

1-1-1997

Life History Characteristics Of *Daphnia Lumholtzi* And Its Susceptibility To An Invertebrate Predator

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LIFE HISTORY CHARACTERISTICS OF DAPHNIA
LUMHOLTZI AND ITS SUSCEPTIBILITY TO
AN INVERTEBRATE PREDATOR

RAWSKI

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LIFE HISTORY CHARACTERISTICS OF
DAPHNIA LUMHOLTZI AND ITS SUSCEPTIBILITY
TO AN INVERTEBRATE PREDATOR

by

EDEN L. RAWSKI

1971 -

THESIS

SUBMITTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
FOR THE DEGREE OF

MASTER OF SCIENCE

IN THE GRADUATE SCHOOL, EASTERN ILLINOIS UNIVERSITY
CHARLESTON, ILLINOIS

1997

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ABSTRACT

Distribution of *Daphnia lumholtzi*, a cladoceran native to Australia, Africa, and southern Asia, has increased rapidly throughout the southeastern and central United States. Reservoirs invaded by *D. lumholtzi* have shown a decrease in the overall density of native zooplankton, perhaps due to the increase in the exotic species population. *Daphnia lumholtzi* is characterized by the presence of a large pointed helmet and tailspine. Native daphnids, such as *Daphnia pulex*, typically lack these structures. In order to determine possible negative impacts *D. lumholtzi* may have on North American reservoirs, I determined the life history characteristics of the exotic and compared the results to that of native species. No significant life history differences were observed which would confer an advantage to the exotic at the expense of native species. While average age at first reproduction and mean number of offspring per brood were similar for the exotic *Daphnia* and similar sized native species, *D. lumholtzi* appears to have a smaller total number of broods and a shorter life span. In addition, I examined vulnerability of different size classes of *D. lumholtzi* and *D. pulex* to an invertebrate predator, *Leptodora kindtii*. Although numerous studies suggest that daphnid spines provide protection against invertebrate predators, my results show that *D. lumholtzi* was more susceptible than *D. pulex* to predation at all sizes. *Daphnia lumholtzi*'s helmet and tailspine may increase likelihood of detection and capture by *Leptodora*, while decreasing the probability of escape. Additional studies following the population dynamics of *D. lumholtzi* and *Leptodora* may determine the role this predator may play in regulating the exotic daphnid population.

ACKNOWLEDGMENTS

I am particularly grateful to Dr. Charles Pederson for the vast amount of time and effort which he devoted to this study, his help with my field work and laboratory experiments, and for his advisement in the preparation of this paper. I am also grateful to Dr. Kipp Kruse for his suggestions and assistance with the statistical analysis of my data and for serving as a member of my graduate committee. I would also like to thank Dr. Robert Fischer for his helpful comments on this study and for serving as a member of my graduate committee.

Special thanks to Sheri Effert for her help with the collection of zooplankton. And I would like to thank my husband, Ken Rawski, for his assistance with my field work, his help feeding the *Daphnia* cultures, and for his support throughout my graduate studies at Eastern Illinois University.

Funding for this project was provided in part by a Tiffany Fund grant from the Botany Department at EIU. In addition, this research was supported by a summer research assistantship from the EIU Graduate Program.

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INTRODUCTION

Predation is a major source of mortality in aquatic ecosystems and thus a powerful component of natural selection. Antipredator defense mechanisms exhibited by zooplankton in a given lake are related to the predation regime (Lysebo, 1995). Predators of freshwater zooplankton are composed of two groups: vertebrate and invertebrate predators (Hanazato and Yasuno, 1989). Vertebrate predators swallow their prey whole and are termed "gape-limited predators" because their mouth diameter, or gape, determines the maximum size of prey they can take (Zaret, 1980). Invertebrate predators differ in part because they typically break apart their prey and then consume it in "bite-sized" pieces. Invertebrates are categorized as "size-dependent predators" with the size of the prey more crucial to prey capture than ingestion (Zaret, 1980). Gape-limited predators and size-dependent predators exhibit prey electivity curves which differ due to distinct limitations on their ability to locate, capture, and retain prey (Figure 1). Both predator types show the lowest electivity for the smallest individuals because these prey items are difficult to locate. Gape-limited predators display the highest electivity for the largest available prey that it can fit into its mouth. Size-dependent predators typically prefer a mid-size prey item due to the increased probability of escape with larger prey sizes.

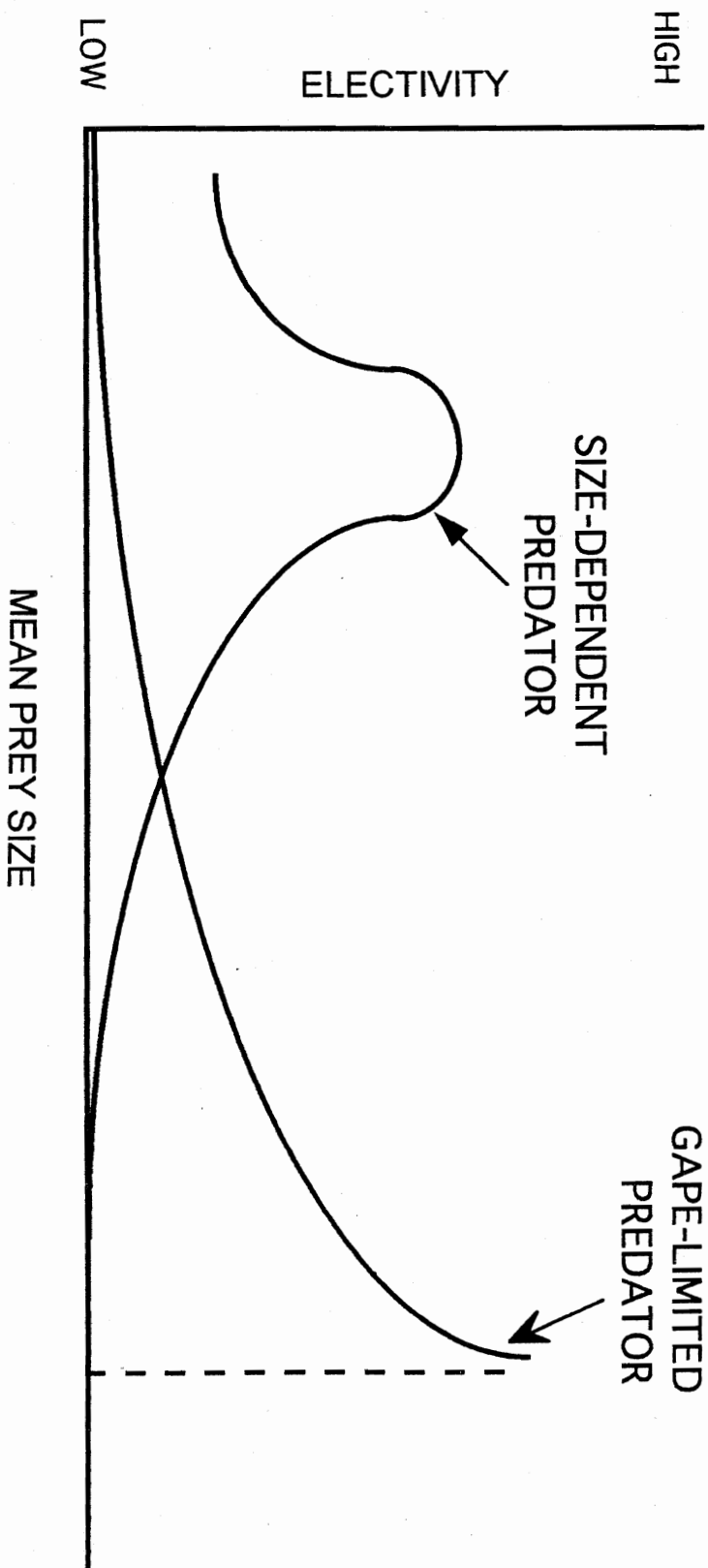
Zooplankton have developed a variety of defenses in an attempt to deter predation by both planktivorous fish (gape-limited) and invertebrate (size-dependent) predators. These defenses can involve life history strategies (e.g., increase reproduction rate), behavioral adaptations (e.g., vertical migration), or morphological changes (e.g., spine production). Morphological variation is a common and well studied defense mechanism found in planktonic animals with zooplankton assuming different shapes and sizes that may reduce

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Figure 1. Prey electivity curves for gape-limited predators and size-dependent predators
(modified after Zaret, 1980).

ELECTIVITY CURVES



their susceptibility to predators. A special case of morphological defense displayed by a few species of zooplankton is cyclomorphosis. Cyclomorphosis is a change in morphologies over time, which can involve formation of a helmet, tailspine, and neckteeth. Studies have found that these changes occur as a response to environmental conditions (Jacobs, 1961; Sorensen and Sterner, 1992) or may be induced by chemicals released by the predator (Dodson, 1974; Havel and Dodson, 1984; Hanazato and Yasuno, 1989; Pijanowska, 1990; Tollrian, 1994). Zooplankton with cyclomorphic morphology are presumably more difficult for predators to capture and consume.

Daphnia are known to show obvious cyclical changes in morphology, including the head spine, tailspine, and carapace length (Hutchinson, 1967). Over the past three decades, numerous studies have suggested that cyclomorphic features protect daphnids against vertebrate and/or invertebrate predators (i.e., Dodson, 1974; Zaret, 1980). Irregularly shaped prey may be difficult to handle and therefore rejected by gape limited predators even though the daphnids are small in size (Swift, 1992). O'Brien et al. (1979) have shown the larger, helmeted morph of *Daphnia longiremis* to be less vulnerable to fish predation than the smaller, non-helmeted morph. Because the shape of the prey can interfere with handling, producing spines may also be an effective defense against size-dependent predators. Pijanowska (1990) suggested that *Daphnia cucullata's* elongated head together with its long tailspine may protect it against invertebrate attacks, or at least alter and prolong the handling sequence. This hypothesis has been further supported by field observations which show that the period of highest helmet formation in daphnids coincided with maximum densities of the invertebrate predators, *Chaoborus* and *Leptodora* (Mort, 1989).

Daphnia lumholtzi, a species of crustacean zooplankton native to Australia, Africa, and southern Asia, has recently appeared in a number of lakes and reservoirs in the south-central and southeastern United States (Sorenson and Sterner, 1992; Havel and Hebert, 1993; Havel et al., 1995). The first documentation of *D. lumholtzi* in North America was at Fairfield Reservoir, Texas (31.7 N, 96.0 W) in 1991 (Sorensen and Sterner, 1992). A possible mode of introduction was the stocking of fish native to Africa, such as Nile perch and *Tilapia*, obtained from systems where *D. lumholtzi* were abundant. To date, it has been found in 20 lakes and reservoirs in five states: Missouri, Florida, Tennessee, Texas, and Illinois (Sorenson and Sterner, 1992; Havel et al., 1995; Kolar et al., 1997). The first observation of *D. lumholtzi* in Illinois was in Lake Springfield in 1992 (Kolar et al., 1997). Since then, this species has quickly spread to at least seven additional reservoirs within the state (Bloomington, Decatur, Charleston, Clinton, Sangchris, Shelbyville, and Taylorville) (Kolar et al., 1997).

Exotic species often lack natural biological controls such as predators, competitors, and parasites. As a result, invading organisms are able to colonize new habitats quite rapidly. This can cause shifts in food webs, extinction of native species, and economic losses. Reservoirs invaded by *D. lumholtzi* already have shown a decrease in the overall density of native zooplankton, perhaps due to the increase in the exotic species population (Havel et al., 1995; Kolar et al., 1997).

Daphnia lumholtzi has several features which distinguish it from native species of *Daphnia* including; a large pointed helmet and tailspine, distinctive lateral fornices, and prominent spines along the ventral carapace margin (Havel and Hebert, 1993). Helmet and tailspine lengths can reach extreme proportions, at times exceeding carapace length.

Individuals found in the United States can achieve total body length over 5 mm (including spines), which is larger than the individuals found in its native range (King and Greenwood, 1992) and larger than other *Daphnia* species found in many lakes in the United States (Work and Gophen, 1995). Although Green (1967) reported both helmeted and non-helmeted morphs of *D. lumholtzi* living in Lake Albert, Africa, only the helmeted morph has been discovered in North American lakes and reservoirs (Havel et al., 1995).

Because it is an exotic species and it displays extreme cyclomorphic features, previous studies suggest that *D. lumholtzi* has the potential to disrupt natural community structure (Sorenson and Sterner, 1992; Havel and Hebert, 1993; Havel et al., 1995; Work and Gophen, 1995; Swaffar and O'Brien, 1996). Swaffar and O'Brien (1996) found that spines of *D. lumholtzi* presented ingestion difficulties to juvenile bluegill and similar structures on other species of *Daphnia* have been shown to reduce predation by invertebrate predators (O'Brien et al., 1979; Havel and Dodson, 1984). Therefore it is possible that the pointed helmet and long tailspine of *D. lumholtzi* may provide a selective advantage over other *Daphnia* and zooplankton competitors.

The effectiveness of daphnid cyclomorphic features against invertebrate predators has been demonstrated. Previous studies have involved the phantom midge larva, *Chaoborus* (Kreuger and Dodson, 1981; Havel and Dodson, 1984) and the predacious copepod *Heterocope* (O'Brien et al., 1979). However, no one has tested the effectiveness of these defenses against the invertebrate predator *Leptodora kindti*.

Leptodora kindti is a large (6-12 mm), predaceous freshwater cladoceran (Haplopoda) that swims continuously through the water column, preying upon a wide range of crustacean zooplankton (e.g., *Bosmina*, *Ceriodaphnia*, *Daphnia*, and *Diaphanosoma*).

They generally prefer cladocerans (Browman *et al.*, 1989), though they have been reported to consume copepods and rotifers (Cummins *et al.*, 1969), and are sometimes cannibalistic (Mordukhai-Boltovskaia, 1958). Most of the studies on predation by *Leptodora* are not based on direct observation, but are inferred from inverse correlations between *Leptodora* abundance and the abundance of potential prey species in field samples (e.g., Wright, 1965; Cummins *et al.*, 1969; Branstrator and Lehman, 1991). These studies estimate that *Leptodora* could consume 25 - 35 % of *Daphnia* production daily. Planktivorous fish have been reported to eliminate 10% of *Daphnia* production on a daily basis (O'Brien *et al.*, 1979) and *Chaoborus* may consume up to 20% over a 24 hour period (Pastorok, 1980). This suggests that predation, in general, and *Leptodora* specifically, can be a significant factor in structuring populations of *Daphnia* (Hovenkamp, 1990).

Many studies on *D. lumholtzi* have been limited to discovering its presence and then determining its density (Sorensen and Sterner, 1992; Havel and Hebert, 1993; Havel *et al.*, 1995). Few have attempted to determine if the exotic actually can interfere with the success of native species or if its morphology truly deters predation. The first objective of this study was to determine if *D. lumholtzi* could displace native daphnids simply because it has life history traits which would confer an advantage to the exotic at the expense of native species. While recent studies on *D. lumholtzi* have been primarily concerned with planktivorous fish predation (Swaffar and O'Brien, 1996), I considered the potential ability of the exotic to avoid invertebrate predation. Thus, the second objective of this study was to compare the vulnerability of *D. lumholtzi* and the native *D. pulex* to the invertebrate predator, *Leptodora kindti*. *Daphnia pulex* was used for this comparison

because they are of similar size, but lack the pronounced tailspine and helmet of *D. lumholtzi*. Also, *D. pulex* is abundant in most of the reservoirs that the exotic species has invaded.

MATERIALS AND METHODS

Collection Methods

For the life history component of this study, *Daphnia lumholtzi* were collected from Lake Taylorville, an impoundment of the Sangaman River located south of Taylorville, IL (Christian Co.). For the predation experiments, *Daphnia lumholtzi* and *Leptodora kindti* were collected from the Charleston Side Channel Reservoir (CSCR) located southeast of Charleston, IL (Coles Co.). Zooplankton were captured with a 80- μm mesh-size Wisconsin Plankton Net by making oblique (bottom to surface) tows from shore. Due to a low density of *Daphnia pulex* in the CSCR during sampling, *D. pulex* was obtained from Aquatic Biosystems Inc., Fort Collins, CO. Zooplankton species were identified according to Pennak (1953) and Benzie (1988). *Daphnia lumholtzi* and *Leptodora* were separated from other zooplankton in the sample using a dissecting microscope and a pipette. *Daphnia* and *Leptodora* were then placed into either aquaria to start mass cultures or into individual culture vessels.

Mass Cultures

Methods for maintaining *Daphnia* cultures were based on guidelines published by the U.S. Environmental Protection Agency (USEPA, 1991). Mass cultures of *Daphnia* were maintained in 5 L aquaria filled with approximately 4 L of filtered lake water (Gelman GA-6 cellulose acetate membrane filters, $d = 45\text{mm}$, pore size=0.45 μm). The medium in each mass culture vessel was replaced twice each week with newly filtered lake water.

Approximately 40 adult *Daphnia* were placed into each aquarium to start the mass cultures, each of which provided up to 400 young per week. At least three mass cultures were maintained to ensure back-up cultures in the event that a population "crashed" in any one vessel. Water temperature of the cultures was uncontrolled but remained in the range

of 20-25 °C. The photoperiod in the laboratory was set at 16 hours of light and 8 hours of darkness. Mass cultures were fed 5.0 mL of YCT (a combination of yeast, dried powdered alfalfa leaves, and fish flake food) and 2.5 mL of *Selenastrum capricornutum* (a unicellular algae) three times per week. Through trial and error, it was determined that this feeding rate and frequency appeared to result in maximum reproduction.

Individual Cultures

Individual organisms were cultured in 30 mL plastic cups which contained 20 mL of filtered lake water. Culture conditions were similar to those for mass cultures. Individual vessels were maintained on a 16 hour day/8 hour night cycle and the water temperature was maintained at approximately 20 °C. Individual cultures were fed 1 drop (ca. 0.1 mL) of YCT and 1 drop of *Selenastrum capricornutum* daily and culture medium was changed three times weekly.

Life History Study

Adult *Daphnia lumholtzi* with eggs deposited in their brood chamber were selected from mass cultures and placed into individual cultures. Offspring produced in the first and second brood while in culture were discarded. Neonates (individuals less than 24 hours old) from the third or subsequent brood were used to compile life history information. One neonate was placed in a 30 mL culture cup. Individual cultures were monitored for age at first reproduction, number of offspring per brood, total number of broods, timing of broods, and total life span. Enough individual cultures were maintained to ensure that at least 30 *D. lumholtzi* were followed throughout their total life span. In addition, 10 individuals representing each instar were preserved in 90% ethanol. The preserved *D.*

lumholtzi were measured with an ocular micrometer on a dissecting microscope.

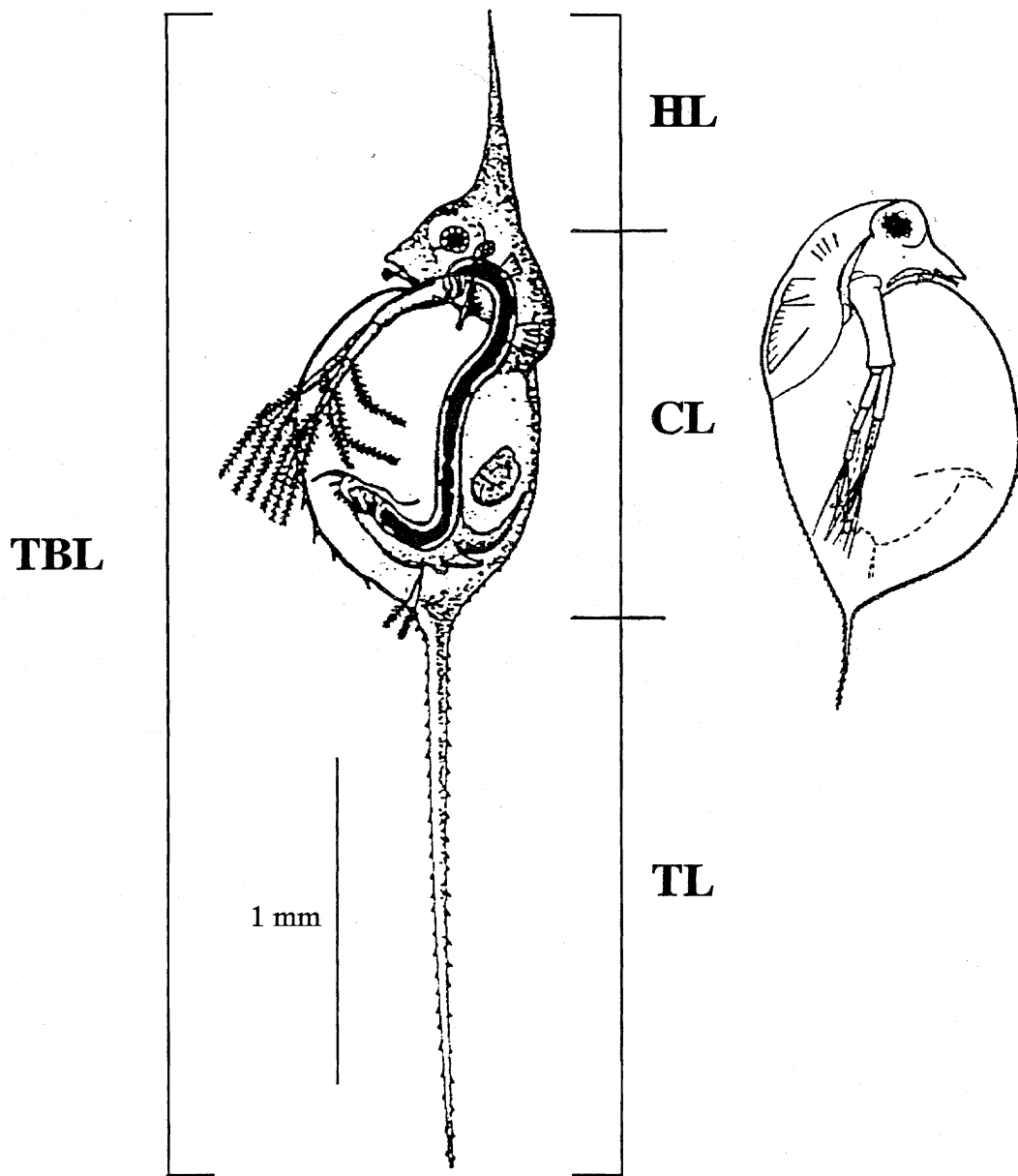
Measurements taken included carapace length (CL), helmet length (HL), and tailspine length (TL), the sum of which equals total body length (TBL) (Fig. 2).

Predation Experiments

Prior to each predation trial, *D. lumholtzi* and *D. pulex* were separated into four different size classes: neonate, small, medium, and large. Neonates were obtained by placing females with eggs deposited in their brood chamber into individual cultures the day before each trial. Second and third instars of each species were defined as the small size class, instars four and five were defined as the medium size class, and instars six or greater were defined as the large size class. To determine mean body size for both species of *Daphnia*, 10 individuals of each size class were preserved in 90% ethanol. *Daphnia* were measured with an ocular micrometer at 40x total magnification. Carapace length (CL) was used to compare size of the two species of *Daphnia* (Fig. 2).

Adult *Leptodora*, greater than 6.0 mm in length, were obtained from samples collected 24 hours prior to each trial. One adult *Leptodora* was placed into an individual culture cup containing approximately 25 mL of filtered lake water. After *Leptodora* were starved for 24 hours, 10 individuals of one size class and species of *Daphnia* were introduced into the predator culture vessel. For example, 10 *D. pulex* neonates were placed into an individual culture containing an adult *Leptodora*. In order to determine the vulnerability of each prey species, the number of *Daphnia* remaining were counted and recorded each hour for the first 12 hours. A dissecting microscope was used to count the smallest prey.

Figure 2. Morphometric measurements taken on *Daphnia lumholtzi* and *Daphnia pulex*. CL = carapace length, HL = helmet length, TL = total length, TBL = total body length. *D. lumholtzi* modified after Havel and Hebert (1993); *D. pulex* from Pennak (1953).



During each count, care was taken to limit disruption of predator-prey interaction. After 12 hours *Leptodora* were left to forage undisturbed for four hours. Additional prey counts were made after 16, 18, 22, and 24 hours. All experiments were terminated after 24 hours. *Leptodora* and any remaining prey were preserved in 90% ethanol. Body size of *Leptodora* was measured from the eye to the end of the caudal fork (Fig. 3).

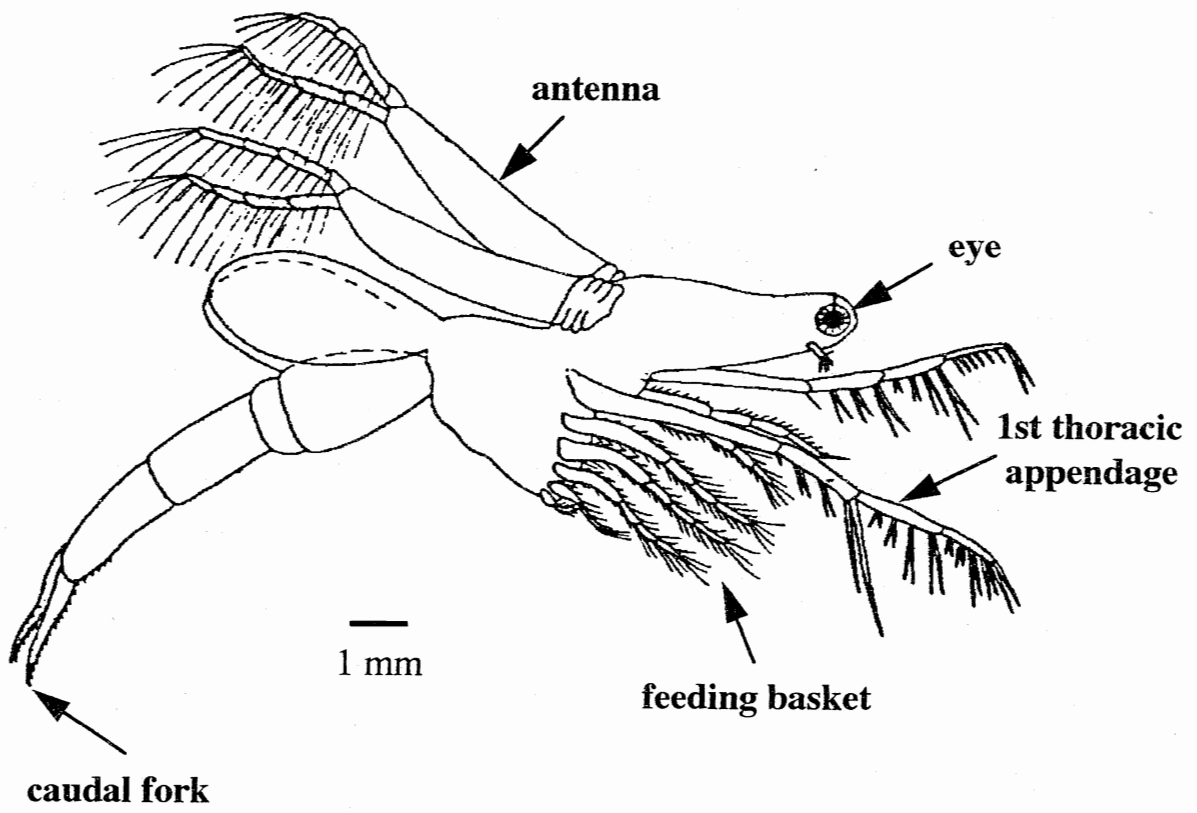
In order to determine selectivity of *Leptodora* for a particular prey item, additional predation experiments were completed by introducing both species of *Daphnia* to the predator at the same time. Experimental procedures were the same as those previously described except for the type of prey available. In these trials, five individuals from one size class of each species of *Daphnia* were placed into an individual culture containing one *Leptodora*. General procedures were the same as the previous predation experiments with the exception of the prey type available. Instead of beginning each trial with 10 prey from a single species, one *Leptodora* was offered five *D. lumholtzi* and five *D. pulex* of the same size class. Combined prey experiments were completed for neonate, small, and medium size classes. (After several weeks in culture the helmet height of adult *D. lumholtzi* declined; as a result, the largest size class was not tested in these combined prey experiments.)

Statistical Analyses

Life History Study

Sample mean and standard deviation were calculated for each life history characteristic monitored: age at first reproduction, number of offspring per brood, total number of

Figure 3. Body size of *Leptodora kindti* measured from eye to caudal fork (modified from Pennak, 1953).



broods, timing of brood, and total life span. A 95% confidence interval was then constructed around each mean. Results for *D. lumholtzi* were compared to published life history characteristics of native cladocerans.

Predation Experiment

Prior to conducting a predation rate analysis, it was necessary to determine if there was a difference between the size of both species of *Daphnia* within each size class and possible size differences between *Leptodora* used in various experiments. Student's t-test was used to test for equality of means within each size class for both species of *Daphnia* (Zar, 1974). Student's t-test was also calculated to detect any significant size difference between neonates, small, medium, and large size classes. Data Desk⁴ was used to conduct all analysis of variance and post hoc tests. In order to determine if there were any differences in the size of *Leptodora* used in the experiments between each size class and prey species, a 2-way ANOVA with interaction was performed with size of *Leptodora* as the dependent variable and size class and prey species as the independent variables.

To compare the vulnerability of *D. lumholtzi* and *D. pulex*, *Leptodora* predation rate was determined for each prey species and size class. A scatterplot was created for the number of prey consumed at the end of each observation hour and slope of the regression line was calculated as an indication of predation rate. For example, a "steep" slope was indicative of a faster predation rate. Data were tested for linearity with a statistical test for the lack-of-fit of a regression model (Montgomery and Peck, 1982). After determining that the data fit a linear equation, a regression line was calculated for each size class and prey species. Subsequently, 2-way ANOVA was used to calculate any significant

differences in the predation rate (slope) between size classes and prey species. The Least Significant Difference (LSD) Post Hoc test was performed to determine the specific differences between each size class and prey species.

RESULTS

Life History Study

Life history data were collected from *D. lumholtzi* individuals followed from neonate through their total life span (n = 31). *D. lumholtzi* helmet length, tailspine length, and carapace length were measured at birth. Mean and standard deviation were calculated for each life history characteristic. Mean total body length at birth of *D. lumholtzi* was 1.08 ± 0.04 mm and mean carapace length at birth was 0.52 ± 0.01 mm. Mean age at first reproduction was 7.8 ± 1.5 days. Mean number of offspring per brood was 8.5 ± 1.0 and mean total number of broods was 11.0 ± 1.7 . Mean total life span of *D. lumholtzi* was 38.5 ± 2.3 days.

In order to compare the life history characteristics of *D. lumholtzi* to native daphnids, 95% confidence intervals were constructed around each mean. Data collected in this study on *D. lumholtzi* were compared to previously reported life history characteristics for *D. pulex* and *D. magna* (Table 1). These species of *Daphnia* were used for this comparison because *D. pulex* carapace length and *D. magna* total body length is similar to the carapace length and total body length of *D. lumholtzi*. Life history characteristics of native species of *Daphnia* were compiled from studies which contained methods similar to those used in this study.

The 95 % C.I. for total body length of *D. lumholtzi* at birth was greater than the size of *D. pulex* and *D. magna* at birth. The difference in total body size was due to *D. lumholtzi*'s relatively long helmet and tailspine at birth. Excluding the helmet and tailspine, *D. lumholtzi* mean carapace length at birth (0.52 mm) was similar to the reported mean carapace length (0.56 mm) of *D. pulex* (Lynch, 1980). *Daphnia lumholtzi* age at first reproduction was similar to previous reports for *D. pulex* but earlier than *D. magna*.

Table 1. *D. lumholtzi* life history data with 95% C.I. compared to previously reported life history characteristics of similar sized native species of *Daphnia*.

References: a) Lynch, 1980; b) USEPA, 1991.

Species	Size at Birth TBL (mm)	Age at 1st Reproduction	Clutch Size	Total # of Broods	Life Span (days)
<i>D. lumholtzi</i>	1.04 - 1.10	7.3 - 8.3	8.1 - 8.8	10.4 - 11.6	37.7 - 39.3
<i>D. pulex</i>	0.69 a	7.7 b	8.5 a	15 b	50 b
<i>D. magna</i>	0.82 a	8.4 b	10.1 a	22 b	56 b

Clutch size, average number of offspring per brood, and total number of broods of *D. lumholtzi* were similar to *D. pulex* but smaller than those of *D. magna*. The greatest differences in life history characteristics were found in the life span of *D. lumholtzi* and the native species of *Daphnia*. Total life span of *D. lumholtzi* was shorter than the life span of both *D. pulex* and *D. magna*.

Predation Experiment

Carapace size of both species of *Daphnia* within each size class were compared. Differences between the mean size of *D. lumholtzi* and *D. pulex* within each size class were not significant ($P > 0.05$, Table 2).

Leptodora ranged in size from 6.30 mm to 10.00 mm. Mean size of *Leptodora* was calculated for each size class of *Daphnia* (Table 3). Overall mean size of *Leptodora* was 7.20 mm for trials with *D. lumholtzi* ($n=19$) and 7.22 mm for trials with *D. pulex* ($n=20$). Since results of a two-way ANOVA showed no significant interaction between prey size and species ($df = 3,31$, $F_{calc} = 0.1022$, $P > 0.05$), the interaction term was combined with the sums of squares error. No significant differences in *Leptodora* size was found between each species of *Daphnia* ($df = 1,34$, $F_{calc} = 0.0078$, $P > 0.05$) or size classes ($df = 3,34$, $F_{calc} = 2.3172$, $P > 0.05$).

Number of prey consumed at the end of each observation hour was recorded and mean number consumed for each prey item was calculated (Appendices A-D). Instead of simply comparing the number of prey consumed at the end of each observation hour, further analyses were completed to get a better estimate of predation rate by *Leptodora* on each prey item. A scatterplot was created for the number of prey consumed at the end of each observation hour and regression lines were calculated for each trial. Results of a lack-of-

Table 2. Mean carapace length of *D. lumholtzi* and *D. pulex* for each prey size class ($\bar{x} \pm SD$) and t-test results from comparisons within each size class ($t_{0.05, 9} = 2.262$).

Size Class	<i>D. lumholtzi</i>	<i>D. pulex</i>	t(calc)	n
Neonate	0.53 \pm 0.04 mm	0.56 \pm 0.02 mm	0.06	10
Small	0.76 \pm 0.02 mm	0.76 \pm 0.01 mm	0.88	10
Medium	1.22 \pm 0.06 mm	1.24 \pm 0.07 mm	0.40	10
Large	1.74 \pm 0.04 mm	1.82 \pm 0.13 mm	0.09	10

Table 3. Mean size of *Leptodora kindti* ($\bar{x} \pm SD$) for each prey size class.

<i>Daphnia</i> Size Class	Mean Size of <i>Leptodora</i>	n
Neonate	6.73 \pm 0.45 mm	10
Small	7.07 \pm 1.22 mm	10
Medium	7.30 \pm 0.56 mm	10
Large	7.73 \pm 0.91 mm	9

fit (LOF) test indicated that the regression function was linear only for data collected through the first 12 hours of all trials (Table 4). Because all 10 prey items had been consumed after 12 hours in three of the trials, the data were not linear when the entire data set (up to 24 hours) was included. Therefore, predation rate analyses were completed by determining a regression line for each size class and prey species using only the data collected during the first 12 hours of each trial (Appendix E).

Because there was no significant interaction between independent variables ($df = 3,31$, $F_{calc} = 2.1689$, $P > 0.05$), the interaction term was combined with the sums of squares error before calculating ANOVA and Post Hoc tests. Two-way ANOVA with slope as the dependent variable and prey items and size code as the independent variables revealed a significant difference in predation rate (i.e., slope) between size classes ($df = 1,34$, $F_{calc} = 7.6147$, $P < 0.05$) and between prey species ($df = 3,34$, $F_{calc} = 5.1254$, $P < 0.05$). Results of a Scheffé Post Hoc test showed a significant difference between neonates and large sizes classes ($P < 0.01$) and between small and large size classes ($P < 0.01$). In addition, slopes for all trials with *D. lumholtzi* were significantly greater than slopes for all trials with *D. pulex* ($P < 0.05$).

In order to determine more specific differences between each size class for each prey item, a one-way ANOVA was calculated with slope as the dependent variable and treatment as the independent variable. Differences between predation of each prey item were significant ($df = 7,31$, $F_{calc} = 5.4832$, $P < 0.01$). LSD Post Hoc tests revealed significant differences in slope for trials with *D. lumholtzi* between neonates and large, neonates and medium, and small and large size classes ($P < 0.05$, Figure 4). Significant differences were also found for trials with *D. pulex* between small and large prey items

Table 4. Linear regression for mean of slopes from the number of prey consumed by *Leptodora* at the end of each hour for 12 hours. Regressions were significant for each prey item (LOF test, $P < 0.05$, $F_0 = 1.99$).

Species	Size	Slope (β_1)	β_0	R^2	n	LOF F(calc)
<i>D. lumholtzi</i>	Neonate	0.5967	1.004	0.972	5	0.132
<i>D. pulex</i>	Neonate	0.3022	0.202	0.523	5	0.283
<i>D. lumholtzi</i>	Small	0.5626	0.209	0.833	5	0.145
<i>D. pulex</i>	Small	0.4209	0.536	0.841	5	0.214
<i>D. lumholtzi</i>	Medium	0.3077	0.246	0.866	5	0.689
<i>D. pulex</i>	Medium	0.2604	0.637	0.473	5	0.648
<i>D. lumholtzi</i>	Large	0.1854	0.099	0.399	4	0.136
<i>D. pulex</i>	Large	0.1176	0.013	0.634	5	1.405

Figure 4. Mean number of *D. lumholtzi* consumed by *Leptodora* at the end of each hour for 12 hours with regression line for each size class (n=5, except large n=4).

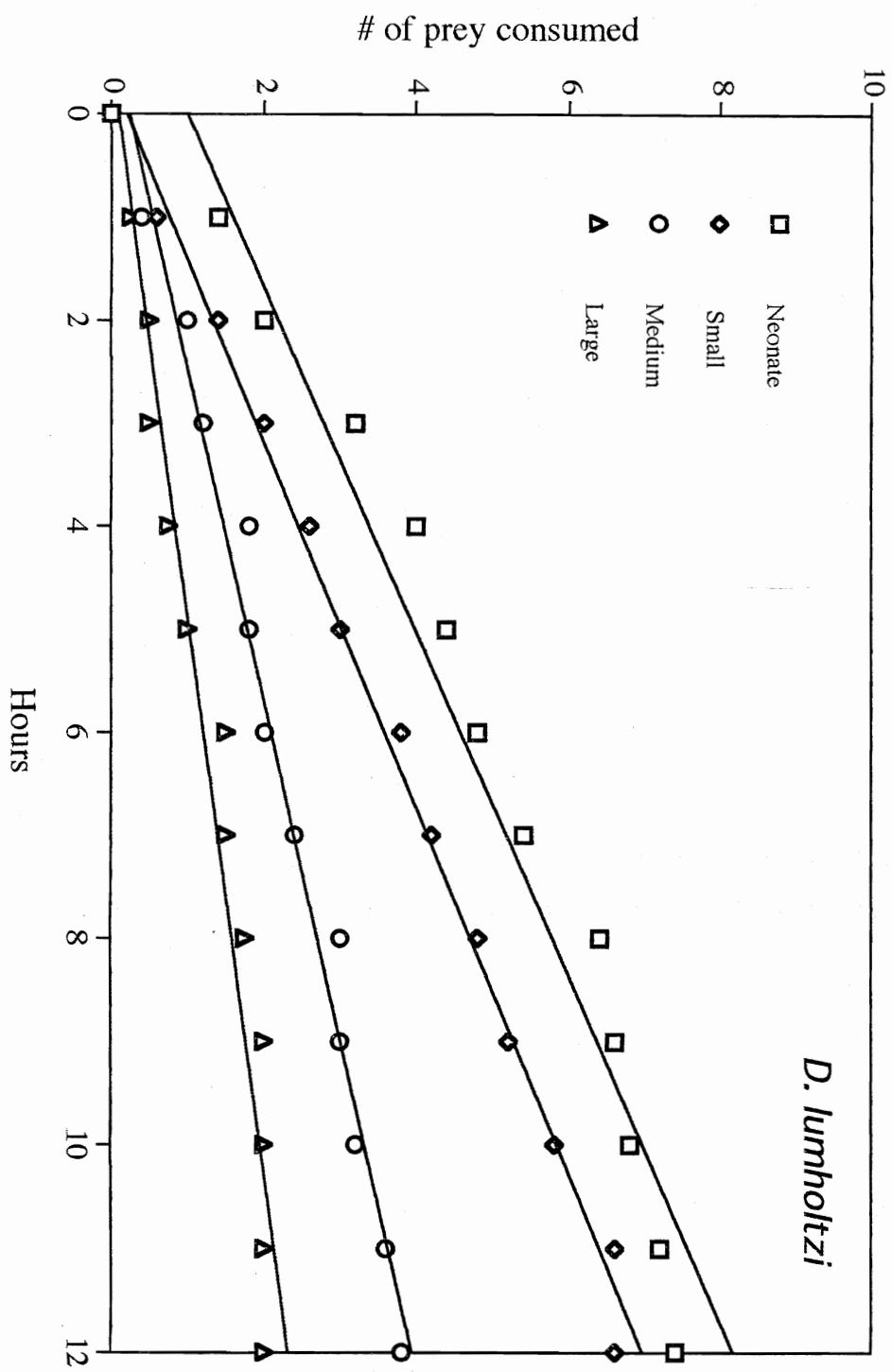


FIG. 12. Consumption of *D. lumholtzi* by *D. lumholtzi*.

($P < 0.05$, Figure 5). A comparison of all slopes revealed that the slope for *D. lumholtzi* neonates was significantly greater than the slopes for *D. pulex* neonates, *D. pulex* medium, and *D. pulex* large ($P < 0.05$, Figure 6). In addition, slope for *D. lumholtzi* small was significantly greater than slope for *D. pulex* large ($P < 0.05$, Figure 7). The expected mean of slopes including all size classes of each prey item was 0.40 for trials with *D. lumholtzi* and 0.29 for trials with *D. pulex*.

Electivity curves for *Leptodora* were created with mean of slopes data for both species of *Daphnia* (Figure 8). *Leptodora* predation of *D. pulex* followed the typical electivity curve of a size dependent predator with small individuals consumed at the fastest rate. However, the electivity curve from predation of *D. lumholtzi* was atypical for that involving a size dependent predator because *D. lumholtzi* neonates, the smallest size class, were consumed at a faster rate than would be expected.

Additional tests were conducted to determine selectivity of *Leptodora* when both prey items were available to the predator at the same time. Because few large prey items were consumed by *Leptodora* during the electivity experiments, the large size class prey were not used in the selectivity tests. Neonate, small, and medium size classes were tested in the combined prey experiments with five replicates for each size class. The number of prey remaining each observation hour was recorded and means were calculated for each prey item (Appendices F-H).

When both prey items were present, *D. lumholtzi* was selected by *Leptodora* at a faster rate than *D. pulex* in all three size classes (Figures 9-11). In many of the trials, *Leptodora* consumed most of the *D. lumholtzi* available before consuming any *D. pulex*. Comparing all three size classes, *Leptodora* displayed the strongest selectivity for *D. lumholtzi*

Figure 5. Mean number of *D. pulex* consumed by *Leptodora* at the end of each hour for 12 hours with regression line for each size class (n=5).

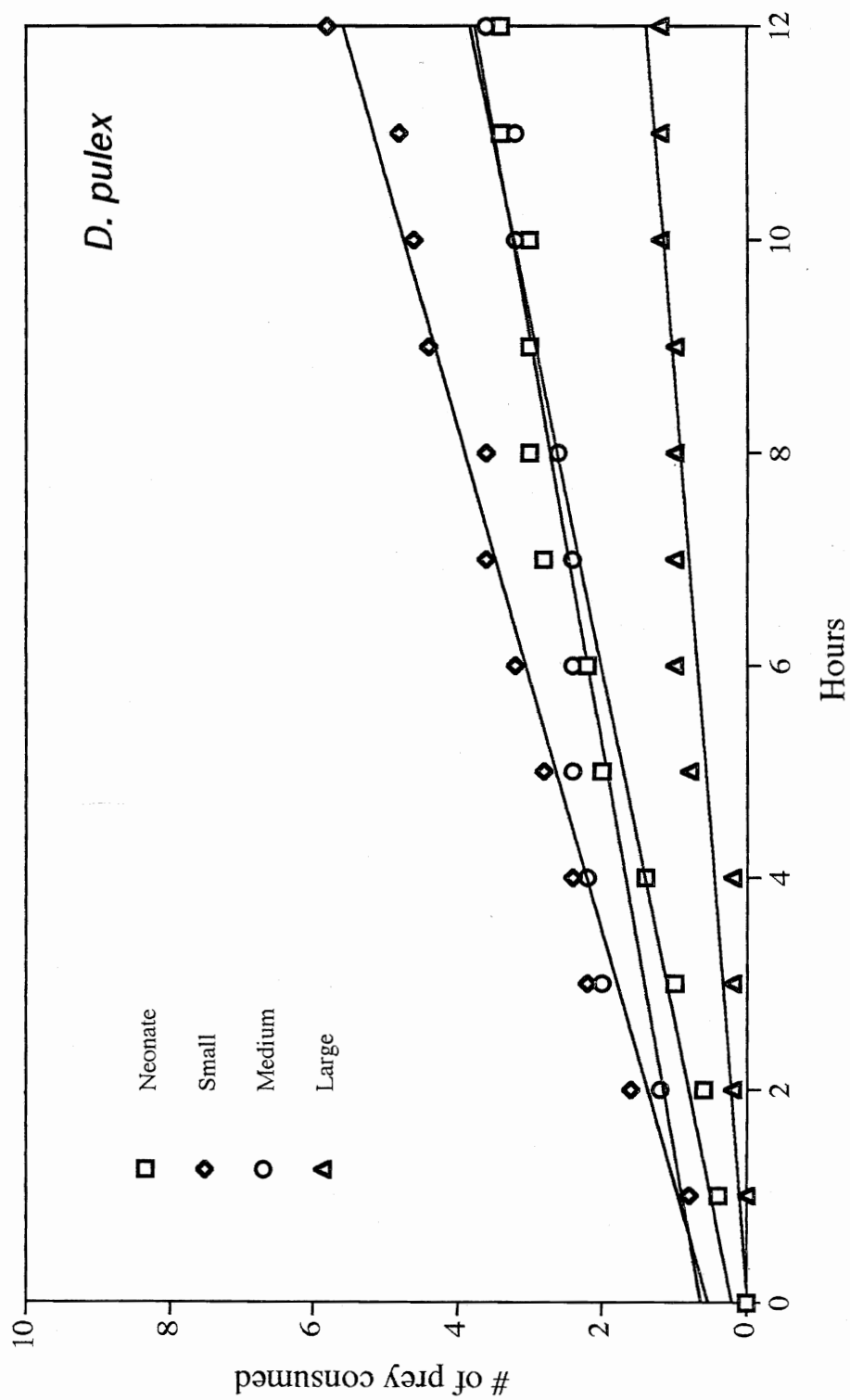


Figure 6. Mean number of prey consumed by *Leptodora* at the end of each hour for 12 hours with regression lines for each prey item. Significant differences in slope of the regression line were found between *D. lumholtzi* neonates and *D. pulex* neonates, medium, and large (Two-way ANOVA, $P < 0.05$).

Figure 6. Mean number of prey consumed by *Leptodora* at the end of each hour for 12 hours with regression lines for each prey item. Significant differences in slope of the regression line were found between *D. lumholtzi* neonates and *D. pulex* neonates, medium, and large (Two-way ANOVA, $P < 0.05$).

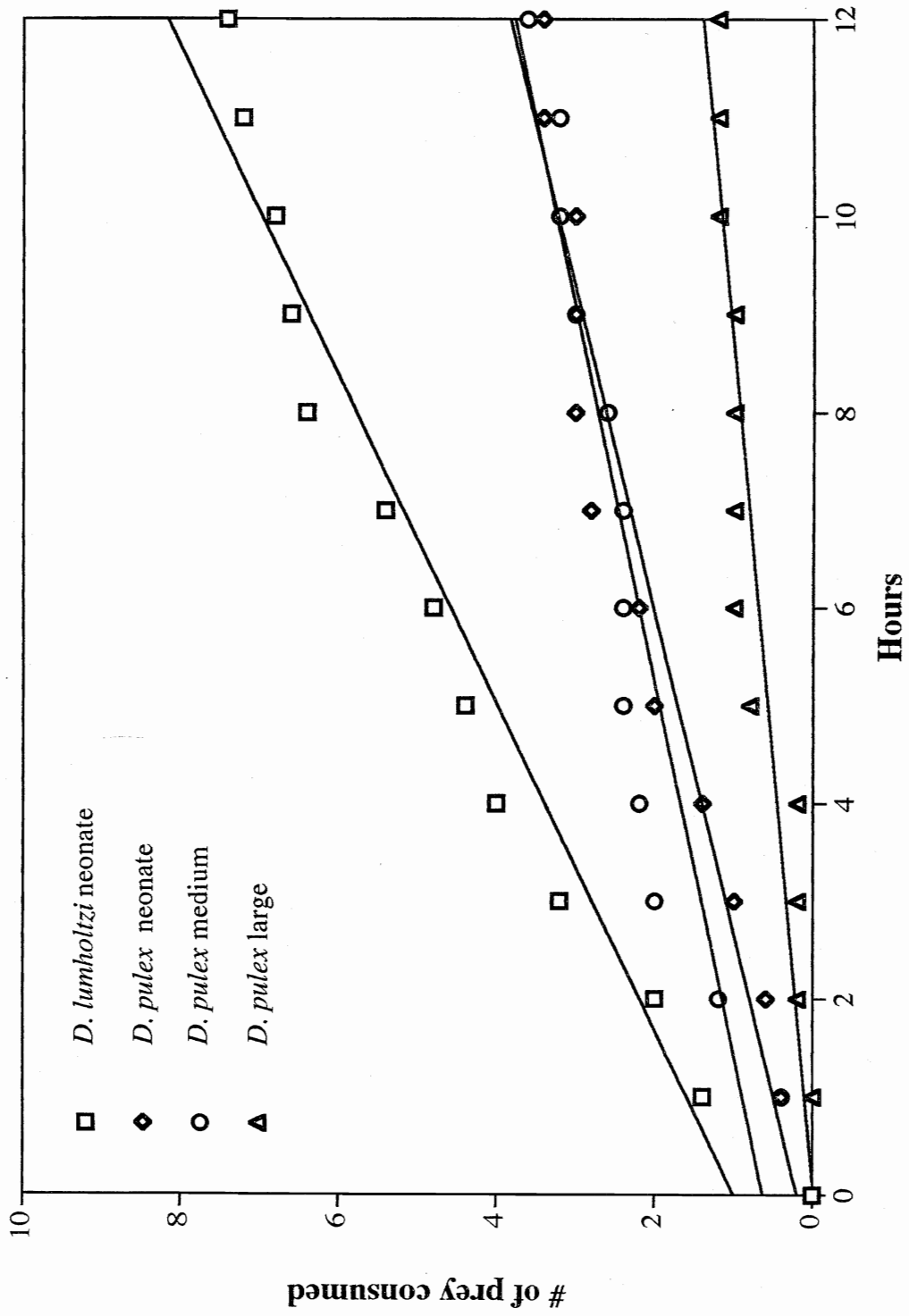


Figure 7. Mean number of prey consumed by *Leptodora* at the end of each hour for 12 hours with regression lines for each prey item. Significant difference in slope was found between *D. lumholtzi* small and *D. pulex* large (Two-way ANOVA, $P < 0.05$).

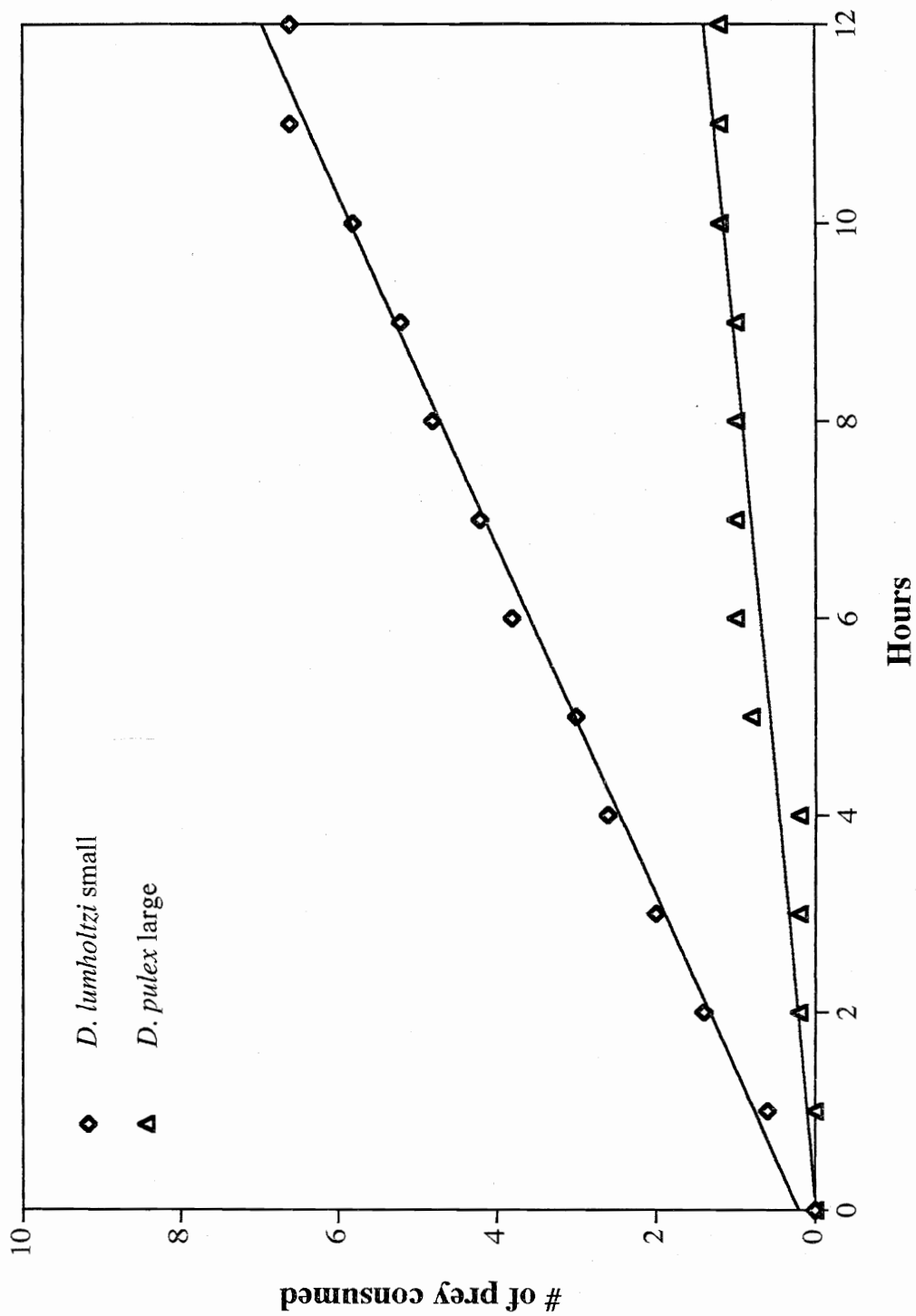


Figure 8. Electivity curves for *Leptodora kindti* created from mean of slopes for each size class of *D. lumholtzi* and *D. pulex*.

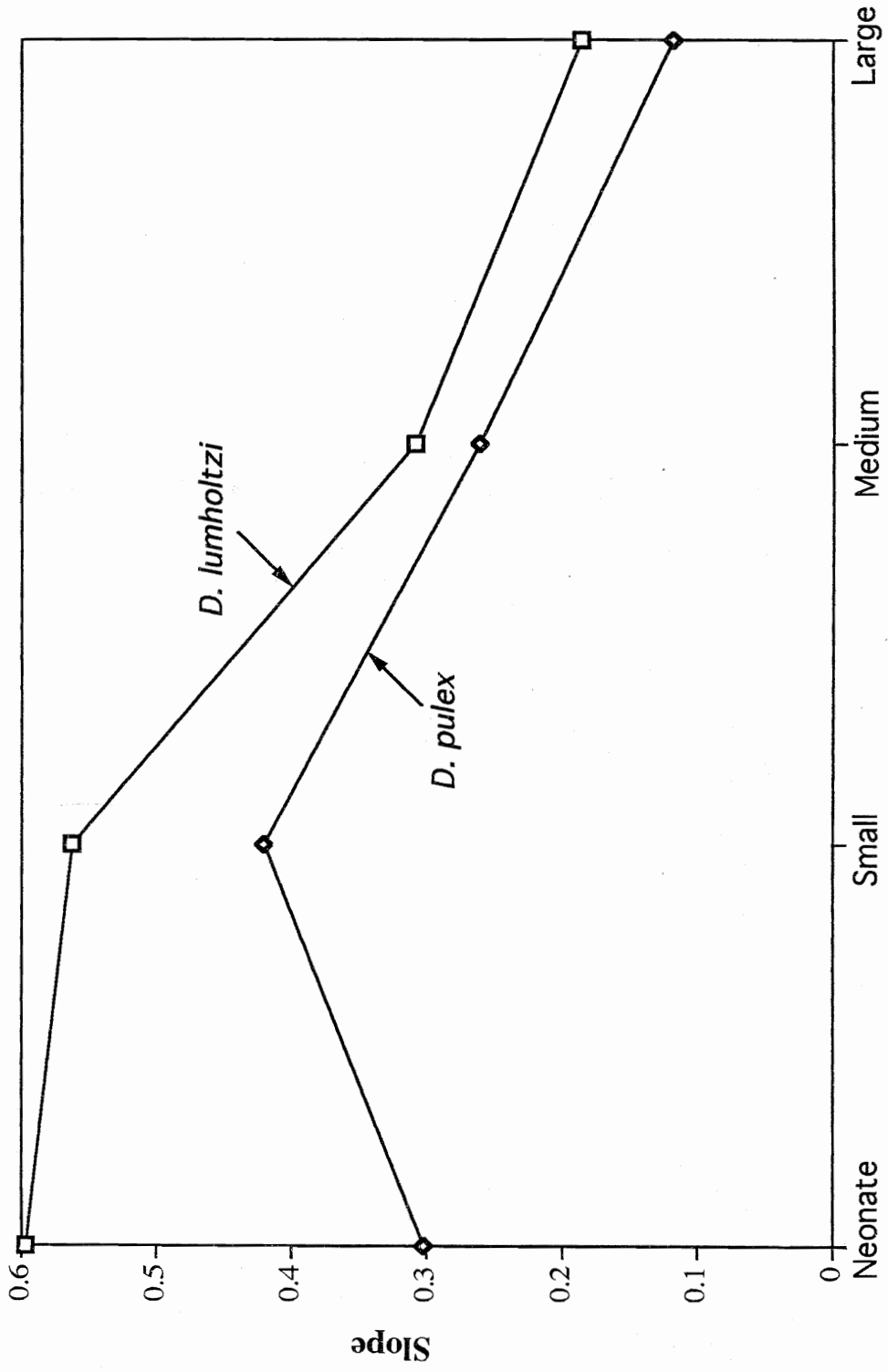


FIG. 10. SLOPE vs. SIZE CLASS

Figure 9. Mean number of neonates consumed at the end of each observation hour for combined prey experiments (n=5). Each trial began with five *D. lumholtzi* and five *D. pulex* introduced to *Leptodora* concurrently.

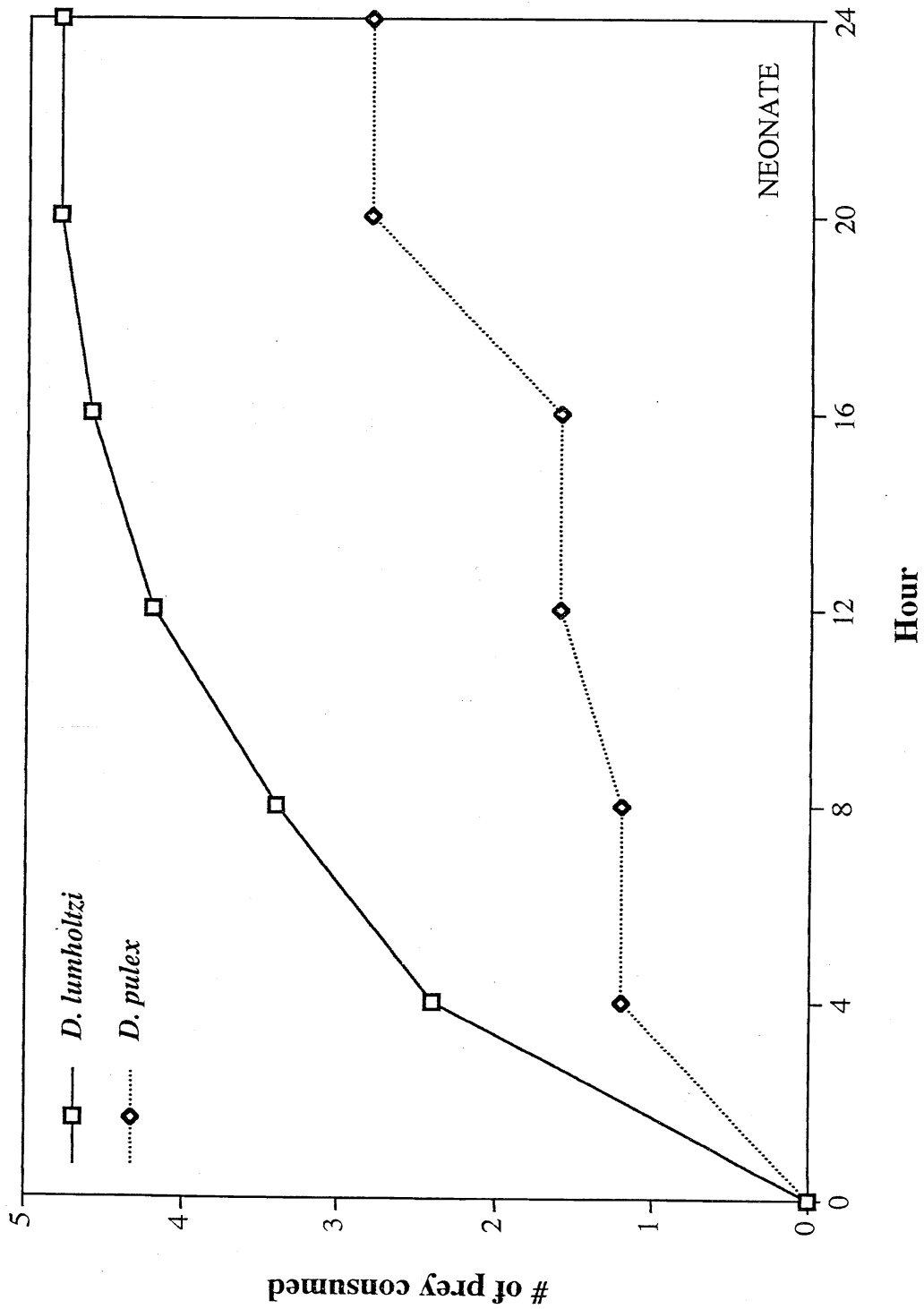


Figure 10. Mean number of small prey items consumed at the end of each observation hour for combined prey experiments (n=5). Each trial began with five *D. lumholtzi* and five *D. pulex* introduced to *Leptodora* concurrently.

PLATE 10
FIGURE 10
MEAN NUMBER OF SMALL PREY ITEMS CONSUMED AT THE END OF EACH OBSERVATION HOUR FOR COMBINED PREY EXPERIMENTS (n=5). EACH TRIAL BEGAN WITH FIVE *D. LUMHOLTZI* AND FIVE *D. PULEX* INTRODUCED TO *LEPTODORA* CONCURRENTLY.

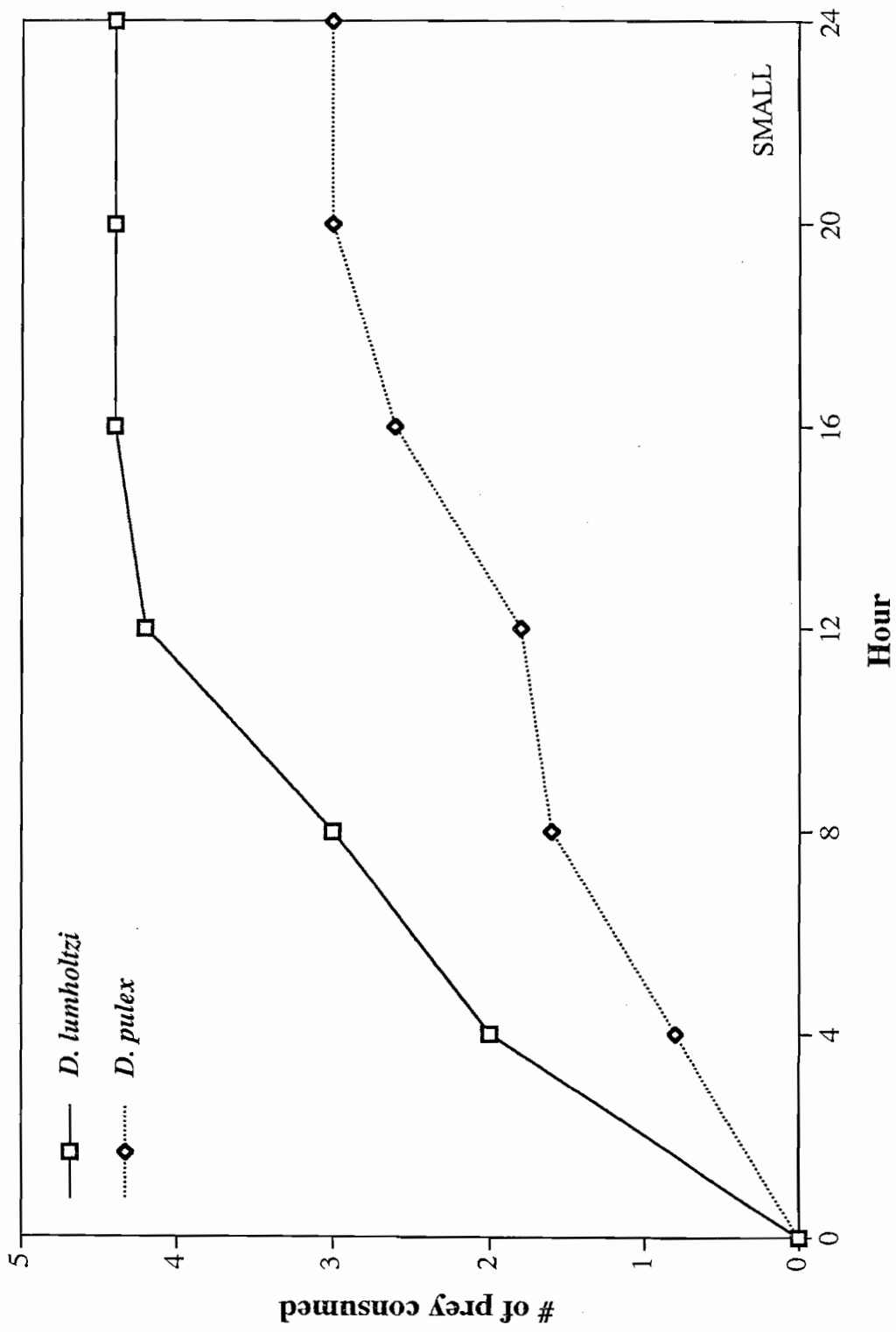


FIG. 10. Consumption of prey by *D. tumholtzi* and *D. pulex*.

Figure 11. Mean number of medium prey items consumed at the end of each observation hour for combined prey experiments (n=5). Each trial began with five *D. lumholtzi* and five *D. pulex* introduced to *Leptodora* concurrently.

neonates over *D. pulex* neonates. In one trial with neonate prey, *Leptodora* consumed all five *D. lumholtzi* within the first 16 hours but failed to consume any of the *D. pulex*.

Results from these selectivity experiments provide further support that *D. lumholtzi* may be more vulnerable than *D. pulex* to predation by *Leptodora*.

DISCUSSION

Life History Study

Life history characteristics of *D. lumholtzi* were compared to that of native species of *Daphnia*. Due to its relatively large helmet and tailspine, total body length of *D. lumholtzi* at birth was greater than the size of both species of native *Daphnia*. Riessen (1984) suggested that larger neonates would be less susceptible to invertebrate predation. Like most studies on size-dependent predation, Riessen used *Chaoborus* as the model for an invertebrate predator. While an increase in size is often considered an effective defense against size-dependent predators, in my predation experiments *Leptodora* consumed *D. lumholtzi* neonates at a faster rate than *D. pulex* neonates. Therefore, *D. lumholtzi*'s larger overall size at birth may not give it an advantage against invertebrate predators when compared to native daphnids.

Carapace length (total body length minus the length of helmet and tailspine) of *D. lumholtzi* at birth was in the same size range as *D. pulex* but smaller than *D. magna*. As a result, *D. lumholtzi*'s life history traits were more similar to *D. pulex* than to *D. magna*. Average age at first reproduction was 7.81 days for *D. lumholtzi* and appears to be very close to the average of 7.7 days reported for *D. pulex*. The similar number of offspring per brood for *D. lumholtzi* and *D. pulex* was probably due to similar carapace size, which may influence brood chamber size. Since total body length of *D. lumholtzi* neonates was larger than *D. pulex* neonates, one would expect a lower number of offspring per brood for *D. lumholtzi*. However, after several weeks in culture the helmet size of *D. lumholtzi* decreased. Studies have shown that the greater the size of the helmet the fewer eggs produced per clutch (Mort, 1986; Riessen, 1984). Reduction in helmet size may have resulted in a larger clutch size than may be found in field samples which could contain

neonates with more extreme helmet formation than was produced in the lab cultures. The tailspine, which accounted for nearly half of the total body length, did not appear to decrease significantly in culture but may not require much additional space in the brood chamber.

D. pulex and *D. magna* had a greater total number of broods than *D. lumholtzi*. Differences in the total number of broods were due to the shorter life span of *D. lumholtzi* compared to both native daphnids. On average, total life span of *D. lumholtzi* was approximately 12 days less than *D. pulex* and 18 days less than *D. magna*. Perhaps the extra energy required to produce offspring with a helmet and tailspine results in a shorter adult life span for *D. lumholtzi*.

My data do not show any life history traits that would confer an apparent advantage to the exotic at the expense of the native species. According to previous research, *D. lumholtzi* may have an advantage against some size-dependent predators (i.e., *Chaoborus*) with a larger overall size at birth. At the same time, the larger size may be disadvantageous in the presence of *Leptodora*. Based on the life history attributes compiled in this study, *D. pulex* and *D. magna* may have an advantage over the exotic species with a larger total number of broods and a longer life span.

Predation Experiments

According to all previous studies on invertebrate predation of *Daphnia*, the extreme cyclomorphic traits displayed by *D. lumholtzi* should have provided protection against *Leptodora*. Dodson (1974) and other studies (O'Brien et al., 1979; Zaret, 1980; Pijanowska, 1990) have proposed that *Daphnia* produce helmets to help protect it against

both fish and invertebrate predation. The production of cyclomorphic structures may complicate prey morphology to such an extent that capture becomes difficult (Lampert and Wolf, 1986). Various experiments conducted with the invertebrate predator *Chaoborus spp.* seem to support this hypothesis. Capture difficulty and lower predation rate by *Chaoborus* have been seen in *D. pulex* displaying a neck spine as compared to non-spined morphs (Repka et al., 1995). In addition, recent studies on *D. lumholtzi* show evidence that its helmet and tailspine may decrease predation by larval fish and *Chaoborus*. Swaffar and O'Brien (1996) reported that fourth instar *Chaoborus punctipennis* were unable to ingest *D. lumholtzi* that are 2.0 mm (TBL) or larger.

Results from my predation experiments contradict the findings of previous research on the effectiveness of cyclomorphosis as a defense mechanism against invertebrate predation. *Leptodora* consumed the extremely cyclomorphic *D. lumholtzi* at a higher rate than the non-spined *D. pulex* in all size classes. *D. lumholtzi* neonates were consumed at a significantly higher rate than *D. pulex* neonates, *D. pulex* medium, and *D. pulex* large size classes. In addition, *D. lumholtzi* small had a significantly higher predation rate by *Leptodora* than *D. pulex* large.

Electivity curves for *Leptodora* show distinct differences between predation rate on the two species of *Daphnia* and suggest a higher electivity for *D. lumholtzi* at all sizes. Because there were no significant differences in carapace length between the two species of *Daphnia* within each size class, vulnerability of *D. lumholtzi* to *Leptodora* may be attributed to aspects other than prey size. Similar results were found during the selectivity experiments. *Leptodora* displayed a preference for the exotic species when offered both at

the same time. On average, when both prey species were available, *Leptodora* consumed *D. lumholtzi* at a faster rate than *D. pulex*. *Leptodora* displayed the highest electivity and selectivity rates for *D. lumholtzi* neonates which suggests a preference for this prey item over all others tested.

While *Leptodora* predation of *D. pulex* followed the electivity curve proposed by Zaret (1980), the electivity curve for predation of *D. lumholtzi* did not follow the typical curve of a size dependent predator. Results from studies with *Chaoborus spp.* were used to form the electivity curve intended to describe all size dependent predators (Zaret, 1980). Due to different predation behaviors and limitations, predictions based on experiments performed with *Chaoborus* may not accurately explain results from similar tests with *Leptodora*. Browman et al. (1989) found that *Daphnia* are more susceptible than copepods to *Leptodora* predation. In contrast, *Chaoborus* prefer copepods over cladocerans due to greater handling problems with cladocerans after predator contact (Riessen et al., 1984). Predation behavior also differs between *Leptodora* and *Chaoborus*. While *Leptodora* continuously moves throughout the water column, *Chaoborus* is an "ambush" predator, remaining motionless until its prey swims into its range of attack (Pastorok, 1990).

Personal observations along with more detailed descriptions of the predation cycle for *Leptodora* yielded additional explanations of my results. The search mode of *Leptodora* is nonvisual and tactile (Herzig and Auer, 1990). Browman et al. (1989) reported that *Leptodora* does not initiate an attack unless it makes direct contact with potential prey. Although quantitative observations are needed to determine if *D. lumholtzi* has a higher

encounter rate with *Leptodora*, I suspect that *D. lumholtzi*'s exterior protrusions and large spines may increase the probability of a direct contact with *Leptodora* making it more vulnerable to predation than non-spined *Daphnia*.

Once the prey has been captured by *Leptodora*, the abdomen and telson are used to manipulate it within the feeding basket, to position it for the mandible or to more securely ensnare the prey. During this prey manipulation, I observed *D. pulex* individuals from the neonate and large size classes escape the feeding basket. Frequently, the relatively round *D. pulex* neonates were small enough to be able to pass between the limbs of the feeding basket before *Leptodora* closed them. Browman *et al.* (1989) found that large *D. pulex* escaped from the feeding basket and swam away in 40% of attacks by *Leptodora*. They concluded that prey capture or escape appears to be related to prey size or shape relative to the feeding basket.

Herzig and Auer (1990) concluded that the feeding basket size was the driving variable in size selection by *Leptodora*. Although the total body length of *D. lumholtzi* was often longer than the size of the feeding basket, I did not observe *D. lumholtzi* escape once captured. *Leptodora* was able to effect capture because the helmet and tailspine could protrude between the appendages of the feeding basket which seemed to stabilize the prey and provide easy access inside the *Daphnia*'s carapace. Instead of protecting the daphnid, the helmet and tailspine appeared to prevent *D. lumholtzi* from escaping once inside the feeding basket by deterring any possible evasive movements. The spines may allow *Leptodora* to get a better grip on its prey and therefore decrease the handling time and probability of escape.

Conclusions

The zooplankton community dynamics of reservoirs invaded by *D. lumholtzi* have been compared to reservoirs without the exotic species (Havel et al., 1995; Kolar et al., 1997). The decrease in native zooplankton populations in the invaded reservoirs does not correspond with normal seasonal population changes observed in reservoirs without the exotic species. This may suggest that native zooplankton populations decreased due to the presence of *D. lumholtzi*. Based on the life history characteristics collected in this study, there appears to be no indication that the exotic daphnid could displace native daphnids. Although average age at first reproduction and total number of offspring per brood do not seem to differ between the exotic species and similar sized native *Daphnia*, *D. lumholtzi* had fewer broods and a shorter life span.

The life history traits observed for *D. lumholtzi* do not appear to provide any inherent advantage to the exotic over native species of *Daphnia*. However, since *D. lumholtzi* is native to hotter climates, it is likely that the dominance of *D. lumholtzi* in local reservoirs at the end of the summer may be due to a higher temperature tolerance than native zooplankton. Additional studies are needed to compare the temperature tolerance and subsequent growth rate of *D. lumholtzi* and *D. pulex*.

My data suggest that *D. lumholtzi*'s cyclomorphic features do not protect it from predation by *Leptodora*. In fact, the helmet and tailspine may make it an easier target for this predator by increasing the likelihood of detection or decreasing its ability to escape once captured. Further studies are needed, which would include a quantitative analysis of each component of *Leptodora*'s predation cycle, to determine the most probable

explanation for my results.

Although cyclomorphic morphology appears to be a disadvantage against *Leptodora* predation, it is likely *D. lumholtzi* produces helmet to help protect it against other invertebrate predators and planktivorous fish. Studies show that chemicals (kairomones) released by *Chaoborus* larvae are effective in inducing helmet growth in *Daphnia* (Dodson, 1988; Hanazato, 1990; Tollrian, 1990). Recently, Tollrian (1994) found that fish kairomones can enhance helmet growth in *D. lumholtzi*.

Due to its relatively large size and extreme cyclomorphic features, previous studies suggest that *D. lumholtzi* has the potential to disrupt native food webs. Researchers have shown that *D. lumholtzi* may be difficult for larval fish (26-35 mm) to consume (Swaffar and O'Brien, 1996). However, the reproductive timing of fish and temporal occurrence of *D. lumholtzi* must be considered before determining possible impacts on fish populations. Since *D. lumholtzi* has been most abundant in late summer, fish that spawn in spring and early summer may not be impacted by the presence of this exotic.

Predation by *Leptodora* can significantly reduce the densities of *Daphnia* populations (Branstrator and Lehman, 1991). Research following the population growth of *D. lumholtzi* and distribution of *Leptodora* in local reservoirs may provide more insight into the role the invertebrate may play in controlling the exotic daphnid population. These additional studies would help determine the potential impact *D. lumholtzi* may have on North American reservoirs.

LITERATURE CITED

- Benzie, J. A. H. 1987. The systematics of Australian *Daphnia* (Cladocera: Daphnidae).
Species descriptions and keys. *Hydrobiologia* 166: 95-161.
- Branstrator, D. K., and J. T. Lehman. 1991. Invertebrate predation in Lake Michigan:
Regulation of *Bosmina longirostris* by *Leptodora kindti*. *Limnol. Oceanogr.* 36: 483-495.
- Browman, H. I., S. Kruse, and W. J. O'Brien. 1989. Foraging behavior of the predaceous
cladoceran, *Leptodora kindti*, and escape responses of their prey. *J. Plankton Res.* 11:
1075-1088.
- Cummins, K. W., R. R. Costa, R. E. Rowe, G. A. Moshiri, R. M. Scanlon, and R. K.
Zajdel. 1969. Ecological energetics of a natural population of the predaceous
zooplankter *Leptodora kindtii* Focke (Cladocera). *Oikos* 20: 189-223.
- Dodson, S. I. 1974. Zooplankton competition and predation: An experimental test of the
size-efficiency hypothesis. *Ecology* 55(3): 605-613.
- Dodson, S. I. 1988. The ecological role of chemical stimuli for the zooplankton:
predator-avoidance behavior in *Daphnia*. *Limnol. Oceanogr.* 33: 1431-1439.
- Green, J. 1967. The distribution and variation of *Daphnia lumholtzi* (Crustacea:
Cladocera) in relation to fish predation in Lake Albert, East Africa. *J. Zool. Lond.*
165: 373-414.
- Hanazato, T. 1990. Induction of helmet development by a *Chaoborus* factor in *Daphnia*
ambigua during juvenile stages. *J. Plankton Res.* 12: 1287-1294.
- Hanazato, T., and M. Yasuno. 1989. Zooplankton community structure driven by
vertebrate and invertebrate predators. *Oecologia* 81: 450-458.

- Havel, J. E., and D. I. Dodson. 1984. *Chaoborus* predation on typical and spined morphs of *Daphnia pulex*: behavioral observations. *Limnol. Oceanogr.* 29: 487-494.
- Havel, J. E., and P. D. Hebert. 1993. *Daphnia lumholtzi* in North America: Another exotic zooplankter. *Limnol. Oceanogr.* 38: 1823-1827.
- Havel, J. E., W. R. Mabee, and J. R. Jones. 1995. Invasion of the exotic cladoceran *Daphnia lumholtzi* into North American reservoirs. *Can. J. Fish Aquat. Sci.* 52: 151-160.
- Herzig, A., and B. Auer. 1990. The feeding behavior of *Leptodora kindti* and its impact on the zooplankton community of Neusiedler See (Austria). *Hydrobiologia* 198: 107-117.
- Hovenkamp, W. 1990. Instar-specific mortalities of coexisting *Daphnia* species in relation to food and invertebrate predation. *J. Plankton Res.* 12: 483-495.
- Hutchinson, G. E. 1967. *A Treatise on Limnology*, Vol II. Wiley, New York.
- Jacobs, J. 1961. Cyclomorphosis in *Daphnia galeata mendotae* Birge, a case of environmentally controlled allometry. *Arch. Hydrobiol.* 58: 7-71.
- King, C. R., and J. G. Greenwood. 1992. The productivity and carbon budget of a natural population of *Daphnia lumholtzi* Sars. *Hydrobiologia* 231: 197-207.
- Kolar, C. S., J. C. Boase, D. F. Clapp, and D. H. Wahl. 1997. Potential effect of invasion by an exotic zooplankter, *Daphnia lumholtzi*. *J. Freshwat. Ecol.* 12: 521-530.
- Krueger, D. A., and S. I. Dodson. 1981. Embryological induction and predation ecology in *Daphnia pulex*. *Limnol. Oceanogr.* 26: 219-223.

- Lambert, W., and H. G. Wolf. 1986. Cyclomorphosis in *Daphnia cucullata*: morphometric and population genetic analyses. *J. Plankton Res.* 8: 289-303.
- Lynch, M. 1980. The evolution of cladoceran life histories. *Quart. Rev. Biol.* 55: 23-42.
- Lysebo, E. M. 1995. Behavioral and morphological changes in polymorphic *Daphnia* related to different predation regimes. *Hydrobiologia* 307: 185-191.
- Montgomery, D. C., and E. A. Peck. 1982. Introduction to linear regression analysis. John Wiley and Sons, Inc., New York. pp. 75-79.
- Mordukhai-Boltovskaia, E. D. 1958. Preliminary notes on the feeding of the carnivorous cladocerans *Leptodora kindtii* and *Bythotrephes*. *Dokl. Acad. Nauk SSSR, Biol. Sci. Sect. Hydrobiol.* 122: 828-830.
- Mort, M. A. 1986. *Chaoborus* predation and the function of phenotypic variation in *Daphnia*. *Hydrobiologia* 133: 39-44.
- Mort, M. A. 1989. Cyclomorphosis in *Daphnia galeata mendotae*: Variation and stability in phenotypic cycles. *Hydrobiologia* 171: 159-170.
- O'Brien, J. W., D. Kettle, and H. Riessen. 1979. Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. *Ecology* 60: 287-294.
- Pastorok, R. A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62: 1311-1324.
- Pennak, R. W. 1953. Fresh-water invertebrates of the United States. The Ronald Press Co., New York.
- Pijanowska, J. 1990. Cyclomorphosis in *Daphnia*: an adaptation to avoid invertebrate predation. *Hydrobiologia* 198: 41-50.

- Repka, S., M. Walls, and M. Ketola. 1995. Neck spine protects *Daphnia pulex* from predation by *Chaoborus*, but individuals with longer tail spine are at a greater risk. *J. Plankton Res.* 17: 393-403.
- Riessen, H. P. 1984. The other side of cyclomorphosis: Why *Daphnia* lose their helmets. *Limnol. Oceanogr.* 29: 1123-1127.
- Riessen, H. P., J. W. O'Brien, and B. Loveless. 1995. An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of relative prey vulnerabilities. *Ecology* 65: 514-522.
- Sorensen, K. H., and R. W. Sterner. 1992. Extreme cyclomorphosis in *Daphnia lumholtzi*. *Freshwat. Biol.* 28: 257-262.
- Swaffar, S. M., and W. J. O'Brien. 1996. Spines of *Daphnia lumholtzi* create feeding difficulties for juvenile bluegill sunfish (*Lepomis macrochirus*). *J. Plankton Res.* 18: 1055-1061.
- Swift, M. C. 1992. Prey capture by the four larval instars of *Chaoborus crystallinus*. *Limnol. Oceanogr.* 37: 14-24.
- Tolliran, R. 1990. Predator-induced helmet formation in *Daphnia cucullata* (Sars). *Arch. Hydrobiol.* 119: 191-196.
- Tolliran, R. 1994. Fish-kairomone induced morphological changes in *Daphnia lumholtzi* (Sars). *Arch. Hydrobiol.* 130: 69-75.
- U. S. Environmental Protection Agency. 1991. Methods for measuring the acute toxicity of effluents and receiving waters to freshwater and marine organisms. U.S. EPA, Office of Research and Development, Washington, DC. pp. 152-168.

- Work, K., and M. Gophen. 1995. The invasion of *Daphnia lumholtzi* (Sars) into Lake Texoma (USA). Arch. Hydrobiol. 133: 287-303.
- Wright, J. C. 1965. The population dynamics of *Daphnia* in Caryon Ferry reservoir, Montana. Limnol. Oceanogr. 10: 583-590.
- Zar, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ. pp. 108.
- Zaret, T. M. 1980. Predation and Freshwater Communities. Yale University Press, New Haven. pp. 3-6, 48-60.

APPENDICES

Appendix A. Number of neonate prey consumed by *Leptodora* at the end of each observation hour and mean number of each prey item consumed. *D. lum* = *D. lumbholtzi*, *D. pul* = *D. pulex*.

Hour	<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. pul</i>		<i>D. pul</i>		<i>D. pul</i>	
	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	neonate	Mean
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
1	1	2	2	1	1	1	1	1	1	1	1	0	0	0	0	0.4
2	2	3	3	1	1	1	1	1	2	2	0	0	0	0	0	0.6
3	2	5	4	3	2	2	2	2	2	2	1	0	0	0	0	1.0
4	3	6	4	4	5	2	2	3	2	2	1	1	0	0	0	1.4
5	3	7	4	4	6	2	2	4	2	2	2	1	1	1	1	2.0
6	3	7	4	4	7	3	3	5	2	2	2	1	1	1	1	2.2
7	4	8	5	5	7	3	3	5	2	2	3	1	3	3	2	2.8
8	6	9	6	6	7	4	4	5	2	2	3	2	3	3	3	3.0
9	6	9	6	6	7	5	5	5	2	2	3	2	3	3	3	3.0
10	6	9	6	6	7	6	6	5	2	2	3	2	3	3	3	3.0
11	6	9	6	6	7	6	6	5	2	2	4	2	4	4	4	3.4
12	6	9	6	6	9	7	7	5	2	2	4	2	4	4	4	3.4
16	7	10	8	9	9	7	7	5	3	3	6	3	6	6	6	4.6
18	7	10	8	10	8	8	8	5	3	3	6	3	6	6	6	4.6
20	7	10	9	10	8	8	8	5	3	3	6	4	6	6	6	4.8
22	7	10	9	10	8	8	8	5	3	3	6	4	6	6	6	4.8
24	7	10	9	10	8	8	8	5	5	5	7	4	7	7	7	5.6

Appendix B. Number of small prey consumed by *Leptodora* at the end of each observation hour and mean number consumed for each prey item. *D. lum* = *D. lumholtzi*, *D. pul* = *D. pulex*.

Hour	<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. pul</i>		<i>D. pul</i>		<i>D. pul</i>	
	small	small	small	small	small	small	small	small	small	small	small	small	small	small	small	small	small	Mean
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
1	0	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0.8
2	2	1	1	2	1	1	2	2	2	2	2	2	2	2	2	2	2	1.6
3	3	2	1	2	2	2	2	3	3	3	3	3	3	3	3	3	3	2.2
4	3	3	1	3	3	3	3	3	3	3	3	3	3	3	3	3	3	2.4
5	3	4	1	4	4	4	4	4	4	4	4	4	4	4	4	4	4	2.8
6	3	6	2	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3.2
7	4	6	3	4	4	4	4	4	4	4	4	4	4	4	4	4	4	3.6
8	5	7	3	4	4	4	5	4	4	4	4	4	4	4	4	4	4	3.6
9	5	7	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	4.4
10	6	8	4	5	5	6	6	6	6	6	6	6	6	6	6	6	6	4.6
11	6	8	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	4.8
12	6	8	6	6	6	7	7	7	7	7	7	7	7	7	7	7	7	5.8
16	8	10	8	7	7	8	8	8	8	8	8	8	8	8	8	8	8	6.2
18	8	10	8	7	7	8	8	8	8	8	8	8	8	8	8	8	8	6.2
20	8	10	8	7	7	9	9	9	9	9	9	9	9	9	9	9	9	6.4
22	8	10	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	6.6
24	9	10	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	6.8

Appendix C. Number of medium prey consumed by *Leptodora* at the end of each observation hour and mean number consumed for each prey item. *D. lum* = *D. lumholtzi*, *D. pul* = *D. pulex*.

Hour	<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. pul</i>		<i>D. pul</i>		<i>D. pul</i>		<i>D. pul</i> Mean
	med	med	med	med	med	med	Mean	med	med	med	med	med	med	med	med	med	Mean		
0	0	0	0	0	0	0	0.0	0	0	0	0	0	0	0	0	0	0.0		
1	0	1	0	1	0	0	0.4	0	1	1	1	0	0	0	0	0	0.4		
2	0	2	1	1	1	1	1.0	1	2	2	2	0	1	1	1	1.2			
3	0	2	2	1	1	1	1.2	2	2	2	3	1	2	2	2	2.0			
4	1	2	2	2	2	2	1.8	3	2	2	3	1	2	2	2	2.2			
5	1	2	2	2	2	2	1.8	4	2	2	3	1	2	2	2	2.4			
6	2	2	2	2	2	2	2.0	4	2	2	3	1	2	2	2	2.4			
7	2	2	3	3	2	2	2.4	4	2	2	3	1	2	2	2	2.4			
8	3	3	3	3	3	3	3.0	4	2	2	4	1	2	2	2	2.6			
9	3	3	3	3	3	3	3.0	5	2	2	4	2	2	2	2	3.0			
10	3	4	3	3	3	3	3.2	5	2	2	4	3	3	2	2	3.2			
11	3	4	3	4	4	4	3.6	5	2	2	4	3	3	2	2	3.2			
12	4	4	3	4	4	4	3.8	5	3	3	5	3	3	2	2	3.6			
16	6	4	6	5	5	5	5.2	5	4	4	6	4	4	2	2	4.2			
18	6	5	6	5	5	5	5.4	5	4	4	6	4	4	3	3	4.4			
20	6	5	6	5	5	5	5.4	5	4	4	6	4	4	3	3	4.4			
22	6	5	6	6	6	6	5.8	5	5	5	6	4	4	3	3	4.6			
24	6	5	6	6	6	6	5.8	6	5	5	6	4	4	3	3	4.8			

Appendix D. Number of large prey consumed by *Leptodora* at the end of each observation hour and mean number consumed for each prey item. *D. lum* = *D. lumholtzi*, *D. pul* = *D. pulex*.

Hour	<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. lum</i>		<i>D. pul</i>		<i>D. pul</i>		<i>D. pul</i>	
	large	large	large	large	large	large	large	large	large	large	large	large	large	large	large	Mean
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
2	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0.2
3	0	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0.2
4	0	3	0	0	0	0	0	0	0	0	1	0	0	0	0	0.2
5	1	3	0	0	0	0	0	1	0	1	1	1	1	1	1	0.8
6	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1.0
7	1	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1.0
8	2	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1.0
9	2	3	1	1	2	2	2	2	2	1	1	1	1	1	1	1.0
10	2	3	1	1	2	2	2	2	2	1	1	2	1	1	1	1.2
11	2	3	1	1	2	2	2	2	2	1	1	2	1	1	1	1.2
12	2	3	1	1	2	2	2	2	2	1	1	2	1	1	1	1.2
16	3	5	2	2	2	2	2	2	2	1	1	2	1	1	1	1.2
18	3	5	2	2	2	2	2	2	2	1	1	2	1	1	1	1.2
20	3	5	2	2	3	3	3	3	3	1	1	2	1	2	2	1.4
22	3	5	2	2	3	3	3	3	3	1	1	2	1	2	2	1.4
24	3	5	2	2	3	3	3	3	3	1	1	2	1	2	2	1.4

Appendix E. Slope of regression line calculated from the number of prey consumed by *Leptodora* at the end of each observation hour for 12 hours.

Prey Item Size Class	Trial 1 Slope	Trial 2 Slope	Trial 3 Slope	Trial 4 Slope	Trial 5 Slope	Mean Slope
<i>D. lumholtzi</i> neonate	0.5275	0.7253	0.4341	0.7418	0.5550	0.5967
<i>D. pulex</i> neonate	0.4400	0.0934	0.3681	0.2088	0.4011	0.3022
<i>D. lumholtzi</i> small	0.5110	0.7472	0.5110	0.4615	0.5824	0.5626
<i>D. pulex</i> small	0.3242	0.4450	0.3736	0.3846	0.5770	0.4209
<i>D. lumholtzi</i> medium	0.3571	0.2857	0.2582	0.3077	0.3297	0.3077
<i>D. pulex</i> medium	0.4505	0.1264	0.3187	0.2637	0.1729	0.2604
<i>D. lumholtzi</i> large	0.2198	0.1923	0.1154	0.2143	-----	0.1854
<i>D. pulex</i> large	0.1099	0.1154	0.1429	0.1099	0.1099	0.1176

Appendix F. Number of neonate prey remaining each observation hour from combined prey experiments. First number in each cell is the number of *D. lumholtzi* remaining followed by the number of *D. pulex* remaining (*D. lumholtzi* / *D. pulex*).

Hour	Neonate	Neonate	Neonate	Neonate	Neonate	Mean
0	5 / 5	5 / 5	5 / 5	5 / 5	5 / 5	5.0 / 5.0
1	3 / 5	3 / 5	4 / 4	4 / 4	5 / 5	3.8 / 4.6
2	3 / 5	2 / 5	4 / 4	3 / 4	3 / 5	3.0 / 4.6
3	3 / 5	1 / 4	4 / 4	2 / 4	3 / 4	2.6 / 4.2
4	3 / 5	1 / 3	4 / 3	2 / 4	3 / 4	2.6 / 3.8
5	3 / 5	1 / 3	4 / 3	2 / 4	3 / 4	2.6 / 3.8
6	3 / 5	1 / 3	3 / 3	2 / 4	2 / 4	2.2 / 3.8
7	3 / 5	1 / 3	2 / 3	2 / 4	2 / 4	2.0 / 3.8
8	3 / 5	1 / 3	2 / 3	1 / 4	1 / 4	1.6 / 3.8
9	3 / 5	1 / 3	1 / 3	1 / 3	1 / 3	1.4 / 3.4
10	3 / 5	0 / 3	1 / 3	1 / 3	1 / 3	1.2 / 3.4
11	3 / 5	0 / 3	1 / 3	1 / 3	1 / 3	1.2 / 3.4
12	2 / 5	0 / 3	0 / 3	1 / 3	1 / 3	0.8 / 3.4
16	0 / 5	0 / 2	0 / 2	1 / 3	1 / 2	0.4 / 2.8
18	0 / 5	0 / 2	0 / 2	1 / 1	1 / 2	0.4 / 2.4
20	0 / 5	0 / 2	0 / 2	1 / 0	0 / 2	0.2 / 2.2
22	0 / 5	0 / 2	0 / 2	1 / 0	0 / 2	0.2 / 2.2
24	0 / 5	0 / 2	0 / 2	1 / 0	0 / 2	0.2 / 2.2

Appendix G. Number of small prey remaining each observation hour from combined prey experiments. First number in each cell is the number of *D. lumholtzi* remaining followed by the number of *D. pulex* remaining (*D. lumholtzi* / *D. pulex*).

Hour	Small	Small	Small	Small	Small	Mean
0	5/5	5/5	5/5	5/5	5/5	5.0/5.0
1	4/5	4/5	5/5	4/5	4/5	4.2/5.0
2	3/5	4/5	5/4	4/5	3/5	3.8/4.8
3	3/4	3/5	4/4	4/4	3/5	3.4/4.4
4	2/4	3/5	4/4	3/4	3/4	3.0/4.2
5	2/3	3/4	4/4	2/4	3/4	2.8/3.8
6	2/3	3/4	4/4	1/3	2/4	2.4/3.6
7	2/2	3/4	4/4	0/3	2/4	2.2/3.4
8	2/2	3/4	4/4	0/3	1/4	2.0/3.4
9	1/2	2/4	4/4	0/3	1/4	1.6/3.4
10	1/2	2/4	4/4	0/3	1/3	1.6/3.2
11	1/2	1/4	3/4	0/3	1/3	1.2/3.2
12	0/2	1/4	3/4	0/3	0/3	0.8/3.2
16	0/1	0/2	3/4	0/2	0/3	0.6/2.4
18	0/1	0/2	3/4	0/2	0/2	0.6/2.2
20	0/1	0/2	3/4	0/1	0/2	0.6/2.0
22	0/1	0/2	3/4	0/1	0/1	0.6/1.8
24	0/1	0/1	3/4	0/1	0/1	0.6/1.6

Appendix H. Number of medium prey remaining each observation hour from combined prey experiments. First number in each cell is the number of *D. lumholtzi* remaining followed by the number of *D. pulex* remaining (*D. lumholtzi* / *D. pulex*).

Hour	Medium	Medium	Medium	Medium	Medium	Mean
0	5 / 5	5 / 5	5 / 5	5 / 5	5 / 5	5.0 / 5.0
1	3 / 5	5 / 5	5 / 5	5 / 5	5 / 5	4.6 / 5.0
2	3 / 4	5 / 5	5 / 5	5 / 5	4 / 4	4.4 / 4.6
3	3 / 4	5 / 5	5 / 5	5 / 5	4 / 4	4.4 / 4.6
4	2 / 4	5 / 5	4 / 5	5 / 5	4 / 4	4.0 / 4.6
5	2 / 4	5 / 5	4 / 5	5 / 5	3 / 4	3.8 / 4.6
6	2 / 4	4 / 5	3 / 5	5 / 4	3 / 4	3.4 / 4.4
7	1 / 4	4 / 5	3 / 5	4 / 4	3 / 4	3.0 / 4.4
8	1 / 4	4 / 5	3 / 5	4 / 4	3 / 4	3.0 / 4.4
9	1 / 3	3 / 5	3 / 5	4 / 4	3 / 4	2.8 / 4.2
10	1 / 3	3 / 5	3 / 5	3 / 4	3 / 4	2.6 / 4.2
11	1 / 3	3 / 5	3 / 5	3 / 4	3 / 4	2.6 / 4.2
12	1 / 3	3 / 4	2 / 5	3 / 4	3 / 4	2.4 / 4.0
16	1 / 2	3 / 4	2 / 4	1 / 4	2 / 4	1.8 / 3.6
18	1 / 2	2 / 4	2 / 4	1 / 4	2 / 4	1.6 / 3.6
20	1 / 2	2 / 4	2 / 4	1 / 4	2 / 4	1.6 / 3.6
22	1 / 2	2 / 4	2 / 4	1 / 4	2 / 4	1.6 / 3.6
24	1 / 2	1 / 4	2 / 4	1 / 3	2 / 4	1.4 / 3.4