

Feeding patterns of migratory and non-migratory fourth instar larvae of two coexisting *Chaoborus* species in an acidic and metal contaminated lake: Importance of prey ingestion rate in predicting metal bioaccumulation

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With 6 figures and 4 tables

Abstract: We studied diel variations in the feeding habits and migratory behaviors of two coexisting *Chaoborus* species in an acidic and metal contaminated lake (Lake Turcotte, QC, Canada). We found that although the zooplankton community was dominated by rotifers, both *Chaoborus* species fed mostly on chironomids and crustaceans despite the relatively low abundance of these prey types in the lake plankton. *Chaoborus americanus* larvae fed on those of *Chaoborus punctipennis*, but not vice versa. The non-migratory species (*C. americanus*) fed throughout the day and night whereas the migratory species (*C. punctipennis*) fed only at night while in the water column. The larger-bodied *C. americanus* consumed more prey and had a more diverse diet than did the smaller-bodied *C. punctipennis*. Differences in feeding habits between the *Chaoborus* species inhabiting Lake Turcotte (prey biomass, prey types) likely explain in part their ability to coexist. Attempts to predict Cd in the *Chaoborus* species using our measurements of Cd in their prey and their prey ingestion rates met with mixed success; although we correctly predicted higher Cd concentrations for *C. americanus* larvae than for *C. punctipennis* larvae, we under-predicted absolute Cd concentrations. We suggest that studies such as ours that are based on analyses of gut contents of larvae collected at intervals of 4 h or longer likely underestimate prey ingestion rates.

Key words: Bioaccumulation, diel vertical migration, feeding habits, coexistence, gut contents, cadmium.

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Introduction

Because larvae of the phantom midge *Chaoborus* (Insecta, Diptera) occur over a large range of chemical conditions (HARE & TESSIER 1996, 1998), are widely distributed (BORKENT 1981), and are able to accumulate and tolerate high concentrations of trace metals without ill effect (CROTEAU et al. 2002 a), they have been proposed for use as biomonitors of cadmium (Cd) in lakes (HARE & TESSIER 1996, 1998). To this end, models have been developed to relate Cd concentrations in *Chaoborus* to those in lakewater (HARE & TESSIER 1996, 1998, CROTEAU et al. 1998). However, such relationships are indirect because larvae of *Chaoborus* take up Cd from their zooplanktonic prey rather than from water (MUNGER & HARE 1997, MUNGER et al. 1999). Information on the feeding habits of *Chaoborus* could, therefore, be used to improve these models. A case in point is Lake Turcotte (Québec, Canada), where model predictions for Cd in *C. punctipennis* did not explain measured Cd concentrations for this species (CROTEAU et al. 1998). Furthermore, Cd concentrations in the two *Chaoborus* species inhabiting this lake (*C. americanus* and *C. punctipennis*) differ markedly (CROTEAU et al. 1998). Although metal bioaccumulation can be influenced by physical (e.g., temperature: CROTEAU et al. 2002 b), chemical (e.g., trace metal speciation: CAMPBELL 1995, HARE & TESSIER 1996) and physiological factors (e.g., metal assimilation efficiency: CROTEAU et al. 2001), diet-related variables such as the type, quantity, quality and Cd content of food are likely central to explaining differences between sympatric species (REINFELDER et al. 1998). Major differences in diet have been reported for coexisting *Chaoborus* species (SARDELLA & CARTER 1983, HARE & CARTER 1987), although there are no published studies comparing the feeding habits of sympatric *C. americanus* and *C. punctipennis* larvae. Differences in feeding habits could also help to explain the coexistence of these species (FEDORENKO 1975, CARTER & KWIK 1977, SARDELLA & CARTER 1983, HARE & CARTER 1987), as could differences in their depths in the water column (TSALKITZIS et al. 1993) and the extent of their vertical migrations (CARTER & KWIK 1977, HARE & CARTER 1987).

To compare the diel feeding habits and vertical distributions of sympatric *C. americanus* and *C. punctipennis* larvae, we collected benthic *Chaoborus* and zooplankton (including *Chaoborus*) from various depths at 4 hour intervals in Lake Turcotte. To compare *Chaoborus* feeding regimes, we examined larval gut contents to estimate ingestion rates, feeding periodicities and types of prey consumed. Lastly, we incorporated our measurements of prey ingestion rates and prey Cd into a mechanistic Cd bioaccumulation model (CROTEAU et al. 2001, 2002 b) to determine if we could predict Cd concentrations in the two *Chaoborus* species.

Methods

Study site

We collected zooplankton on September 19–20 2000 (stations A and B) as well as benthic *Chaoborus* on September 19–20 (station A) and September 23–24 (station B) 2000 from Lake Turcotte (48° 18' N, 79° 04' W), Québec, Canada. Stations A and B were located at the same depth (5 m) on opposite sides of the central basin (50 m apart) so as to encompass any horizontal heterogeneity in zooplankton composition (PINEL-ALLOUL 1995, FOLT & BURNS 1999). Samples were collected at 4 h intervals over 24 h, with sampling at stations A and B ending and beginning, respectively, on the hour. This small (5 ha), shallow (5 m maximum depth), highly acidic (pH 5) and fishless lake has been strongly influenced by nearby metal smelters in Rouyn-Noranda, QC. CROTEAU et al. (1998) reported that the dissolved concentrations of several trace metals in this lake are very high, e.g., 20 nM for Cd and 5000 nM for Zn, compared with concentrations of these metals in pristine lakes (0.2 and 8 nM for Cd and Zn, respectively; HARE & TESSIER 1998). At the time of sampling, the fall overturn of Lake Turcotte had already occurred since temperature, oxygen and pH were fairly constant with depth, i.e., 13.9 ± 0.2 °C, 8.5 ± 0.1 mg O₂ l⁻¹ and 4.9 ± 0.1 , respectively (means \pm S.D. of measurements at 1 m intervals on 19 September).

Sample collection

We collected planktonic *Chaoborus* larvae and their potential zooplanktonic prey at 1200h, 1600h, 2000h, 2400h, 0400h and 0800h (times of sunset and sunrise were 0645h and 1905h, respectively). Samples were collected using a 0.05 m³ Plexiglas plankton trap equipped with a 64- μ m mesh-aperture net. Collections were made at 0.5 m intervals from the surface to the bottom at both stations A and B. Samples were placed in 250 mL jars, to which chloroform was added, to anaesthetize animals so that they would not regurgitate their gut contents, followed by 10% formalin for preservation. We also collected benthic *Chaoborus* larvae at every sampling time by taking a single sample at each station using a 15 \times 15 \times 15-cm Ekman grab. Larvae were isolated from the sediment by sieving through a 0.5-mm mesh-aperture net then placed in a 1-L jar, anaesthetized in chloroform and preserved in 10% formalin.

For Cd measurements, we collected large numbers of zooplankton at mid-day on September 22 by hauling a 64- μ m mesh-aperture net at lake centre; the net's path ensured that plankton was collected from all depths. This plankton was placed in plastic bags with lakewater. In the laboratory, we prepared two subsamples of this bulk plankton using a 64- μ m mesh-aperture nylon sieve. Subsamples were placed on pieces of pre-weighed acid-washed Teflon sheeting that were frozen until Cd analysis. We did not measure zooplankton Cd over several weeks prior to collecting *Chaoborus* (so as to integrate possible temporal changes in prey Cd) because unpublished data (M.-N. Croteau) show that Cd concentrations in calanoid copepods as well as in bulk plankton vary little over the 2 weeks that it takes *Chaoborus* larvae to achieve a steady state in their Cd concentrations in the early spring (CROTEAU et al. 2001, 2002 b).

Chaoborus crop contents

In the laboratory, all *Chaoborus* collected were sorted to species (SAETHER 1972) and final (fourth) instar larvae were differentiated by head capsule length, as given in LAROW & MARZOLF (1970) for *C. punctipennis* and in FEDORENKO & SWIFT (1972) for *C. americanus*. All fourth instar larvae of each *Chaoborus* species were dissected to remove their crop (SWIFT & FEDORENKO 1973) and larval bodies and crops, opened to reveal their contents, were individually mounted on microscope slides. Food items in crops were identified and prey densities in crops were converted to biomass based on the dry weights of various taxa given in YAN & STRUS (1980) and MALLEY et al. (1989).

Zooplankton community analysis

All crustaceans and chironomids were counted in plankton samples. Cladocerans and chironomids were identified to either genus or family levels. Copepods collected at Station A were assigned to one of four groups: calanoid adults, cyclopoid adults, copepodids or nauplii, whereas only the adult stages were enumerated in samples collected at Station B. Rotifers were identified from samples collected at Station A to the genus level and counted in 1/16 subsamples obtained using a Folsom plankton splitter. Although some algae (mainly diatoms) were present in plankton samples, we did not estimate their densities since they were likely under-represented.

Ivlev selectivity index

Chaoborus food selectivity was expressed by the IVLEV (1961) coefficient (E):

$$E = \frac{r_i - p_i}{r_i + p_i} \quad (1)$$

where r_i is the mean relative biomass of a taxon in the crop of *Chaoborus* and p_i is the mean relative biomass of the taxon in the lake plankton; means in both cases are for 6 samples collected at 4 h intervals over 24 h. Positive electivity values indicate that the prey type is over represented in the diet compared to its density in the plankton, 0 the absence of electivity and negative electivity values indicate that the prey type is under-represented in the diet compared to its abundance in the plankton.

Cadmium analyses

To minimize inadvertent trace metal contamination, we soaked all labware and sampling material in 15% nitric acid and rinsed them in ultrapure water ($> 18 \text{ M}\Omega \text{ cm}$) prior to use. Zooplankton samples were freeze-dried (FTS SystemsTM), weighed on a microbalance (Mettler ME30) and digested in concentrated nitric acid at room temperature as described in CROTEAU et al. (2001). We submitted samples of similar weight of a certified reference material (lobster hepatopancreas, TORT-1, NRCC) to the same digestion procedure during each run. Cadmium concentrations in animal digests were analyzed by flameless AAS (Varian Spectra AA-30); Cd concentrations measured in TORT-1 were within the certified range and the recovery of Cd in spiked samples was within 10% of the amount added.

Results and discussion

Zooplankton community composition

The low total zooplankton biomass found in Lake Turcotte ($\approx 10 \text{ mg d.w. m}^{-3}$, Fig. 1) is typical of many acidic and trace-metal contaminated Shield lakes (YAN & GEILING 1985, YAN & WELBOURN 1990). Circum-neutral Shield lakes can contain 4–5 times this biomass (YAN & GEILING 1985). The zooplankton community of Lake Turcotte was largely dominated, in both density and biomass terms, by rotifers; 79 to 91 % of the animal biomass collected belonged to this group (Fig. 1, Table 1). The importance of rotifers in acidified and metal-contaminated lakes has been attributed to a reduction in the abundance of crustacean competitors and predators owing to the effects of either acidification or metals or both (NEILL 1984, YAN & GEILING 1985, YAN et al. 1988). In contrast, the richness of rotifer communities is reported to be less reduced by acidification than is that of crustacean communities (YAN & LAFRANCE 1984). Although our study was limited to the autumn, CROTEAU et al. (1998, 2002 b) reported a similar dominance of rotifers in spring plankton samples from this lake.

Although *Keratella* was the most abundant rotifer, the much larger *Asplanchna* (MALLEY et al. 1989) made up the majority (49–67 %) of the total biomass (Table 1). Ours is the first study to report dominance of the biomass

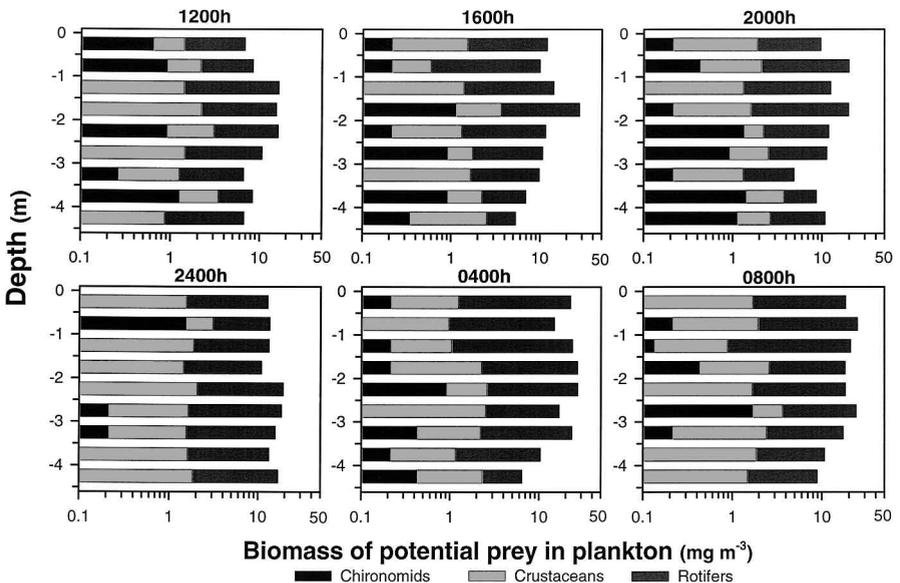


Fig. 1. Diel vertical changes in the biomass of potential prey for *Chaoborus* larvae (Station A, 19–20 September 2000).

Table 1. Mean density (individuals m^{-3} , $n = 9$) and percentage contribution to the total zooplankton biomass (in parentheses) of major animal taxa collected at various times of the day at station A on September 19–20, 2000.

Taxa	Time (hour)					
	1200 h	1600 h	2000 h	2400 h	0400 h	0800 h
Rotifera						
<i>Asplanchna</i> sp.	12836 (61)	15680 (67)	15609 (67)	16676 (57)	17742 (49)	11520 (51)
<i>Conochiloides</i> sp.	1067 (0.5)	249 (0.1)	213 (0.1)	36 (<0.1)	178 (<0.1)	71 (<0.1)
<i>Gastropus</i> sp.	36 (<0.1)	36 (<0.1)	36 (<0.1)	36 (<0.1)	36 (<0.1)	0 (0)
<i>Kellicotia</i> sp.	36 (<0.1)	36 (<0.1)	36 (<0.1)	0 (0)	0 (0)	0 (0)
<i>Keratella</i> sp.	41138 (6.7)	35413 (5.2)	33209 (4.9)	44978 (5.3)	48427 (4.6)	35022 (5.3)
<i>Polyarthra</i> sp.	6293 (7.2)	8284 (8.6)	9280 (9.6)	26240 (22)	53618 (36)	25493 (28)
<i>Synchaeta</i> sp.	2916 (3.9)	2169 (2.7)	320 (0.4)	1067 (1.1)	1529 (1.2)	1707 (2.2)
Copepoda, Cyclopoida						
Adults	2 (0.1)	2 (0.1)	0 (0)	7 (0.1)	7 (0.1)	0 (0)
copepodids	178 (1.6)	36 (0.3)	36 (0.3)	0 (0)	71 (0.4)	0 (0)
nauplii	3378 (11)	3520 (11)	3733 (11)	4196 (10)	3449 (6.7)	2738 (8.6)
Cladocera						
Chydoridae	28 (0.2)	30 (0.2)	23 (0.2)	30 (0.2)	18 (0.1)	29 (0.2)
Bosminidae	7 (0.1)	8 (<0.1)	6 (<0.1)	8 (<0.1)	4 (<0.1)	7 (<0.1)
Macrothricidae	0 (0)	9 (0.2)	18 (0.5)	2 (<0.1)	9 (0.1)	11 (0.3)
Insecta						
Chironomidae	22 (7.2)	20 (4.6)	31 (6.0)	7 (4.2)	20 (2.0)	18 (4.5)
Total	67937 (100)	65492 (100)	62550 (100)	93283 (100)	125108 (100)	76616 (100)

by *Asplanchna* in acidic and metal contaminated lakes, where *Keratella* usually dominates (YAN & GEILING 1985). The second most important planktonic group was copepods, which were mainly present as immatures (i.e., copepodids and nauplii, Table 1). All adult copepods collected were cyclopoids, and the examination of several sub-samples indicated predominance by *Cyclops scutifer* and, in lesser numbers, *Eucyclops* sp. Cladocerans were rare, with chydorids being the major taxon in most samples (Table 1). The absence of calanoid copepods and the rarity of cladocerans in Lake Turcotte are likely explained both by the sensitivity of most cladocerans to high acidity (HAVENS & HANAZATO 1993) and the sensitivity of both of these groups to the toxic metal cadmium (LAWRENCE & HOLOKA 1987). Chironomid larvae were collected at most depths and sampling times (Fig. 1); all identifiable larvae were ascribed to one of four genera: *Chironomus*, *Polypedilum*, *Procladius* or *Psectrocladius*. The head capsule sizes of these larvae suggest that although many were first instars, which are known to be planktonic (DAVIES 1976), the majority were later instars. The consistent presence of post first instar chironomid larvae in the plankton appears to be very uncommon.

Chaoborus diel behavior

Despite remaining in the water column throughout the day (Fig. 2) in contact with potential zooplanktonic prey (Fig. 1), the crop of 40 to 80% of *C. americanus* larvae was empty at any one time (Fig. 3). Judging from the number of prey in the crop (Fig. 4), feeding activity by *C. americanus* increased at night. FEDORENKO (1975) reported a similar tendency for *C. americanus* in a British Columbia lake. Prey biomass in *C. americanus* crops was also greater at night (Fig. 5). However, this trend was only evident at Station B (Fig. 5); it was obscured at Station A by the presence of a few large insects in the crops of *C. americanus* collected at 1600h and 0800h (Fig. 5). This diel variation could be explained if larvae are either more active at night or if preferred prey are more available at this time, as reported by NEILL (1990). Our data support the former possibility because we saw no evidence of prey movement with depth (Fig. 1).

We collected *C. americanus* larvae in the sediment both during the day and at night, with largest numbers being present at night (Fig. 6). Approximately 90% of benthic *C. americanus* larvae were fourth instars. Although TSALKITZIS et al. (1993) showed that *C. americanus* larvae can migrate vertically in the water column, ours is the first to report that they enter sediment. The shallow depth of Lake Turcotte ($Z_{\max} \approx 5$ m) might have favored this behavior.

Feeding activity of *C. punctipennis* larvae in the water column increased at night, as evidenced by the large increase in the proportion of larvae with food

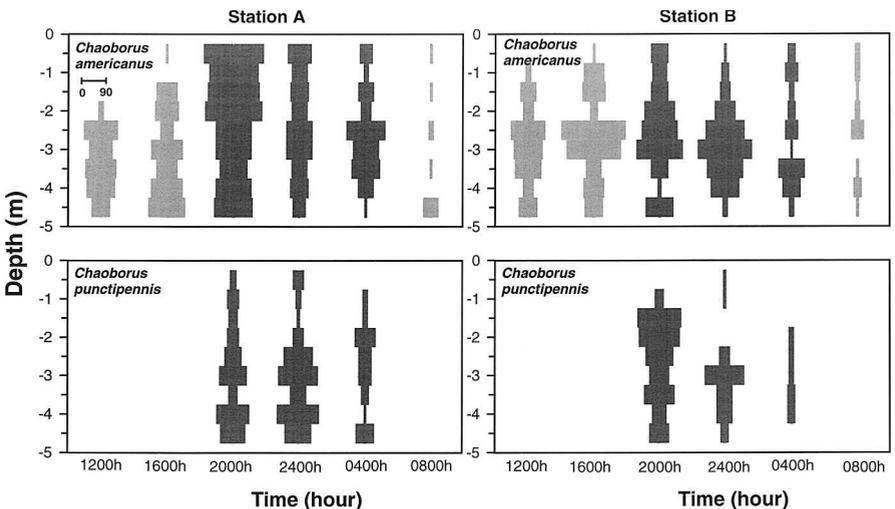


Fig. 2. Diel vertical changes in the density (individuals m^{-3}) of planktonic *Chaoborus* larvae at both Station A (19–20 September 2000) and Station B (23–24 September 2000).

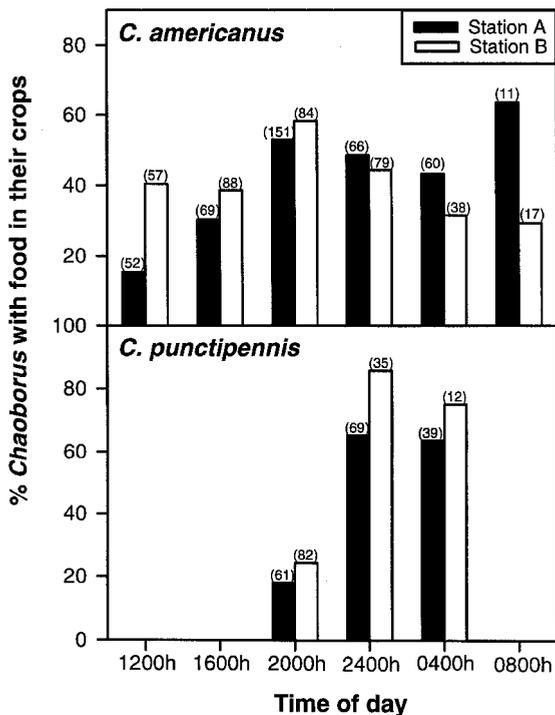


Fig. 3. Diel changes in the proportion of *Chaoborus* larvae with prey in their crop. The total number of *Chaoborus* larvae that were dissected is shown in parenthesis.

in their crop between 2000h and 2400h (Fig. 3). Crops of all *C. punctipennis* larvae collected in sediment at 0800h were empty (Fig. 6), suggesting that all prey consumed between 0400h and sunrise (0645h) were digested within a few hours. Given that the temperature of Lake Turcotte water was around 14 °C at the time of our study, this rate of digestion is somewhat higher than that reported for *Chaoborus trivittatus*; this animal is reported to take from 4 (at 25 °C) to 24 hours (at 5 °C) to digest a single copepod (FEDORENKO 1975). Digestion rates are, however, reported to vary greatly with prey type (FEDORENKO 1975), and our *Chaoborus* species consumed a variety of other prey types. Our results suggest that larvae of *C. punctipennis* experience a starvation period of around 12 hours (from sunrise at 0645h to sunset at 1905h), which could influence their subsequent selection of prey. PASTOROK (1980 a, 1980 b) reported that satiated *C. trivittatus* larvae fed preferentially on *Diaptomus* (Copepoda) compared with *Daphnia* (Cladocera), whereas starved larvae attacked prey indiscriminately. Because prey types tend to differ in their Cd content and because the assimilation of trace metals varies according to the type of prey consumed (REINFELDER et al. 1998), the existence or not of a daily star-

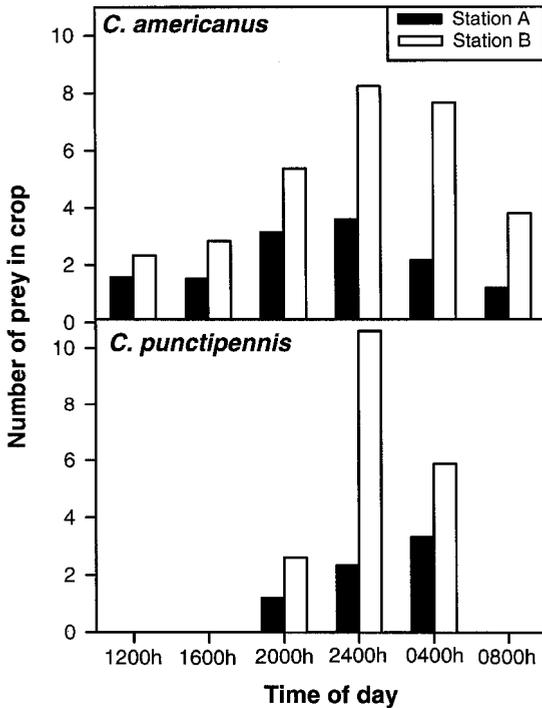


Fig. 4. Diel variations in the numbers of prey present in the crops of *Chaoborus* collected at our two study stations.

variation period could contribute to differences in the Cd concentrations of *C. americanus* and *C. punctipennis*.

We found no benthic prey in the crops of *C. punctipennis* larvae collected in the sediment (Fig. 6), suggesting that larvae do not feed in the sediment. Although there has been some speculation that larvae might feed during the benthic phase of their migration cycle (GOLDSPIK & SCOTT 1971, SWÜSTE et al. 1973, FEDORENKO 1975, PASTOROK 1980 a), it is difficult to imagine that mechano-receptors for prey movement would be effective when *Chaoborus* larvae are surrounded by sediment particles.

Because *C. punctipennis* daytime benthic density (Fig. 6) did not approximate its night time planktonic density, as was the case for *C. americanus* (Fig. 2), some horizontal displacement of larvae likely took place during their migration, as has been reported by TSALKITZIS et al. (1993) and VOSS & MUMM (1999). A strong horizontal component to the vertical migration of *Chaoborus* could also explain in part the variability in the total density of *Chaoborus* observed between our stations and among sampling times (Fig. 2). However, because our density estimates for benthic *Chaoborus* are based on

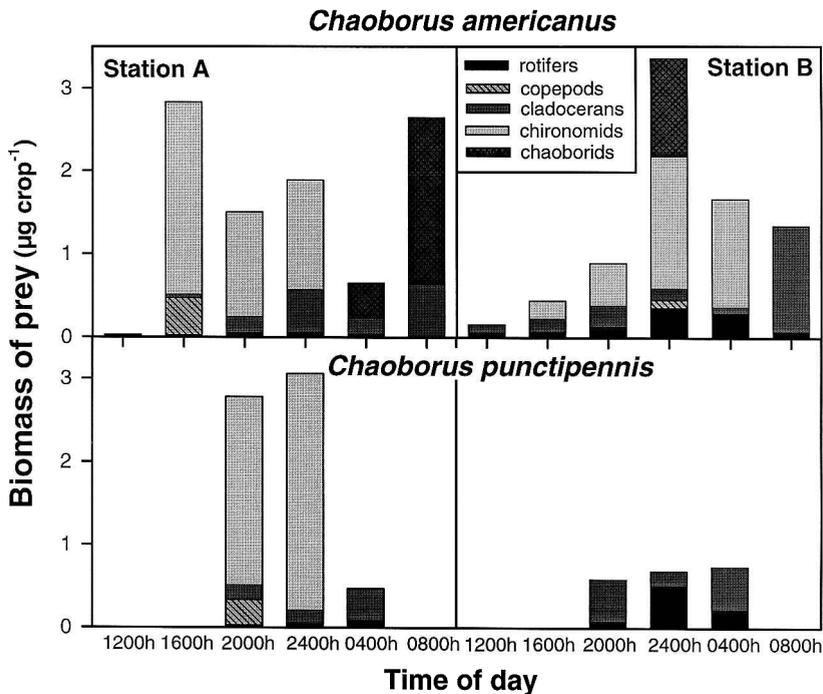


Fig. 5. Diel variations in the biomass of the various prey types found in the crops of *Chaoborus* collected at our two study stations.

single grab samples (per station per time), trends such as the nocturnal increase in benthic *C. punctipennis* larvae at Station B (Fig. 6) could be artifacts.

Diet of the *Chaoborus* species

Both *Chaoborus* species fed on crustaceans, rotifers and chironomid larvae (Fig. 5). Although fairly abundant in the Lake Turcotte zooplankton (Table 1), copepod nauplii were never encountered in the crops of either *Chaoborus* species. SWIFT (1992) has suggested that cyclopoid nauplii reduce encounter frequencies with first-instar *Chaoborus* larvae by remaining motionless for long periods. The virtual absence of nauplii in the diet of *Chaoborus* has been reported in several studies (SARDELLA & CARTER 1983, HARE & CARTER 1987, MOORE 1988, IRVINE 1997). High positive Ivlev selectivity values suggest that cladocerans are elected by both *Chaoborus* species (Table 2); LEWIS (1977) also reported high positive electivity values for cladocerans by *Chaoborus*. Algae (mainly diatoms) were found in the crops of both species at most times and depths (results not shown), supporting their importance in the diet of *Chaoborus* larvae (HARE & CARTER 1987, MOORE et al. 1994). PASTOROK

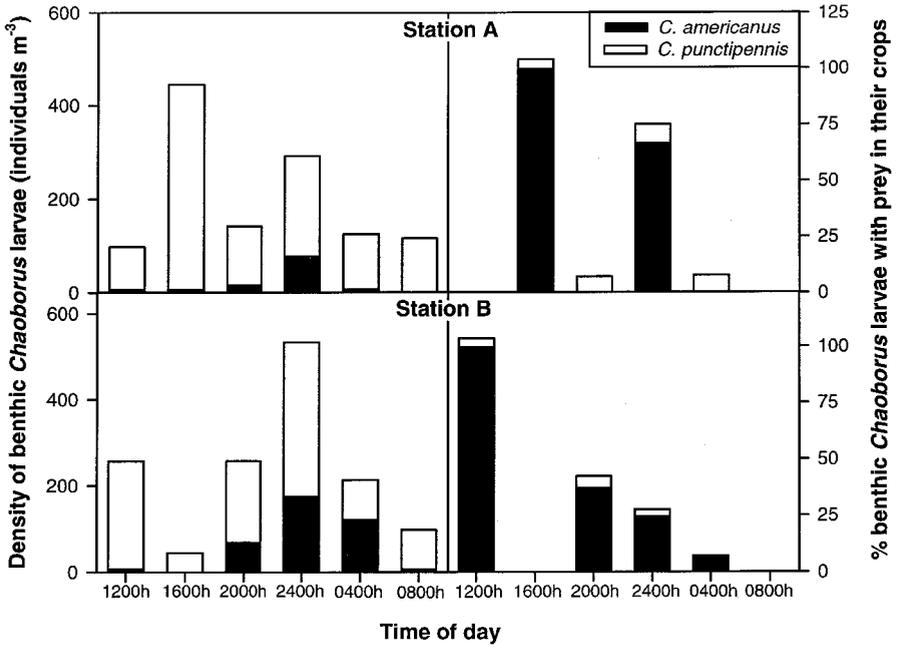


Fig. 6. Diel variations in the density (individuals per m^3) of benthic fourth instar *Chaoborus* larvae (left panels; benthic densities averaged over the height of the water column to permit comparison with Fig. 2) as well as the proportion of these larvae with identifiable prey items in their crop (right panels) at our two study stations.

(1980 a) suggested that *Chaoborus* switch to feeding on algae whenever animal prey are scarce, which could be the case in Lake Turcotte given its very low zooplankton biomass (Fig. 1, Table 1). Chironomid larvae, because of their large size (Table 4), contributed greatly to the biomass of prey consumed by both *Chaoborus* species. Second and third instar *C. punctipennis* larvae were also important in the diet of *C. americanus* (Fig. 5). As evidenced by the mostly positive electivity values for chironomids (Table 2), the high biomass (Fig. 5) and frequency of chironomids in *Chaoborus* crops was more than expected based on their low biomass and abundance in the plankton (Fig. 1, Table 1). At some sampling times and depths, the very low abundance of chironomids and cladocerans in the plankton meant that very few were available to be eaten by *Chaoborus* and thus none were present in their guts; this led to some negative selectivity indexes for these prey (Table 2). SWIFT & FEDORENKO (1975) reported a similar finding in Eunice Lake where the large copepod *Diaptomus kenai*, although the primary source of biomass for *C. trivittatus*, was almost never available to *Chaoborus* because their depth distributions seldom overlapped. The most common rotifer in *Chaoborus* crops was *Keratella* (Fig. 5), although non-loricata taxa that are more easily digested

Table 2. Values of the IVLEV (1961) selectivity index calculated for fourth instars of two *Chaoborus* species and four major prey types collected at various times at Station A on September 19–20, 2000. Mean (\pm S. D.) mouth gapes of larvae are presented in parentheses.

<i>Chaoborus</i> species	Time	Rotifera	Copepoda	Cladocera	Chironomidae
<i>C. americanus</i> (0.71 \pm 0.06 mm) ¹	1200 h	0.34	-1	-1	-1
	1600 h	-0.97	0.93	-0.53	0.30
	2000 h	-0.83	-	0.38	0.24
	2400 h	-0.89	-1	0.82	0.24
	0400 h	-0.58	-1	0.92	-1
	0800 h	-0.93	-	0.92	-1
	Mean	-0.64	-0.52	0.25	-0.37
<i>C. punctipennis</i> (0.45 \pm 0.02 mm) ²	1200 h	-	-	-	-
	1600 h	-	-	-	-
	2000 h	-0.98	1	0.08	0.23
	2400 h	-0.93	-1	0.33	0.37
	0400 h	-0.52	-1	0.91	-1
	0800 h	-	-	-	-
	Mean	-0.81	-0.33	0.44	-0.13

¹ FEDORENKO (1975).

² MOORE (1988).

Table 3. Values of variables and parameters used for predicting Cd concentrations in fourth instar *Chaoborus* larvae from Lake Turcotte.

Variable or Parameter	<i>C. punctipennis</i>	<i>C. americanus</i>	Reference
Weight (mg larva ⁻¹) \pm S. D.	0.17 \pm 0.03	0.43 \pm 07	CROTEAU & HARE, unpubl. results
<i>Chaoborus</i> Cd concentration (μ g g ⁻¹) \pm S. D.	2.21 \pm 0.73	6.34 \pm 0.77	CROTEAU & HARE, unpubl. results
Biomass of prey consumed (μ g d ⁻¹)	6.31	9.54	This study
Prey ingestion rate (g prey g <i>Chaoborus</i> ⁻¹ d ⁻¹)	0.0371	0.0222	This study
Cd concentration in food (μ g g ⁻¹) \pm S. D.	7.43 \pm 0.01	7.43 \pm 0.01	This study
Cd assimilation efficiency (%)	0.057	0.58	CROTEAU et al. (2001)
Cd loss rate constant (d ⁻¹)	0.0029	0.0368	CROTEAU et al. (2001)
Growth rate constant (d ⁻¹)	0.0134	0.0253	CROTEAU et al. (2001)
Predicted <i>Chaoborus</i> Cd concentration (μ g g ⁻¹)	0.98	1.54	This study

could have been under-represented (e.g., *Asplanchna*) since soft-bodied prey were not seen in crops. Ingestion of rotifers by *C. punctipennis* (CHIMNEY et

Table 4. Zooplankton body sizes from MALLEY et al. (1989).

Taxa	Prey size (length × width in μm)
Rotifera	
<i>Asplanchna</i> sp.	304 × 244
<i>Conochiloides</i> sp.	150 × 97
<i>Gastropus stylifer</i>	88 × 71
<i>Kellicotia longispina</i>	132 × 56
<i>Keratella taurocephala</i>	119 × 73
<i>Polyarthra vulgaris</i>	120 × 71
<i>Synchaeta</i> sp.	74 × 70
Copepoda, Cyclopoida¹	
adults	1238 × 349
copepodid V	917 × 280
copepodid I	363 × 140
nauplius VI	242 × 127
nauplius I	110 × 71
Cladocera	
<i>Chydorus sphaericus</i> ²	250 × 320
<i>Bosmina longirostris</i> ³	210 × 160
Macrothricidae ⁴	[200–400] × [280–720]
Insecta	
Chironomidae ⁴	[500–1200] × [60–120]

¹ Data for *Cyclops bicuspidatus thomasi*.

² From SWIFT (1992).

³ From FEDORENKO (1975).

⁴ Range of sizes for individuals examined in our study.

al. 1981, MOORE 1988) and most other *Chaoborus* species (FEDORENKO 1975, SARDELLA & CARTER 1983, HARE & CARTER 1987) is common. Although rotifers were the most important potential prey in the Lake Turcotte plankton (Fig. 1, Table 1), they contributed little to the total biomass of prey in *Chaoborus* crops (Fig. 5). *Chaoborus* electivity indexes for this prey type are correspondingly highly negative (Table 2).

The diet of *C. americanus* larvae was in general more diverse than that of *C. punctipennis*, with more prey types being found in crops of the former species at most sampling times and stations (Fig. 5). This is surprising given the fact that feeding selectivity is reported to be inversely proportional to larval hunger state (IVLEV 1961, PASTOROK 1980 b) and because *C. punctipennis* larvae experience a starvation period of at least 12 h whereas *C. americanus* larvae do not (Figs. 3–5). FEDORENKO (1975) suggested however, that a more diverse diet is likely a consequence of the fact that larger larvae can handle a greater range of prey sizes due to their larger mouth gape (Table 2). Larvae of

C. americanus also had (on average) a larger biomass of prey in their crops that did larvae of *C. punctipennis* (Fig. 5).

Based on our estimates of prey biomass in crops (Fig. 5, Table 3), larvae of *C. punctipennis* and *C. americanus* consumed 3.7 and 2.2 %, respectively, of their weight per day (Table 3). When offered prey in excess of their needs (in the laboratory at a temperature similar to that in Lake Turcotte, i.e., 14 °C), mass-normalized consumption values are 3 to 6 times greater (CROTEAU et al. 2002 b). Although our field values are probably underestimates (discussed above), the major explanation for these differences likely lies in the near absence of the food groups (crustaceans in Table 1) usually exploited by *Chaoborus* in Lake Turcotte. The slightly higher prey ingestion rates for *C. punctipennis* could be the result of their daily starvation period, i.e., JOHNSON et al. (1975) reported that many arthropods exhibit “compensatory feeding” in which the intake of food is elevated after going without food for a short time.

Predicting Cd in *Chaoborus*

In lakes in which *C. punctipennis* coexists with *C. americanus*, CROTEAU et al. (2001) reported that Cd concentrations in the latter species exceeded those in the former species by a factor of from 1.1 to 3.2 depending of the lake. Results of the present study are consistent with this trend because Cd concentrations in *C. americanus* larvae were almost 3 times those of *C. punctipennis* in Lake Turcotte (Table 3). Because *Chaoborus* larvae are known to take up all of their Cd from food (MUNGER & HARE 1997, MUNGER et al. 1999), the consumption by *C. americanus* of a greater prey biomass (Table 3) would have contributed to the higher Cd concentrations measured in this species. However, if prey consumption is expressed as a rate per unit mass of predator (g prey per g predator per day), the rate of prey ingestion by *C. americanus* was actually somewhat lower than that of *C. punctipennis* (Table 3). Rather than attempt to explain specific differences in Cd accumulation on the basis of a single variable (ingestion rate), we used a model that incorporates the key variables influencing metal bioaccumulation. Thus, steady-state Cd concentrations in *Chaoborus* ($[Cd]_{Chaoborus}$) should be related to the rate at which it ingests prey (IR), the efficiency with which it assimilates Cd from food (AE), the concentration of Cd in its food ($[Cd]_{food}$) and the rate constants for Cd loss (k_e) and larval growth (k_g), as expressed by the following equation (THOMANN 1981),

$$[Cd]_{Chaoborus} = \frac{AE \times IR \times [Cd]_{Food}}{k_e + k_g} \quad (2)$$

Using the values of AE, k_e and k_g reported from laboratory experiments (CROTEAU et al. 2001) along with our measurements of prey ingestion rates and Cd

concentrations in bulk plankton (Table 3), we predicted Cd concentrations in our two study species. We used concentrations of Cd in bulk zooplankton rather than in specific prey taxa because it was not feasible to hand pick and aggregate individual prey types into samples of sufficient biomass for Cd analyses (due to the low densities and small sizes of most prey types). On the one hand, our model predictions confirm previous findings that Cd concentrations in *C. americanus* should exceed those of *C. punctipennis*, that is, predicted Cd concentrations in *C. americanus* were 1.6 times those of *C. punctipennis* (Table 3). On the other hand, measured values of Cd concentrations in Lake Turcotte *Chaoborus* were 2.5 to 4 times greater than model predictions (Table 3). There are several possible explanations for this discrepancy. First, the estimates of model variables obtained in the laboratory are for *Chaoborus* consuming a calanoid copepod rather than the mixture of prey types available to the predator in Lake Turcotte. Second, and likely more important, CROTEAU et al. (2002 b) showed that prey ingestion rate strongly influences Cd concentrations in *Chaoborus*. Prey ingestion rates based on identifiable items in gut contents, as in this study, almost certainly underestimate prey consumption. For example, soft bodied prey leave little trace (for example, some rotifers), and *Chaoborus* larvae do not retain whole prey but crush and eject their exoskeleta via their mouth. As discussed above, our data suggest that exoskeleta are ejected within our sampling interval of 4 h. Our model underestimates could be explained if prey ingestion rates were higher by a factor of approximately 2 to 4, depending on the species (Table 3). Using a simple feeding rate model (ELLIOT & PERSSON 1978), we estimate that digestion times of 2.0 and 2.9 hours for *C. americanus* and *C. punctipennis*, respectively, would increase *Chaoborus* daily food consumption (by factors of 2 and 1.3) to fit these "target" ingestion rate values. If our estimates of prey ingestion rate are indeed too low, then most previous estimates of prey consumption by *Chaoborus* larvae in nature are also likely underestimates. In most field dietary studies, sampling intervals are not less than 4 h (MOORE 1988, IRVINE 1997) and such studies are made almost exclusively in the summer when water temperatures and digestion rates are likely to be highest. Another possible limitation of our study is that we measured prey ingestion over one day, whereas the Cd concentration in *Chaoborus* larvae likely depends on the numbers of prey consumed over the previous week or two (CROTEAU et al. 2001, 2002 b). Furthermore, our measurements were made in early autumn, at a time of declining water temperatures, and ingestion rates of *Chaoborus* are reported to decrease with declining temperature (CROTEAU et al. 2002 b). Overall, measurements of prey consumption rates at short intervals and at several times prior to the measurement of predator Cd would likely improve model predictions.

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