<td>&lt;0.001</td>
<td>−168.93</td>
<td>2.00</td>
<td>0.37</td>
</tr>
<tr>
<td>C2</td>
<td>Temp, <em>L. siciloides</em>, <em>Daphnia</em>, Chl a</td>
<td>4</td>
<td>0.58</td>
<td>&lt;0.001</td>
<td>−148.90</td>
<td>22.03</td>
<td>0</td>
</tr>
<tr>
<td>C3</td>
<td>Temp, <em>L. siciloides</em>, <em>Daphnia</em>, <em>D. thomasi</em></td>
<td>4</td>
<td>0.53</td>
<td>&lt;0.001</td>
<td>−155.65</td>
<td>15.27</td>
<td>0</td>
</tr>
</tbody>
</table>

**Horizontal distribution of *Leptodora***—Horizontal survey of daytime *Leptodora* abundance revealed that 61.3% of adults were located in the lowest 3 m of the water column, with adults concentrated near the center of the lake rather than at its periphery. At the central station, *Leptodora* densities (± SD) in the bottom 3 m (0.83 ± 0.01 ind. L$^{-1}$) were over three-fold higher than in the overlying water column (0.24 ± 0.01 ind. L$^{-1}$). Similar patterns were observed at the 15.5 m station (0.58 ind. L$^{-1}$ and 0.11 ind. L$^{-1}$, respectively), and at the 12 m station (0.33 ind. L$^{-1}$ and 0.10 ind. L$^{-1}$, respectively). At all stations, *Leptodora* were absent from the surface sediment samples. Such an absence did not appear to reflect profound anoxia in sediments, because adult *Leptodora* were abundant in the deepest waters where dissolved oxygen concentrations were consistently < 1 mg L$^{-1}$ during most of the summer.

**Fish predation experiment**—Predation by fish accounted for 100% of *Leptodora* mortality during the experiment, because there was no mortality in the no-fish controls (Table 4). Mortality did not differ between illuminated and dark treatments ($t$-test, $t = 0.056$, df = 1, $p = 0.825$). Body lengths were significantly reduced by perch predation when compared with controls (Table 4; ANOVA, $F_2 = 6.454$, $p = 0.032$). Post-hoc comparisons with the Tukey Honestly Significant Difference test indicated that although body lengths did not differ between dark and illuminated treatments ($p = 0.994$), both had reduced average body lengths relative to controls ($p = 0.04$, 0.05). Males were shorter than females irrespective of treatment ($t$-test, $t = 17.893$, df = 1, $p = 0.01$).

**Modeled predation rates**—Predation rates of individual *Leptodora* declined with increases in prey body size for both daytime and nighttime zooplankton assemblages (Fig. 5A), reflecting increased handling time for large items by *Leptodora* (Eq. 2). However, as adults migrated into surface waters at night predation by *Leptodora* increased substantially, particularly for intermediate-sized prey (Fig. 5A). The increase in the mean size of the *Leptodora* population at night (by ~2 mm) changed the estimated predation rates on specific prey species by up to three-fold (Fig. 5B, open squares). Together, the nighttime changes in *Leptodora* size and density increased species-specific predation rates by up to five-fold (Fig. 5B, closed squares). Species-specific predation rates averaged across all four sampling dates increased by factors of 6.2 for *Daphnia retrocurva*, 3.6 for *Leptodiaptomus siciloides*, 3.4 for *Diacyclops thomasi*, 2.1 for *Diaphanosoma birgei*, and 1.2 for *Bosmina longirostris*. Predation rates did not increase at night for the largest species, *Daphnia galeata mendotae*.

Sensitivity analysis revealed that the magnitude of diurnal variation in total predation by *Leptodora* (Fig. 5) was insensitive to the precise parameter values used in the predation models. Variation in parameters by ± 2 SEM generally resulted in less than a 10% change in predation rate estimates (Table 2). In addition, a widely varying attack rate had little influence on the qualitative nature of our conclusions shown in Fig. 5C. Overall, our results suggest that variation in size structure of *Leptodora* populations owing to DVM can result in a substantial underestimate of invertebrate predation on zooplankton communities in eutrophic lakes, when *Leptodora* are collected solely during daylight hours.

**Discussion**

Analysis of 11 yr of survey data from five productive lakes, intensive study of vertical and horizontal distribution in Katepwa Lake, and a fish-feeding experiment support the hypothesis that DVM is a dynamic anti-predator defense trait of *Leptodora* that can substantially alter its predatory effects on freshwater zooplankton (Vijverberg 1991). Specifically, adult *Leptodora* exhibited DVM in Katepwa Lake (Fig. 2), resulting in a two-fold increase in population densities at night relative to during the day. Taken in concert with an ~2 mm increase of mean nighttime body size, elevated densities increased estimates of total predation at night by up to five-fold relative to daytime assemblages, particularly for those intermediate-sized prey favored by *Leptodora* (Fig. 5B). Because zooplankton prey did not exhibit typical patterns of
DVM, we infer that *Leptodora* migration was primarily a response to diel changes in predation by fish, an interpretation supported by the size-selective feeding by perch on large adult *Leptodora* under both illuminated and darkened conditions (Table 4). These findings suggest that although mean *Leptodora* density is correlated to aspects of resource availability across lakes (e.g., primary production as Chl a prey density), the extent of DVM within individual lakes is driven mainly by predation risk, especially given the very low water transparency in these lakes during late summer (< 0.5 m; Leavitt et al. 2006). Furthermore, modeling exercises suggest that such diurnal changes in *Leptodora* density and size-structure lead to as high as five-fold underestimates of invertebrate predation on zooplankton in productive lakes when compared with standard models parameterized with estimates of *Leptodora* populations based on daytime assemblages.

Leptodora abundance in relation to limnological conditions—Most previous studies of *Leptodora* have focused on individual, shallow (max. depth < 8 m), productive lakes (Costa and Cummins 1969; Herzig and Auer 1990; Alajarvi and Horppila 2004), and typically consider effects based on daytime population parameters (Lunte and Luecke 1990; Branstrator and Lehman 1991). Here, we confirm that daytime densities of *Leptodora* in these five chemically and morphologically diverse lakes are within the ranges reported for most meso- and eutrophic sites (Lunte and Luecke 1990; Uusitalo et al. 2003), but demonstrate further that variation in mean daytime density is correlated with indicators of their resource abundance (prey abundance and size structure; McNaught 1993b). As with previous research, we observed that seasonal timing of maximum population density was closely linked to the thermal properties of lakes (Fig. 1B), with daytime population
densities typically peaking in late summer (Herzig and Auer 1990; Branstrator and Lehman 1991; Alajarvi and Horppila 2004). Such patterns are thought to arise because of the strong temperature dependence of Leptodora growth (Vijverberg and Koelewijn 2004) and because migratory adult Leptodora rarely appear in the water column when temperatures are < 10°C (Garton et al. 1990). This interpretation is consistent with the composition of the best multiple-regression model to predict Leptodora density in Qu’Appelle lakes, which included temperature, as well as two prey densities (Daphnia spp., Leptodiaptomus siciloides).
Unexplained variance in *Leptodora* density in our regression models may reflect differences in abundances of fish predators among lakes; however, reliable estimates of vertebrate abundance are not available for these years.

**Size-selective diel vertical migration of *Leptodora*—**

*Leptodora* and other large-bodied zooplankton are a common prey item of many planktivorous fish, including bluegill (*Lepomis macrochirus*; Branstrator and Holl 2000), razor fish (*Pelecus cultratus*; Liu and Herzig 1996), bleak (*Alburnus alburnus*; Liu and Uiblein 1996), and perch (*Perca fluviatilis*; Horppila et al. 2000). However, among the zooplankton only adult *Leptodora* underwent pronounced DVM in Qu’Appelle lakes (Fig. 2). This pattern suggests that size-selective DVM arises from ontogenetic changes in predation risk to *Leptodora*. Consistent with this hypothesis, previous research establishes that zooplanktivorous fish can exhibit size-selective predation on *Leptodora* (Branstrator and Holl 2000), with adult invertebrates more vulnerable to predation than juveniles (Liu and Herzig 1996). Similarly, our feeding experiment confirms that adult *Leptodora* did not migrate as a means of tracking migratory prey. Similarly, *Leptodora* did not demonstrate lateral migration during the day in response to the use of shallow water refugia by large-bodied cladocera, as known from shallow lake ecosystems (Burks et al. 2002). Instead, *Daphnia retrocurva*, a prey preferred by raptorial copepods (Havel 1985), exhibited an inverse DVM in Katepwa Lake (Fig. 3), possibly as a means of avoiding predation by *Leptodora*. Further, the metabolic hypothesis for DVM (Enright 1977) is not consistent with the observed *Leptodora* migration, because Katepwa Lake did not always thermally stratify, and the anoxic hypolimnion would not confer the typical metabolic advantage of cooler, well-oxygenated deep waters during the day. Finally, we additionally infer that *Leptodora* migration was not a response to avoiding damage by high energy irradiance as suggested for some zooplankton (Leech and Williamson 2001), because juveniles were abundant throughout the water column during the day, yet have a higher body transparency than adults (Johnsen 2001). In addition, the high levels of DOC in Katepwa Lake (11 mg C L$^{-1}$) mean that 1% UV-B penetration should be < 3 m (Schindler et al. 1996), even accounting for the low specific attenuation coefficient of prairie lake DOC (uncolored; Leavitt et al. 2006), and thus exposure to ultraviolet radiation is not a suitable explanation for *Leptodora* DVM.

**Potential effects of *Leptodora* DVM on predation regimes in lakes—** Recent research suggests that invertebrate predation is an underappreciated but potentially important force
structuring the food web of aquatic ecosystems (Yan et al. 2002; Borer et al. 2005; Shurin and Seabloom 2005). Vertebrate and invertebrate predators have both direct and indirect effects on lower trophic levels (Halpern et al. 2005) and, although predation can be intense, the transmission of predator effects down the food chain varies widely among and within ecosystems (Pace et al. 1999). Interestingly, invertebrate predators may have particularly strong cascading effects (Borer et al. 2005), a result that is at odds with the research bias toward studies of the effects of fish on lacustrine food webs (Lane 1979; Carpenter and Kitchell 1993). Further, even though invertebrate predator biomass is often substantially lower than fish biomass, mass- and metabolism-specific predation rates are often much higher for invertebrates than vertebrates (Yodzis and Innis 1992; Shurin and Seabloom 2005) and need to be fully accounted for in food-web models to accurately assess the predation regime of aquatic ecosystems (Blumenshine and Hambright 2003).

Our analysis of simple predator–prey models (Pichlova and Vijverberg 2001; Branstrator 2005) demonstrates that DVM can increase predation rates of Leptodora by as much as five-fold at night as a result of increases in both the mean size and density of invertebrate predators in the water column. This finding contrasts sharply with the results of other food-web analyses, which often find that invertebrate predation is of marginal significance when compared with that of planktivorous fish (Carpenter and Kitchell 1993). For example, zooplanktivorous fish were found to account for 50–95% of estimated total consumption of daphniids in eutrophic Lake Mendota, a system similar to Katepwa Lake (Luecke et al. 1992). In this case, substantial invertebrate effects were evident only in early spring, or in years where fish abundances were reduced to low numbers (Lunte and Luecke 1990; Luecke et al. 1992). Here, we suggest that the importance of Leptodora predation may have been greatly underestimated in prior studies because of the prevalence of size-selective zooplanktivory by fish (see above), the pronounced occurrence of DVM by adult Leptodora, and the strong effect of diel changes in size and density on estimates of predation by Leptodora (Branstrator 1998; Pichlova and Vijverberg 2001). Although we recognize that our model did not capture the full range of possible prey-capture coefficients (e.g., fast-swimming copepods), our findings were stable across a wide range of attack rates and handling times. Given the potential for strong ecological effects of Leptodora, we implore further research to quantify functional responses across a broad range of prey types, and we suggest that realistic comparisons of vertebrate and invertebrate predation must include not only analysis of invertebrate abundance and size structure, but also the influence of anti-predator defense behavior such as DVM.

In summary, we have demonstrated that a common and important invertebrate predator (Leptodora kindtii) undergoes pronounced size-selective DVM in response to predation from fish. As a consequence of diel changes in size structure and density of invertebrate assemblages, prey-specific predation by Leptodora and its effects on aquatic food webs may be underestimated by up to five-
fold, even in lakes with abundant planktivorous fish. Our analysis of size-specific predation rates suggests that this effect is particularly pronounced for intermediate-sized prey (Fig. 5), where predation rates averaged across all sampling periods increased 3–5-fold. Such a style of predation can act as a diversifying selective force that favors extreme phenotypes (i.e., large and small species), as well as the coexistence of multiple prey species (McNaught 1993a). In comparison, fish predation imparts a more directional selection because larger size classes are always at a disadvantage. Together, these findings suggest that invertebrate predation may be a stronger force structuring lake communities than was previously thought, particularly for eutrophic lakes with low water clarity and abundant *Leptodora*.

**Acknowledgments**

We thank members of the Limnology Laboratory for assistance with data collection and experiments. Beatrice Beisner, Kerri Finlay, Norman Yan, Luc De Meester, and one anonymous reviewer provided insightful comments that improved the manuscript.

This work was supported by the Natural Sciences and Engineering Research Council of Canada Discovery Grants, the Canada Research Chair Program, Canada Foundation for Innovation, the Province of Saskatchewan, and the University of Regina.

**References**


Vertically migration of Leptodora

Associate editor: Luc De Meester

Received: 12 September 2012
Accepted: 15 May 2013
Amended: 13 June 2013