

Foraging behavior of the predaceous cladoceran, *Leptodora kindti*, and escape responses of their prey

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Abstract. Using silhouette video photography we have made the first quantitative observations of foraging behavior in *Leptodora kindti*, a predaceous cladoceran (Haplopoda). *Leptodora* swims with a mean velocity of 13.4 ± 4.0 mm s⁻¹ and initiates an attack only upon direct contact with potential prey. The attack sequence is as follows: *Leptodora* swims randomly through the water column with all five pairs of thoracic appendages spread to form a 'feeding basket' and, seemingly by chance, encounters prey. Shortly after prey make contact with any part of *Leptodora*'s body (usually ventral), the abdomen is rapidly pulled forward, clamping itself under the feeding basket so that the telson closes it at the posterior end. The duration of this movement is always the same and we conclude that it is an indiscriminate reflex. If the prey is encountered anywhere but a short distance directly in front and slightly below the *Leptodora*, it is not captured. The speed of copepod escape responses effectively allows them to avoid contact with the predator. *Daphnia*'s escape response, particularly that of juveniles, is slower and leaves them far more susceptible to *Leptodora* predation.

Introduction

Predation can be a powerful force in aquatic ecosystems. That predation by planktivorous fish can structure zooplankton communities is well documented: small species and individuals predominate when zooplanktivorous fish are abundant (e.g. Brooks and Dodson, 1965; Hall *et al.*, 1976; O'Brien, 1979). When zooplanktivorous fish are scarce or absent, zooplanktivorous invertebrates are often abundant and can exert strong predation pressure on the smaller size fractions of the zooplankton community, consuming significant portions of their prey populations every day (Dodson, 1974; Kerfoot, 1977; Pastorok, 1981; Greene, 1983; Luecke and O'Brien, 1983).

The copepod *Mesocyclops edax* can consume up to 17% of the standing crop of its prey (Williamson, 1984) and *Chaoborus*, a larval midge, can remove 20% of its prey population per day and be an important determinant of population structure (Pastorok, 1980; Riessen *et al.*, 1988).

Leptodora kindti is a large (6–12 mm), carnivorous freshwater cladoceran (Haplopoda) that swims continuously through the water column, preying upon a range of zooplanktonic crustaceans (e.g. *Bosmina*, *Ceriodaphnia*, *Daphnia*, *Diaphanosoma*, *Diatomus*, *Polyphemus* and *Cyclops*). They generally prefer cladocerans approximately one-tenth their own size (Mordukhai-Boltovskaia, 1958, 1960; Auer, 1988), though they have been reported to consume copepods (Cummins *et al.*, 1969) and rotifers (Mordukhai-Bolotovskaia, 1958; Cummins *et al.*, 1969), and are sometimes cannibalistic (Mordukhai-Boltovskaia, 1958). Several reports of selective predation by *Leptodora*, particularly those for

copepods and rotifers, are not based on direct observation but are inferred from inverse correlations between *Leptodora* abundance (or birth rate) and the abundance (or death rate) of potential prey species in field samples (e.g. Hall, 1964; Wright, 1965; Cummins *et al.*, 1969; Karabin, 1974).

Leptodora predation can be a significant factor in structuring populations of its prey. Mordukhai-Boltovskaia (1958) estimates that it can consume considerably more zooplankton than young-of-the-year fishes. Hall (1964) estimated that, in Base Line Lake Michigan, it could consume 25–35% of *Daphnia galeata mendotae* production. Wright (1965) compared the standing crop of *Leptodora* and instantaneous death rates of *Daphnia schodleri* in a reservoir and inferred that *Leptodora* was responsible for a significant mid-summer decline in the abundance of *D. schodleri*. He estimated that *Leptodora* consumed 33% of *Daphnia* production. Similar results have been obtained by Cummins *et al.* (1969), Hillbricht-Ilkowska and Karabin (1970), and Karabin (1974). On the other hand, *Leptodora* is often an important component in the diet of zooplanktivorous fishes (Mordukhai-Boltovskaia, 1958; Sebestyen, 1960; Cummins *et al.*, 1969; Engel, 1976) and is also apparently fed upon by the copepods *Macrocyclus albidus*, *Acanthocyclops* spp. and *Cyclops* spp. (Mordukhai-Boltovskaia, 1958, 1960).

While a considerable amount is known about the importance of invertebrate predation on zooplankton at the population level, relatively little is known about the predatory behavior of these organisms. To date, all observations of *Leptodora* feeding behavior have been conducted in small containers (a drop of water, Petri plates, or small beakers) under unrealistic conditions. It has been described as a 'fluid' or 'suction' feeder, piercing the carapace of its prey near the head with sharp protuberances of its pointed mandibles and sucking out the juices (Sebestyen, 1931, 1960; Mordukhai-Boltovskaia, 1958; Auer, 1988). This interpretation of its feeding behavior seems to have arisen because hard parts of their prey are only rarely observed in the gut. Nonetheless, a suction feeding interpretation prevails in virtually all publications on *Leptodora* predation and/or ecology (Cummins *et al.*, 1969; Moshiri *et al.*, 1969; Hillbricht-Ilkowska and Karabin, 1970; Karabin, 1974; Havel, 1985).

Using shadow video photography, we have made the first detailed observations of the predation cycle and predatory behavior in *Leptodora*. Here we present a qualitative and quantitative description of foraging behavior in *Leptodora* and report on the escape responses of its prey. On the basis of the results, and those in the literature, we address *Leptodora's* mode of feeding, search tactics, prey selectivity and energy budget, and set out the components of its predation cycle. We suggest that the components of this cycle must be quantified for several prey species before a realistic evaluation of *Leptodora's* effect on zooplankton populations can be obtained.

Materials and methods

Silhouette videotaping system

Silhouette (shadow) video photography (Arnold and Nutall-Smith, 1974;

Edgerton, 1977) was used to observe the predatory and search behavior of *Leptodora*. This technique has been applied effectively in studies of the swimming movements and feeding behavior of fish larvae (Hunter, 1972; Drost and van den Boogaart, 1986; Drost, 1987) and has several important advantages over standard photographic or video techniques. It allows filming of events in a large depth of field (~15 cm) with a relatively large field of view (here 18 cm): the free-swimming predators and their prey can be observed under relatively natural conditions. Magnification is independent of distance from the camera, and the resolution of the system is extremely good: objects as small as 0.2 mm in diameter can be resolved. Furthermore, the system does not require intense light sources [1–50 lux (Arnold and Nutall-Smith, 1974; this study)], so organisms are not disturbed by excessive light or increased water temperature.

Shadow images were focused on the lens (Nikon 35 mm f/2.0) of Panasonic WV-140 black and white (b&w) video cameras, recorded with Panasonic NV-8420 and General Electric 1CVD5025X video tape recorders, and monitored on b&w television screens. The frame advance rate of these recorders is 30 frames s^{-1} , which is sufficient for frame-by-frame analysis of predatory behavior in these crustaceans. Small, under-run microscope lamps (12 V, 100 W, filament area 4×2 mm) were used as point sources of light and placed at the first focus of each of the optical-quality biconvex collimating lenses (18 cm dia., 333 mm focal length—Edmund Scientific catalogue number N94893). From the point source of light, these lenses 'project' a collimated beam through a $10 \times 10 \times 10$ cm all-glass observation tank filled with 500–800 ml of water. The use of a collimated beam prevents perspective distortion; clear, sharp shadows of any organism (even transparent ones) in the beam's path are produced and recorded by the video cameras. In some experiments, synchronous lateral and ventral views were obtained by using two cameras simultaneously, one recording in the vertical plane (from above) and one in the horizontal plane (from the side). This allowed exact determination of the three-dimensional position of both predator and prey.

Frame-by-frame analysis of the tapes was carried out using a Panasonic Professional AG-1950 videotape machine and an AG-A95 editing console projecting to a 20" Hitachi CT-2077B color video monitor. For simultaneous examination and analysis of vertical and horizontal views, two such set-ups were used side-by-side. All time intervals were measured with increments of 1/30 s from frame counts of the videotape. At the beginning of each experiment a transparent ruler was placed in the collimated beam. Its image was recorded and, when displayed on the monitor screen, the ratio of actual distance to screen distance was established by measuring the length of the ruler on the screen. This ratio was then used to convert distances measured on the monitor screen to real distances.

General procedures

Leptodora were collected in September–October 1988 from local reservoirs and maintained in 10 l aquaria at 20°C without food for 24 h prior to an experiment.

Both males and females were present, in approximately equal numbers. All observations were made within 48 h of collection. In each experiment five or six *Leptodora* were placed in the 1000 cm³ observation cube in at least 500 ml of water. Each experiment lasted 2 h (the duration of the videotape) and we have analyzed data from a total of 20 h of experiments. Events occurring near the sides of the observation cube were not analyzed. For each feeding trial, a known number of zooplankters—either juvenile (1.06 ± 0.09 mm) or adult (1.50 ± 0.15 mm) *Daphnia pulex*, or a mixture of *D. pulex* and copepods (*Diaptomus* sp., *Mesocyclops* sp.)—were added to the aquarium. An estimate of prey size was determined by measuring 20 individuals under a dissecting microscope. *Leptodora* size was measured on the TV monitor.

Observations and measurements

Swimming speed was calculated from measurements of distance moved over time along a straight-line trajectory. Only trajectories with a minimum of vertical movement were measured, although since the vertical dimension was not considered, our measurements may represent slight underestimates.

Several variables associated with prey encounters were measured. The point between *Leptodora*'s swimming appendages (second antennae) was chosen as a reference point for these measurements because it appears as a sharply defined dark spot on the video tapes. For *Leptodora* attacks, the angle of encounter with prey (long axis of *Leptodora* is forward-directed = 0°), and its distance from the predator when contacted, were measured from this point of reference (Figure 1). For prey escape responses, the angle and distance from *Leptodora* at which it was initiated was measured. Escape speeds were calculated from measurements of their distance and duration. The time between contact with prey and the initiation of the abdominal reflex (described below) was measured for both successful and unsuccessful attacks, as was its duration. The time taken for the abdomen to flex, and the duration of flexion, were also measured.

Results

Swimming behavior

Leptodora swims continuously through the water column using its large second antennae. Vertical movement is extensive. The speed (mean \pm SD) is 13.4 ± 4.0 mm s⁻¹ (range = 5.3–28.3 mm s⁻¹, $n = 51$; Table I). We could not discern any difference in swimming speed for individuals ranging from 3 to 8 mm in size. We observed two swimming patterns: smooth motion powered by continuous strokes of the antennae, and a more jerky stop-and-go pattern powered by intermittent strokes. We could not discern any reason for changes in swimming pattern.

Abdominal reflex

Shortly after prey touches any part of *Leptodora*'s body, the abdomen is rapidly pulled forward, clamping itself under the feeding basket so that the telson closes

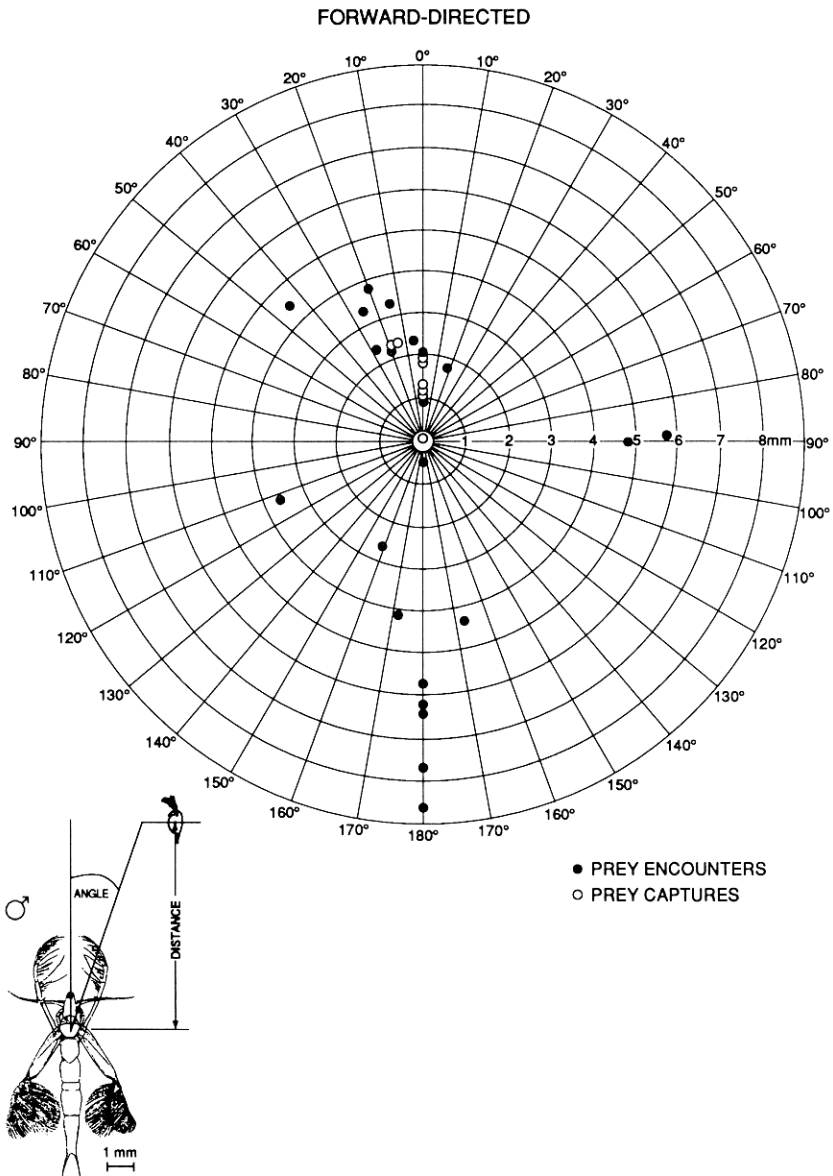


Fig. 1. The inset at the bottom illustrates the manner in which the parameters of *Leptodora* behavior were measured. The area between the second antennae is the reference point from which distance measurements were made. The midline of the body was taken as 0° forward-directed: angles of incidence with prey were measured relative to this. The polar projection illustrates the distances and angles at which *Leptodora* encountered prey. The center of the projection is the point of reference. Open circles represent prey contacts that resulted in successful attacks. All other points represent contacts that resulted in an abdominal reflex but no prey capture.

Table I. Summary statistics of *Leptodora* swimming speed, prey capture behavior and prey escape

	Swimming speed of <i>Leptodora kindtii</i> (mm s ⁻¹)	Distance from predator to prey before escape (mm)			Escape distance (mm)		
		Copepods	<i>Daphnia</i>		Copepods	<i>Daphnia</i>	
			Adult	Juveniles		Adult	Juveniles
<i>n</i>	51	25	24	25	27	24	25
$\bar{x} \pm SD$	13.4 ± 4.0	3.7 ± 2.2	6.2 ± 1.5	4.5 ± 1.5	6.0 ± 3.2	7.7 ± 3.2	5.4 ± 1.8
Observed range	9.4–17.4	1.5–5.9	4.7–7.7	3.0–6.0	2.8–9.2	4.5–10.9	3.4–7.2
Predicted range	5.3–28.3	0.8–10.8	4.3–8.8	1.4–6.9	1.9–19.2	3.0–16.0	2.5–8.6

it at the posterior end. The time from contact with prey to the first movement of the abdomen ranges from 0.33 to 1.9 s and is apparently not correlated with prey size or any other variable that we measured. The duration of this movement—from the first movement of the abdomen until it clamps to the feeding basket—is always the same: 0.2 ± 0.07 s (Table I). We conclude that this response is a reflex, here termed the 'abdominal reflex'.

If prey has been captured, the abdomen and telson are seemingly used to manipulate it within the feeding basket, perhaps to position it for the mandibles or to more securely ensnare it. The antennae continue to stroke during flexion and *Leptodora* continues to swim, though in a markedly different pattern. When the abdomen relaxes, smooth swimming begins again, with the prey still in the feeding basket.

The duration of abdominal flexion—the length of time that the abdomen remains clamped in the feeding basket—depends upon whether prey has been captured and retained in the feeding basket. When prey is contacted but not captured, the abdomen remains flexed for 0.63 ± 0.23 s (Table I). When prey is captured and does not escape from the feeding basket, the duration of flexion is significantly longer (>2 min 55 s) and there are generally several relaxations and flexions. This can be considered as handling time.

Attacks on prey and strike efficiency

Leptodora does not initiate an attack unless it makes direct contact with potential prey. The attack sequence is as follows: *Leptodora* swims through the water column, in a seemingly undirected manner, with all five pairs of thoracic appendages spread to form a 'feeding basket' and, apparently by chance, encounters prey. After hitting the prey, the abdominal reflex is initiated. If prey is encountered anywhere other than a short distance (<2.5 mm from our arbitrary reference point between the second antennae) directly in front (0–15° from forward-directed) and slightly below (i.e. at the level of the open feeding basket; determined from side views) the *Leptodora*, it is not captured (Figure 1). We have observed prey encountered slightly off center being directed into the feeding basket by the first pair of thoracic appendages. We also observed males using their elongated first antennae (used to grasp females during reproduction) to bat prey items towards the feeding basket. It should be noted that the first antennae of females are reduced and cannot be used in this manner.

responses

Escape time (s)			Escape speed (mm s ⁻¹)			Duration of abdominal reflex (s)		Duration of abdominal flexion (s):
Copepods	<i>Daphnia</i>		Copepods	<i>Daphnia</i>		Prey not captured	Prey captured	Prey not captured
	Adult	Juveniles		Adult	Juveniles			
27	24	25	27	24	25	25	8	25
0.07 ± 0.03	0.23 ± 0.06	0.2 ± 0.03	90.4 ± 43.1	31.5 ± 8.4	24.8 ± 5.5	0.23 ± 0.07	0.2 ± 0.07	0.63 ± 0.23
0.03–0.10	0.17–0.29	0.17–0.23	47.3–133.5	23.1–39.9	19.3–30.3	0.16–0.30	0.13–0.27	0.40–0.86
0.03–0.13	0.13–0.5	0.13–0.30	36.0–174.0	18.0–53.6	15.5–36.0	0.13–0.47	0.13–0.30	0.20–0.97

Most prey are contacted by the forward-extending first pair of thoracic appendages, the abdomen or the stroking antennae (Figure 1). *Leptodora* usually (>90% of contacts) initiates the abdominal reflex in response to such contact, despite the fact that in most instances it has little chance of capturing the prey.

Only the largest individuals were able to attack adult *D. pulex* successfully and we did not observe attacks by individuals of <6 mm. In over 20 h of observation, no copepod was successfully attacked; they were always able to avoid direct contact with *Leptodora*. We occasionally observed two *Leptodora* clamped together with the thoracic appendages and they could remain so entwined for several minutes. Both individuals involved in such interactions always swam away, seemingly unharmed. As the individuals involved were always about the same size it is unlikely that these incidents represent attempts at cannibalism, but we could not distinguish the individuals as male or female.

At the prey abundances used in these experiments (80–100 l⁻¹), the maximum number of successful attacks observed during any single 2 h experiment was 1.2 individual⁻¹, or a maximum feeding rate of ~14 prey items *Leptodora*⁻¹ day⁻¹.

Prey escape responses

Copepod escape behavior consists of one long, rapid jump. The mean escape distance of 6.0 ± 3.2 mm is attained in 0.07 ± 0.03 s (Table I). Escape velocity is 90.4 ± 43.1 mm s⁻¹. When the escape response is initiated, the distance between the copepod and *Leptodora* is 3.7 ± 2.2 mm (Table I).

Daphnia escape behavior consists of a sequence of jumps requiring a longer time than that of copepods. Adult *Daphnia* jump 7.7 ± 3.2 mm in 0.23 ± 0.06 s, while juveniles jump 5.4 ± 1.8 mm in 0.20 ± 0.03 s (Table I). Escape velocity is 31.5 ± 8.4 mm s⁻¹ for adults and 24.8 ± 5.5 mm s⁻¹ for juveniles (Table I). When the escape response is initiated, the distance between adult *Daphnia* and *Leptodora* is 6.2 ± 1.5 mm while for juveniles this distance is 4.5 ± 1.5 mm (Table I). In several instances large *Daphnia* escaped from the feeding basket and swam away. This occurred in ~40% of attacks in which they were enclosed in the food basket.

Comparison of escape velocities in these three prey categories by *t*-test reveals that copepods are significantly faster than both adult and juvenile *Daphnia*

(Tables I and II). Adult *Daphnia* escape responses were significantly faster than those of juveniles. Adult *Daphnia* initiate their escapes at a significantly greater distance from the predator than both copepods and juvenile *Daphnia*. There is no statistically discernible difference in the distance from the predator at which copepods and juvenile *Daphnia* initiate an escape response (Table II).

Discussion

Unlike some raptorially feeding calanoid copepods, in which the same appendages are employed for both swimming and feeding (Gauld, 1966; Greene, 1988), *Leptodora* uses different appendages for these two activities. *Leptodora* swims, albeit at a slower speed, while attacking and consuming prey so that the interaction between swimming and feeding is probably not as important as it is for predatory copepods (Greene, 1988). Our measurement of *Leptodora* swimming speed is similar to the only other published estimate of 12 mm s^{-1} (Sebestyen, 1960).

Though it has been suggested that *Leptodora* is a visually guided predator (Mordukai-Boltovskaia, 1958; Cummins *et al.*, 1969), our observations indicate strongly that prey location and attack are entirely tactile and require direct contact. This interpretation is supported by Auer (1988), and by the observation that *Leptodora* never feeds upon sessile or semi-sessile prey (Andrews, 1949; Mordukhai-Boltovskaia, 1956, 1958, 1960). Further, we commonly observed *Leptodora* swimming past potential prey without changing direction or initiating any form of pursuit, and we have observed attacks on empty carapaces and detrital material. These latter items are always ejected from the feeding basket shortly after being trapped. When prey escapes from the feeding basket *Leptodora* does not perform any type of looping back or area-restricted searching as do some predaceous copepods (Williamson, 1986).

We have not studied the feeding mechanism of *Leptodora*. However, recent observations imply that it is not strictly a 'fluid feeder'. Auer (1988) states that the mandibles tear a hole in the carapace, usually near the head, rip up the tissue inside, and suck it in through the esophagus. The empty carapace is discarded. *Leptodora* gut contents reveal the presence of *Bosmina* and *Daphnia* post-abdominal claws and copepod abdomens (D.Brandstrator, personal communication), disassembled but unshredded components of two entire copepods along with whole *Polyarthra*, clumps of *Microcystis* and 48 trophi of the rotifer *Conochilus hippocrepis* (Edmondson and Litt, 1987), chitinous remains (Sebestyen, 1931) and a lorica of the rotifer *Keratella cochlearis* (Mordukhai-Boltovskaia, 1958). Zaret (1980, p. 62) observed that *Leptodora* occasionally swallow prey whole. All of these reports suggest that *Leptodora* ingest particles and is not exclusively a fluid sucker.

Auer (1988) mentions a movement of the abdomen towards the feeding basket, but we have found no other description of this behavior. We conclude that it is a reflex activated by direct contact. Its indiscriminate nature, that is, its activation by contact with prey or non-prey particles anywhere on the body's ventral surface, supports this view.

Table II. Statistical comparisons of prey escape responses and *Leptodora* feeding behavior

	Distance from predator to prey before escape		Escape speed		Duration of abdominal reflex	
	Copepods versus adult <i>Daphnia</i>	Copepods versus juvenile <i>Daphnia</i>	Copepods versus adult <i>Daphnia</i>	Copepods versus juvenile <i>Daphnia</i>	Adult versus juvenile <i>Daphnia</i>	Prey not captured versus prey captured
d.f.	42	42	24	27	47	31
<i>t</i>	4.69	1.50	6.95	7.84	3.32	1.23
<i>P</i>	<0.01	>0.05	<0.01	<0.01	<0.01	>0.05

Some authors have suggested that *Leptodora* feeds on copepods (Cummins *et al.*, 1969), but we are not aware of any published reports based upon direct observations. Hillbricht-Ilkowska and Karabin (1970) report that it does not eat copepods or rotifers, and Mordukhai-Boltovskaia (1958) reported that copepods, kept in the same vessel with *Leptodora* for 2 weeks in the absence of any other food source, were not eaten. He concluded that 'the dashing movements of the copepods save them from the predators' (p. 829). In feeding trials, *Leptodora* could not capture the copepod *Arctodiaptomus spinosus* (Auer, 1988). These reports are consistent with observations of copepod escape responses presented here and elsewhere: copepods are able to avoid contact with free-swimming *Leptodora* because they can detect the hydrodynamic disturbance resulting from its swimming movements (Strickler, 1975; Haury *et al.*, 1980; Williamson, 1983). We conclude that copepods are not an important food source for *Leptodora* and will not be consumed unless they are so abundant as to be encountered with high frequency.

The escape response of adult *Daphnia* is slower than that of copepods. That it is initiated at a greater distance from the predator, at least for the adults (Table I), may in part compensate for its slower speed. Nonetheless, *Daphnia* (particularly juveniles) is highly susceptible to *Leptodora* predation. The speed that it can attain during an escape movement is only slightly faster than *Leptodora*'s mean swimming speed, whereas that attained by copepods is considerably greater (Table I).

No attacks by the smallest *Leptodora* were observed. This was probably because we did not conduct any experiments with small prey items. However, Sebastyen (1949) observed carnivorous behavior in *Leptodora* immediately after the thoracic appendages had developed and Mordukhai-Boltovskaia (1956) observed carnivory by small individuals. It has also been suggested that small (<5 mm) *Leptodora* ingest yeast, bacterial and algal cells (Moshiri, 1968; Moshiri *et al.*, 1969), although this should be treated with skepticism.

Estimates of feeding rates in *Leptodora* vary widely: six *Daphnia retrocurva* day⁻¹ (Havel, 1985), 30 *Polyphemus pediculus* day⁻¹ (Mordukhai-Boltovskaia, 1958), 2.5 *Diaphanosoma brachyurum* day⁻¹ (Auer, 1988), 14 *D. pulex* day⁻¹ (this study). The great variability in these feeding rates is probably due to the prey type used and to differences in methodologies, most notably prey abundance, size of the experimental chamber (e.g. O'Brien, 1988) and temperature. We have not been able to determine a reliable estimate of the amount of time between attacks for a given *Leptodora*, although a single prey item can remain in the feeding basket for over 60 min (Sebastyen, 1931).

Using these feeding rates, and measurements of *Leptodora* respiration, it is possible to make a first-order comparison between energy intake and the cost of maintenance metabolism (Table III). Published estimates of *Leptodora* respiration vary greatly: 1.75 cal *Leptodora*⁻¹ day⁻¹ (Moshiri *et al.*, 1969) and 0.11 cal *Leptodora*⁻¹ day⁻¹ in maintenance metabolism at 20°C (Hillbricht-Ilkowska and Karabin, 1970; Table III). None of the published feeding rate estimates would provide >64% of a 1.75 cal day⁻¹ minimum energy requirement while they all provide >100% of a 0.11 cal day⁻¹ requirement (Table III). More measure-

Table III. Comparison of *Leptodora* energy intake and assimilation with energy expended in respiration

Prey species (size)	Calorific content (cal individual ⁻¹)	Feeding rate (no. day ⁻¹)	Energy ingested (cal day ⁻¹)	Energy assimilated = energy ingested × 0.87 ^a (cal day ⁻¹)	Ratio of energy assimilated to energy consumed in respiration ^b Energy assimilated 0.11 cal <i>Leptodora</i> ⁻¹ day ^{-1c}	Energy assimilated 1.75 cal <i>Leptodora</i> ⁻¹ day ^{-1d}
<i>Daphnia retrocurva</i> (~0.5 mm)	0.051 ^e	6 ^f	0.31	0.27	2.45	0.15
<i>Daphnia pulex</i> (1.1–1.5 mm)	0.092 ^g	14 ^h	1.29	1.12	10.18	0.64
<i>Diaphanosoma brachyurum</i> (0.6–0.9 mm)	0.048 ⁱ	4.5 ^j	0.22	0.19	1.73	0.11

^aHillbricht-Ilkowska and Karabin (1970).

^bValues for respiration (maintenance metabolism) were converted from ml O₂ *Leptodora*⁻¹ day⁻¹ to calories by multiplying by 4.8, the conversion factor for the number of calories consumed by 1 ml of O₂ in oxidative metabolism (Schmidt-Nielsen, 1983, p. 587).

^cHillbricht-Ilkowska and Karabin (1970): based upon a value of 9.65 × 10⁻⁴ ml O₂ respired h⁻¹ by 'mature' *Leptodora* at 20°C.

^dMoshiri *et al.* (1969): taken as the mean of values for 6–7 and 8–9 mm individuals drawn from the curves in Figure 1, at 20°C.

^eCummins and Wuycheck (1971): calculated from the mean of all the *Daphnia* spp. measurements, assuming 10 µg *D. retrocurva*.

^fHavel (1985): at 24.5°C.

^gCummins and Wuycheck (1971): calculated from the mean of the values for 1.3 and 1.8 mm specimens, assuming 20 µg *D. pulex*.

^hThis study: maximum feeding rate at 20°C.

ⁱAuer (1988).

^jAuer (1988): drawn from Figure 5, at 20°C.

ments of prey-specific feeding rate and energy consumption are needed in order to achieve firmer estimates of these parameters.

Within the current framework for foraging tactics in invertebrate predators, *Leptodora* must be considered a cruise predator (Greene, 1983, 1985, 1988; O'Brien *et al.*, 1989). Unlike ambush predators such as *Chaoborus*, which have a cylindrical strike volume surrounding their entire length (Riessen *et al.*, 1988), and other invertebrate cruise predators (reviewed in Greene, 1988), the location space for *Leptodora* is limited to a small forward-directed area and direct contact with the prey is required before an attack is initiated. This means that *Leptodora* encounter rates with prey are much lower than might be expected, certainly far lower than some ambush and other cruising invertebrate predators (Gerritsen and Strickler, 1977). Whereas differences in prey swimming speeds largely determine their encounter rates with an ambush predator and thereby play a large part in prey selection (Gerritsen and Strickler, 1977; Riessen *et al.*, 1988), this is not the case for a cruising predator such as *Leptodora*, particularly given its small prey location volume.

Given the indiscriminate nature of the abdominal reflex, strike efficiency [the probability that an initial attack results in an ingestion (Swift and Fedorenko, 1975; Pastorok, 1981)] is difficult to estimate. If all abdominal reflexes, even those that could not possibly result in a successful attack (>90% of encounters), are considered as attacks, then strike efficiency in this species would be extremely low. It is difficult to discriminate between a successful attack and an unsuccessful abdominal reflex from casual observations and we suggest that this might lead to overestimates of *Leptodora*'s feeding rate.

Prey selection in *Leptodora* is probably passive, being determined strictly by prey vulnerability [defined as the product of encounter rate and strike efficiency (Pastorok, 1981; Greene, 1988)]. Prey encounter rate for *Leptodora* will be low and is determined by the probability of contacting a given prey item, which is related in turn to abundance, relative swimming speed and avoidance or escape responses. Striking at prey is an automatic and indiscriminate reflex activated by direct contact with any particle, while prey capture or escape appears to be related to its size relative to the feeding basket and possibly to its shape.

We propose the following predation cycle for *Leptodora*: encounter (contact), strike (abdominal reflex), capture (retained in the feeding basket, or escape), ingestion. Probabilistic estimates of each of these components for the major prey species in the diet must be determined before a realistic estimate of the effect of *Leptodora* predation on zooplankton communities can be made.

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