

## Predicting diet composition from body length in the zooplankton predator *Leptodora kindti*

**Abstract**—*Leptodora kindti* and many other species of zooplankton predator range widely throughout temperate-zone lakes, yet these species are rarely included in size-based studies of food webs. This oversight derives mainly from a lack of predictive functions that quantify their effects on prey communities. With laboratory experiments I measured the handling time and phosphorus ingestion of *L. kindti* fed three cladoceran species radiolabeled with  $^{33}\text{P}$  as a tracer of dry weight (DW). In general, laboratory results show that predator body length exerts strong influence on maximum prey length, on prey handling time (and indirectly predation rate), and on prey profitability (expressed as  $\mu\text{g DW ingested time}^{-1}$ ) in systematic ways that may be useful in predicting predatory effects of *L. kindti* on natural prey communities. The prey-capturing structure of *L. kindti*, called the trap basket, constrains the maximum length of prey that is consumable, and handling times on prey increase exponentially as prey length approaches the maximum dimensions of the trap basket. The empirical relationship is given by the following equation: Handling time =  $1/[0.067(\text{Trap basket length}/\text{Prey length} - 1)^{0.436}]$ . I use handling time and body length data to evaluate the predictive nature of two previously published regression models that relate *L. kindti* trap basket length to body length. This note offers a length-based approach to analysis of diet composition in *L. kindti* that will hopefully encourage increased consideration of this species in future studies of food webs.

In freshwater and marine communities, body size has dominant structuring effects on patterns of predation and diet composition (Werner and Gilliam 1984). These effects are particularly evident in pelagic communities where predators capture and engulf their prey whole (Zaret 1980). For these predators, maximum prey size is set by the dimensions of the mouth or capturing structure. Consequently, diet breadth and patterns of diet expansion often correlate closely with body size. This has been shown in fishes (Grossman 1980; Zaret 1980), amphibians (Christian 1982), crustaceans (Neill and Peacock 1980; Murtaugh 1981), and insects (Lewis 1977; McArdle and Lawton 1979).

Patterns in diet breadth that correlate with ontogenetic growth are well documented in the larger zooplankton predators, including *Leptodora kindti* (Branstrator and Lehman 1991), mysids (Murtaugh 1981), and midge larvae (Lewis 1977). Their population effects on prey communities can shift seasonally and spatially within a lake as the average body length of the predator population changes (Lunte and Luecke 1990; Manca and Comoli 1995). As a result, the effects of zooplankton predators on trophic interactions are likely to be more dynamic and therefore more difficult to model and predict in comparison to planktivorous fishes that tend to always crop the largest prey from the community. Difficulty in modeling the effects of zooplankton predators is one reason why they are frequently ignored in community models of trophic interaction such as trophic cascades.

As a means to develop a more rigorous, length-based approach to predicting trophic interactions of zooplankton predators, I carried out laboratory feeding experiments with *L. kindti*. The experiments measured handling time and prey profitability (expressed as  $\mu\text{g DW ingested time}^{-1}$ ) for juvenile and adult *L. kindti* predators and three cladoceran prey species. I used *L. kindti* specimens that spanned a broad range in body length, and this permitted me to assess the effects of body length on predation. The experimental methods and a brief data analysis were originally reported by Branstrator (1994). In this note, I expand that analysis in order to describe some useful empirical relationships between *L. kindti* body length, prey handling time, and prey profitability. The experimental results also provide an opportunity to compare two recently published regression models that relate maximum prey length to predator body length (Herzig and Auer 1990; Manca and Comoli 1995).

*L. kindti* are exclusively carnivorous and range in body length from 2 mm as juveniles to ~15 mm as adults. This large range admits them to a variety of prey species and sizes over a lifetime (Branstrator and Lehman 1991). Descriptions of the prey capture and feeding processes were made originally by Weismann (1874) and Sebestyen (1931), and later studied by Browman et al. (1989). Prey capture is performed by six pairs of thoracic legs, called the trap basket, that are positioned around the mouth. When a prey item is encountered, grasping action of the legs pulls the prey toward the body cavity and creates an enclosed space where the prey can be restrained and fed upon. *L. kindti* feeds by excavating prey tissue with its long mandibles and then by sucking the tissue into its mouth. Recognizable fragments of prey, including filtering combs and postabdominal claws, are consumed, but *L. kindti* discards the entire carapace of cladoceran prey (Branstrator and Lehman 1991).

The experimental approach was to label prey tissues of *Bosmina longirostris*, *Ceriodaphnia quadrangula*, and *Daphnia rosea* with radioactive phosphorus ( $^{33}\text{P}$ ), and to use the isotope as a tracer of total phosphorus (TP) ingested from the prey (Dagg 1974). This technique permitted me to quantify the rate of tissue consumption by *L. kindti* as well as the total weight of tissue consumed from the prey. I chose P as a tracer, over C, because the chemical techniques for P determination are precise, and the element has no gaseous phase, which eliminated the need for air-tight incubation vessels. Because intraspecific elemental stoichiometries in crustacean zooplankton are relatively constant, P served as a reasonable proxy for DW (Sterner 1990; Andersen and Hessen 1991). But P content of crustacean zooplankton is variable among species, and this required the conversion of P to DW for comparative analyses of interspecific prey profitability ( $\mu\text{g DW ingested time}^{-1}$ ). One caveat with using P as the tracer is that weight-specific P content is larger in

juvenile than adult zooplankton, apparently due to increased RNA concentrations associated with higher growth rates in juveniles (Hessen and Lyche 1991). In my experiments, *B. longirostris* and *D. rosea* varied little in length and probably exhibited minor variation in P content; however, age may have influenced the intraspecific P content in *C. quadrangula* prey that ranged from 0.4 to 0.8 mm. Hessen (1990) estimated that weight-specific P content of *Daphnia magna* differs by 23% between juveniles and adults. I therefore suspect that the magnitude of variation in P content among the *C. quadrangula* was  $<2\times$ .

Experiments were performed in a walk-in environmental chamber at 16°C. SYSTAT 5.0 was used for all statistical applications.

An initial experiment identified the incubation time required to achieve uniform labeling of the  $^{33}\text{P}$  tracer in body tissues of the prey (when the ratio of radioactive P:TP achieved a stable maximum). Detailed methods are presented in Branstrator (1994). Under the experimental conditions, all three prey species reached 90% of uniform labeling at 105 h. This result is consistent with Lehman and Naumoski (1985), who measured uptake kinetics of  $^{33}\text{P}$  by *Daphnia pulex* with methods similar to mine.

Subsequently, a predation experiment measured the handling time and TP ingested by *L. kindti*. For this experiment, fresh prey were uniformly labeled with  $^{33}\text{P}$  by the procedure described in Branstrator (1994). *L. kindti* were collected from Whitmore Lake, Michigan. They were isolated in 10-ml plastic containers and starved for 1–2 d before feeding. To start a feeding trial, one  $^{33}\text{P}$ -labeled prey was removed from culture and measured for body length. *C. quadrangula* and *D. rosea* were measured from the center of the eye to the base of the tailspine. *B. longirostris* length was measured as the greatest distance from the anterior edge of the carapace above the eye to the posteroventral corner of the carapace. Prey were offered individually to *L. kindti* with watchmaker forceps, making sure not to kill the prey or even rupture the carapace. The feeding trial began when *L. kindti* grasped the prey from the forceps. The entire feeding process was viewed by microscope under darkfield illumination. *L. kindti* eventually released the prey carapace from the trap basket, and this marked the end of the feeding trial. At that time, *L. kindti* was transferred from the container by wide-bore pipette to a rinse container with 10 ml of lake water for 30 s. *L. kindti* was then placed on a glass slide, measured for body length from the eye to the base of the bifurcation in the tailspine, and saved in a 7-ml scintillation vial. Water and uningested prey debris in the feeding and rinse containers were collected in a 22-ml scintillation vial. Handling time was recorded as the time elapsed between initial seizure of the prey by *L. kindti* to the moment the predator released the carapace from its trap basket.

Contents of the scintillation vials were frozen and then freeze-dried. Bio-Safe II counting cocktail was added to each vial and samples were counted by the same procedure used in the uniform labeling experiment (Branstrator 1994).

Inventory of  $^{33}\text{P}$  was defined by

$$P_{\text{tot}} = P_{\text{feed}} + P_{\text{debris}} \quad (1)$$

where the subscript "feed" is the amount of  $^{33}\text{P}$  present in

the *L. kindti* and "debris" is the amount of  $^{33}\text{P}$  present in the feeding and rinse wells, including uningested prey material. Profitability of prey ( $P_p$ ) was computed as

$$P_p = P_{\text{feed}}/\text{Handling time.} \quad (2)$$

Ingestion efficiency of P ( $IE_p$ ) was computed as

$$IE_p = P_{\text{feed}}/P_{\text{tot}} \quad (3)$$

Quantitative estimates of TP ingested were transformed into DW ingested for individual prey taxa following Hessen et al. (1992). The results of profitability and ingestion efficiency are all reported here in terms of DW.

Successful consumption of prey by *L. kindti* depends on the length of the trap basket appendages and their ability to ensnare and immobilize prey. Because maximum trap basket length sets an upper bound on prey length, it serves as a convenient predictor of diet breadth in *L. kindti*. Herzig and Auer (1990) were the first to point this out and to report a correlation between *L. kindti* trap basket length and maximum prey length. Later, Manca and Comoli (1995) studied the trap basket in an attempt to predict length-dependent effects of *L. kindti* predation in Lago Maggiore, Italy. Both Herzig and Auer (1990) and Manca and Comoli (1995) report linear regressions that predict trap basket length from body length; however, the separate studies based their regressions on different linear dimensions of the trap basket. Consequently, they make different predictions regarding maximum prey length. Herzig and Auer (1990) measured the internal diameter of the trap basket from the base of the first to the base of the sixth pair of appendages, and they report the following relationship:

$$\text{Trap basket length} = 0.057 \times \text{Body length} + 0.244 \\ (R^2 = 0.738). \quad (4)$$

Manca and Comoli (1995) considered that a more accurate descriptor of effective trap basket length should be the outer diameter of the trap basket. They therefore measured the distance between the distal tips of the second and sixth pairs of outstretched appendages since the appendages are spread in this fashion when *L. kindti* hunts prey. They reported

$$\text{Trap basket length} = 0.145 \times \text{Body length} + 0.152 \\ (R^2 = 0.805). \quad (5)$$

Although Manca and Comoli (1995) proposed that their own regression equation more accurately predicts maximum prey length for *L. kindti*, they did not test it experimentally. Because Eq. 4 and 5 should each predict the capture success of prey species in my experiment, I used my results to compare the accuracy of the two published equations. I made two assumptions: (1) *L. kindti* cannot capture prey that exceed its trap basket length, and (2) handling times increase as prey length approaches trap basket length. I predicted a priori that no prey that exceed the length of the trap basket should be included in the diet and that handling times on prey should scale positively with prey length. To compare the two equations on these criteria, I transformed the body lengths of all 94 *L. kindti* from the feeding experiment into trap basket lengths by the authors' own equations (Eq. 4 and 5). Handling times on prey were then plotted against the ratio of *L. kindti* trap basket length to prey length for both

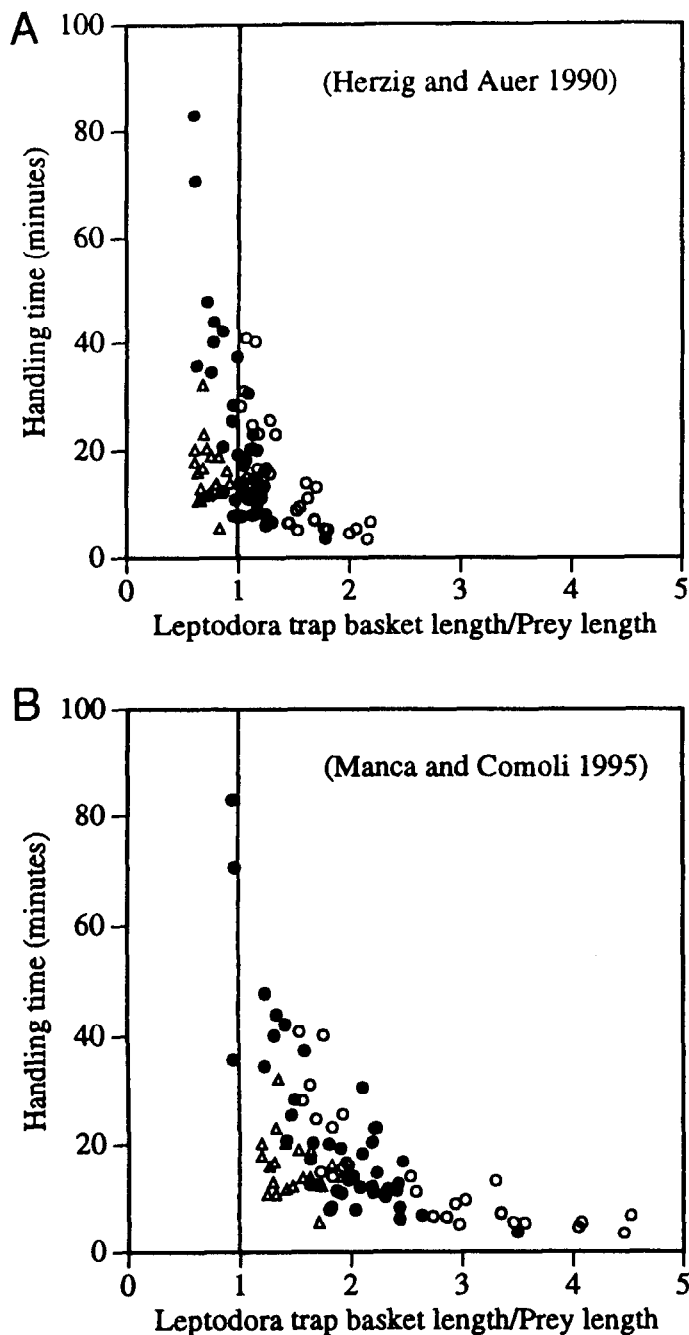


Fig. 1. The relationship between prey handling time and the ratio *L. kindti* trap basket length to prey length ( $n = 94$ ). *L. kindti* trap basket length was estimated from body length by (A) Eq. 4 (Herzig and Auer 1990) and by (B) Eq. 5 (Manca and Comoli 1995). The asymptote at  $X$  of 1 defines the theoretical lower bound of the independent variable.  $\circ$ , *B. longirostris*;  $\bullet$ , *C. quadrangula*;  $\triangle$ , *D. rosea*.

sets of transformed data (Fig. 1). Because *L. kindti* theoretically cannot capture prey that are larger than the trap basket, an asymptote at 1 of *L. kindti* trap basket length:prey length was set to define the individual-specific, upper bound on relative length. Predator-prey combinations falling in the do-

main to the left of the asymptote are theoretically prohibited (Fig. 1).

The two plots in Fig. 1 were evaluated by visual inspection. Fig. 1A shows that body lengths transformed by Eq. 4 (Herzig and Auer 1990) produced several data points within the domain to the left of the asymptote where the ratio *L. kindti* trap basket length:prey length was  $<1$ . Some of those data points suggest that *L. kindti* consumed prey that were as much as twice the length of the trap basket. Specifically, the regression of Herzig and Auer (1990) predicted that 36 prey longer than the trap basket, as defined by themselves, were successfully eaten by *L. kindti* in my feeding trials (Fig. 1A). The same original set of body lengths for all 94 *L. kindti* were transformed to trap basket lengths by Eq. 5 (Manca and Comoli 1995) and are shown in Fig. 1B. Results there show that the ratio of *L. kindti* trap basket length:prey length ranges below  $X$  of 1 in only three cases, and that most prey that even approach the full length of the trap basket require long handling times. Eq. 4, reported by Herzig and Auer (1990), appears to underestimate the maximum holding capacity of the trap basket perhaps because it is based on a linear measure of the internal diameter of the basket that is too conservative to accurately predict maximum prey length (Fig. 1A). My experimental data thus support Eq. 5 (Manca and Comoli 1995) as the better predictor of maximum prey length, at least for the prey species used in this study (Fig. 1B).

Because *L. kindti* attack and consume prey individually, handling time underlies the economics of prey choice and predation rate. Theoretically, the upper bound on predation rate should be set by the time costs incurred to search for prey as well as to handle prey (*sensu* Werner and Hall 1974). As a means to estimate maximum predation rates achievable by *L. kindti*, the data from Fig. 1B were fit by nonlinear regression to the following equation:

$$\begin{aligned} \text{Handling time} &= 1/[0.067 \text{ (SE}=0.004) \\ &\quad \times (\text{Trap basket length/Prey length} - 1)^{0.436 \text{ (SE: } 0.067)}] \\ &\quad (R^2 = 0.316). \end{aligned} \quad (6)$$

The choice of a power function was based on the assumption that handling time is primarily a function of prey length and the volume of prey consumed (proportional to length cubed). The vertical asymptote in Eq. 6 at  $X$  of 1 was a necessary constraint to prevent prey length from exceeding trap basket length. Three data points in Fig. 1B, where  $X < 1$ , are excluded from the nonlinear regression (Eq. 6).

With Eq. 5 and 6, I computed handling times and maximum daily predation rates for *L. kindti* and prey of 0.4–1.6 mm length (Table 1). In most cases my estimated predation rates, based on the constraint of handling time alone, are high in comparison to the following rates of predation measured in the laboratory: 30 *Polyphemus pediculus*  $d^{-1}$  (Mordukhai-Boltovskaia 1958), 14 *Daphnia pulex*  $d^{-1}$  (Browman et al. 1989), upwards of 13 *Daphnia retrocurva*  $d^{-1}$  (Havel 1985), and 6 *Diaphanosoma brachyurum*  $d^{-1}$  (Herzig and Auer 1990). The general disparity between these published laboratory values and my estimates in Table 1 probably owe to additional time costs that were not explicitly included in

Table 1. Estimated handling times (from Eq. 5 and 6) and predation rates (computed as the reciprocal of handling time over 24 h) for *L. kindti* and prey of variable body lengths.

<i>L. kindti</i> length	Prey length (mm)	Handling time (min)	Predation rate (prey d <sup>-1</sup> )
6 mm	0.4	12.3	117
	0.6	17.4	83
	0.8	26.1	55
	1.0	78.8	18
12 mm	0.4	8.4	171
	0.6	10.7	135
	0.8	13.0	111
	1.0	15.7	92
	1.2	19.0	76
	1.4	23.5	61
	1.6	31.3	46

my estimates—such as search time, between-meal satiation, and time devoted to nonfeeding activities such as vertical migration—that would reduce the total time for feeding and lower true predation rates measured in the laboratory.

If all time-consuming activities other than handling are a constant portion of the daily budget of *L. kindti*, then a steep rise in handling time, associated with handling larger prey (Fig. 1), should decrease predation rates. I tested this hypothesis with published data from Havel (1985). In the laboratory, Havel (1985) measured clearance rates (ml predator<sup>-1</sup> d<sup>-1</sup>) for *L. kindti* that were fed *Daphnia retrocurva* prey. He used *L. kindti* of similar length (mean body length of 8.8 mm; SE = 1.46 mm) for the experiment, but he allowed carapace length of *D. retrocurva* to range from ~0.38 to 0.54 mm. Havel (1985) reported:

$$\log k = 9.1 - 11.3 \times C \quad (7)$$

as an estimate of predator clearance rate where  $k$  represents milliliters of water cleared predator<sup>-1</sup> d<sup>-1</sup> and  $C$  is carapace length of *D. retrocurva*. Eq. 7 is depicted in Fig. 2 where the variable  $C$  is expressed as the *L. kindti* trap basket length-to-*D. retrocurva* length ratio. I transformed *L. kindti* body length (constant, 8.8 mm) into trap basket length by Eq. 5 and let *D. retrocurva* carapace length vary over a broad range. Results in Fig. 2 show that clearance rates approach zero as the ratio of *L. kindti* trap basket length to *D. retrocurva* length approaches one. A general agreement between the curvilinear shape and position of the data in Fig. 1B and the curve in Fig. 2 supports the hypothesis that handling time, and indirectly prey length, defines an upper bound on clearance or predation rate for *L. kindti*.

Relative body length of *L. kindti* and its prey clearly has a large effect on prey profitability. Results show that *L. kindti* devotes increased handling time to prey of larger relative body length, and this reduces the profitability ( $\mu\text{g DW ingested min}^{-1}$ ) of these prey. Figure 3 shows a consistent, positive effect of relative body length on prey profitability for all three species. Linear regression revealed significant relationships between profitability (Prof.) and relative length for *B. longirostris* (*B.l.*) and *C. quadrangula* (*C.q.*), and a marginally significant relationship for *D. rosea* (*D.r.*):

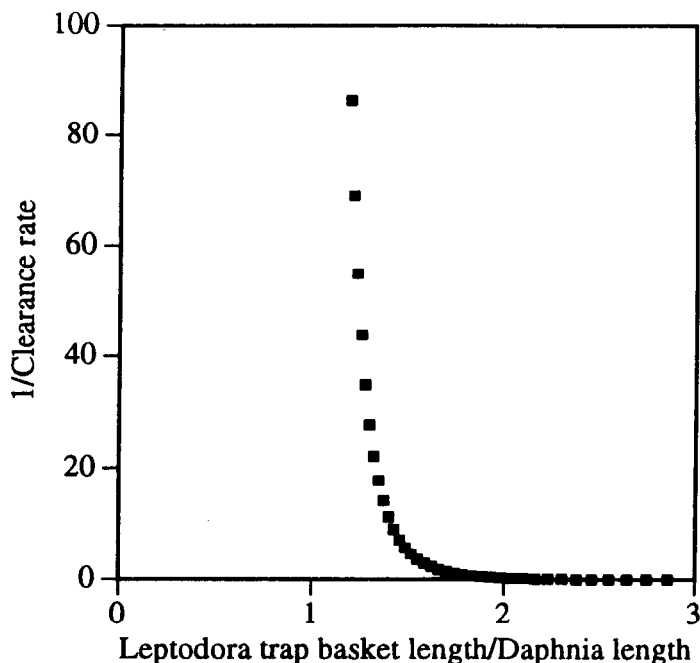


Fig. 2. *Daphnia retrocurva* clearance rates (ml predator<sup>-1</sup> d<sup>-1</sup>), originally reported by Havel (1985), are presented here as the relationship between 1/Clearance rate and the ratio *L. kindti* trap basket length to prey length. *L. kindti* trap basket length was estimated from body length by Eq. 5.

$$\text{Prof.}_{B.l.} = 0.092 \times \text{RL} - 0.138 \quad (R^2 = 0.538, P < 0.001) \quad (8)$$

$$\text{Prof.}_{C.q.} = 0.052 \times \text{RL} - 0.055 \quad (R^2 = 0.408, P < 0.001), \quad (9)$$

$$\text{Prof.}_{D.r.} = 0.078 \times \text{RL} - 0.019 \quad (R^2 = 0.098, P = 0.096), \quad (10)$$

where RL is relative length defined as the ratio of *L. kindti* trap basket length to prey length.

Although body length is a major contributor to prey profitability (Fig. 3), there are also species-specific differences in profitability that are unrelated to length. To show this effect I used results on juvenile *L. kindti* only because I could eliminate relative length (*L. kindti* trap basket length:prey length) as a variable. For adult *L. kindti*, the three prey species differed so greatly in their range of relative lengths that a comparison among species was not really that useful. Combining all trials that used juvenile *L. kindti* (3.2–5.3 mm in length,  $n = 35$ ), I performed an ANCOVA with prey profitability as the dependent variable, *L. kindti* trap basket length:prey length as the covariate, and prey species (*B. longirostris* and *C. quadrangula*) as the treatment or categorical variable. The assumption of homogeneity of slopes was met (treatment by covariate interaction,  $P = 0.936$ ), and ANCOVA detected a highly significant effect of species ( $P = 0.003$ ), with *B. longirostris* more profitable than *C. quadrangula*. The basis for this difference in profitability between the two species is unknown. In general, it seems likely that prey species that possess considerable spines and ornamentation would demand more handling time and this would

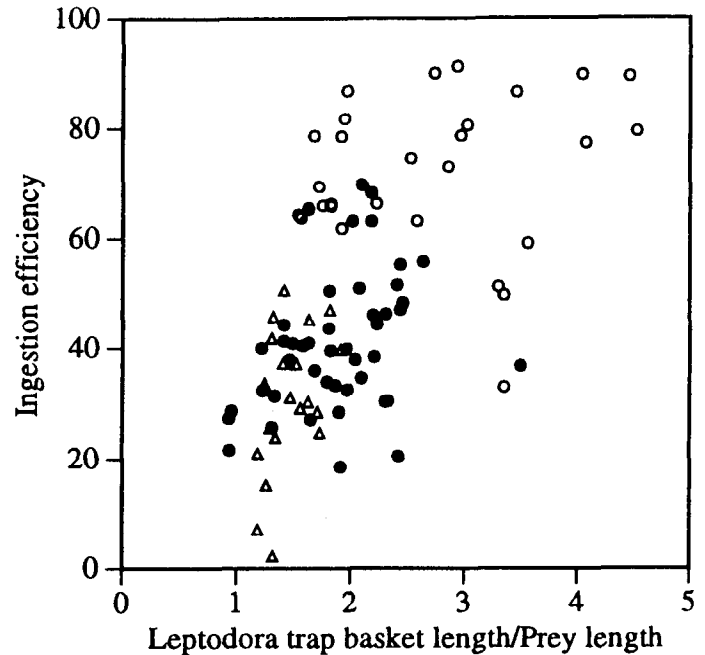
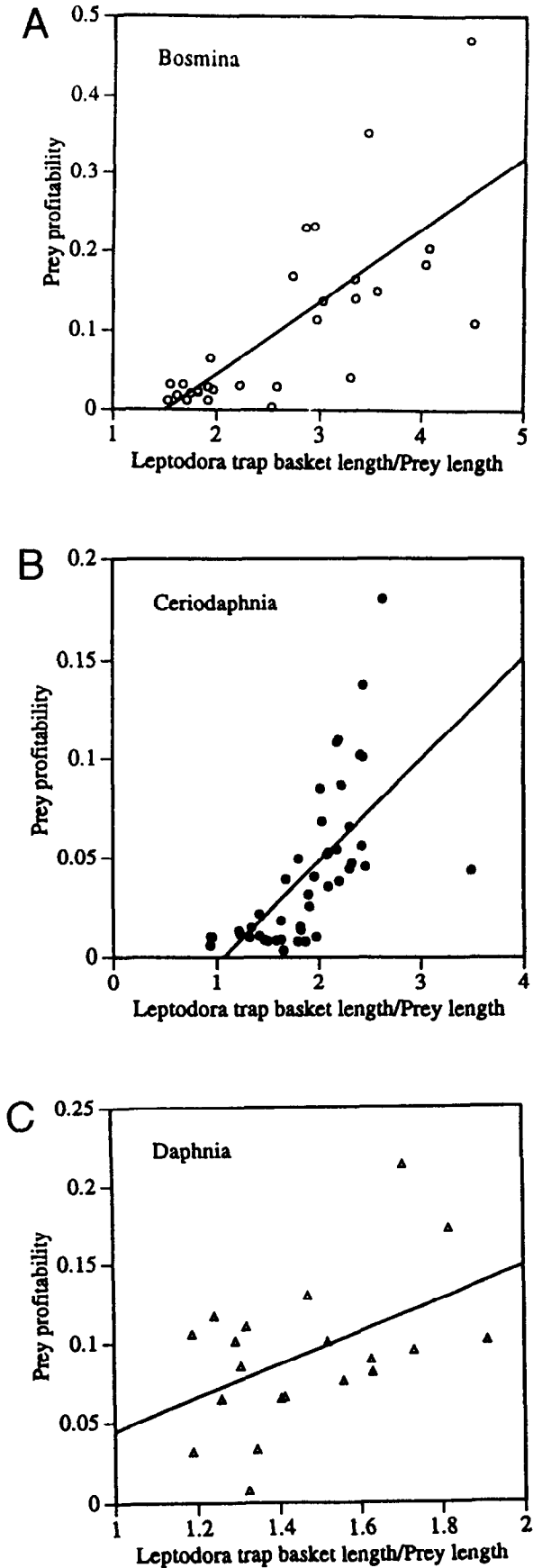


Fig. 4. The relationship between ingestion efficiency (percentage of prey ingested) and the ratio of *L. kindti* trap basket length to prey length for *Bosmina longirostris* (○), *Ceriodaphnia quadrangula* (●), and *Daphnia rosea* (△). *L. kindti* trap basket length was estimated from body length by Eq. 5. Mean ingestion efficiencies, presented as percentage ingested  $\pm$  1 SE, are *B. longirostris* ( $71.9 \pm 2.5$ ), *C. quadrangula* ( $41.0 \pm 1.9$ ), and *D. rosea* ( $31.0 \pm 2.9$ ). Independent *t*-tests on ingestion efficiency revealed significant differences ( $P < 0.05$ ) among all three species.

reduce their overall profitability to *L. kindti*. Additionally, spines and other body armor that limit the extent to which *L. kindti* can excavate tissues from the prey body could negatively affect prey profitability by reducing the total amount of tissue consumed. Predator ingestion efficiency (Eq. 3) was largest for *B. longirostris* (71.9%) compared to *C. quadrangula* (41.0%) and *D. rosea* (31.0%) (Fig. 4). However, there were no obvious differences in body shape between *B. longirostris* and *C. quadrangula* that are noteworthy.

In conclusion, trap basket length appears to be a powerful predictor of diet composition in *L. kindti*. Trap basket length, as defined by Manca and Comoli (1995), sets an upper limit on the length spectrum of edible prey (Fig. 1B) that is generally consistent with estimated clearance rates of the predator (Havel 1985; Fig. 2) and trends in handling times and prey profitability measured here (Figs. 1B, 3). A variety of population-level questions can be addressed with a length-based approach suggested by Eq. 5–7. For example, targeted

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Fig. 3. The relationship between prey profitability ( $\mu\text{g DW ingested min}^{-1}$ ) and the ratio of *L. kindti* trap basket length to prey length for *Bosmina longirostris* (A), *Ceriodaphnia quadrangula* (B), and *Daphnia rosea* (C). *L. kindti* trap basket length was estimated from body length by Eq. 5. See text for equations of regression lines.

effects of *L. kindti* predation can be predicted from data on the length distribution of natural *L. kindti* populations. An analysis of this sort would be usefully applied in seasonal environments when the length structure of the predator population is variable through time or between lakes (Manca and Comoli 1995). A length-based approach of this sort would also permit quantitative estimates of resource overlap, and hence the ability to quantify interspecific competition, for invertebrate predators that occupy similar trophic guilds. One caution is that actual diet composition of *L. kindti* in the field may be more conservative than predicted by trap basket dimensions alone. Note that daphnids that exceed two-thirds the length of the trap basket were poorly utilized by *L. kindti* in predation experiments reported by Havel (1985) (Fig. 2), and that all three species of cladoceran prey tested here were considerably less profitable at lengths that exceeded two-thirds to one-half the length of the trap basket (Fig. 3). In addition, prey can vary in their profitability to *L. kindti*, regardless of relative body length. These problems invite further inquiry of the length-based equations presented here, yet they pose minor limitations for application of these equations in future models of food webs.

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