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Influence of temperature on Cd accumulation by species of the biomonitor *Chaoborus*

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Abstract

We exposed larvae of several species of the phantom midge *Chaoborus* to the trace metal cadmium (Cd) to determine whether Cd accumulation rates varied with ambient temperature. Because this predator is known to accumulate its Cd mainly from food rather than from water, we presented the Cd in food, that is, Cd-rich copepods taken from a lake near a metal smelter. Rates of Cd accumulation by larvae of *Chaoborus americanus, C. flavicans,* and *C. punctipennis* were measured at three temperatures (5, 14, and 22°C) covering the seasonal range encountered by these animals. The rates at which all species accumulated Cd increased with temperature. To explain these results, we fit our experimental data to a bioaccumulation model that allowed us to estimate Cd assimilation efficiency, Cd-efflux rate, and larval growth rate. Temperature-related changes in Cd accumulation rates were best explained by changes in the rate at which *Chaoborus* larvae ingested prey as well as the efficiency with which they assimilated Cd from their food. Neither the rate of larval growth nor the rate at which larvae lost Cd was influenced by temperature. Extrapolations of our laboratory results to the field suggest that our model results provide a realistic representation of the processes involved in Cd accumulation by larvae of this common aquatic insect.

A rise in temperature generally increases the metabolic rate of animals (Robinson et al. 1983; Ratte 1985), which usually leads to an increase in the ingestion and assimilation of carbon and other essential elements (Heiman and Knight 1975; Giguère and Dill 1980; Gresens 2001). The concentrations of nonessential trace metals such as cadmium are also reported to rise in organisms with increasing ambient temperature (Douben 1989; Janssen and Bergema 1991; Van Hattum et al. 1993; Bervoets et al. 1996), in part because these metals likely enter animals at uptake sites for essential metals such as calcium (Craig et al. 1998). Exceptionally, the opposite (e.g., Pb accumulation by *Asellus*; Van Hattum et al. 1993) or no effect of temperature (e.g., Cd uptake by *Mytilus edulis,* Jackim et al. 1977) has occasionally been reported. Reports of temperature influencing metal bioaccumulation are generally not followed up with an identification of the biological processes responsible for the effect. Speculations to explain metal bioaccumulation–temperature interactions have included changes in the rates at which food is ingested (Odin et al. 1994), water is passed over the gills (White and Rainbow 1984), metals cross biological membranes (Bervoets et al. 1996), and metal binding proteins are produced (Douben 1989). However, there are no published experimental studies explaining how temperature influences trace metal accumulation by freshwater invertebrates. For soil-dwelling invertebrates, we found only one study that addressed this question (Janssen and Bergema 1991).

Cadmium is a toxic and carcinogenic trace metal that commonly appears on government priority-substances lists (for example, the Canadian Environmental Protection Act). This metal is released by mining, smelting, and other industrial activities (Pacyna et al. 1995) into aquatic environments where it is accumulated by organisms (Hare 1992). To improve our ability to predict the impact of toxic trace metals such as cadmium, we need a better understanding of the processes controlling their accumulation by animals (Pace 2001).

We set out to study the influence of temperature on Cd accumulation by larvae of the phantom midge *Chaoborus,* a predatory insect proposed for use as a Cd biomonitor in lakes (Hare and Tessier 1996; Croteau et al. 1998). Because *Chaoborus* larvae take up Cd almost exclusively from their planktonic prey rather than from ambient water (Munger and Hare 1997; Munger et al. 1999), we measured the influence of temperature on Cd uptake by larvae from their food. Using a model that takes into account key processes in metal uptake and loss, we quantified the rate at which this insect ingests its Cd-containing prey, the proportion of ingested Cd that is assimilated, the rate at which the animal loses its Cd, as well as the rate at which the insect grows. If temperature influences Cd concentrations in *Chaoborus* larvae, then study of these processes should help us to explain how such an effect occurs. Because metal concentrations can differ among congeners (Janssen and Bergema 1991; Ritterhoff and Zauke 1997; Croteau et al. 2001), we compared the influence of temperature on Cd accumulation by three species of the genus. Lastly, we compared our model predictions with Cd concentrations measured in field collected *Chaoborus.*

Methods

We conducted experiments at three temperatures (5, 14, and 22°C) encompassing the range likely to be encountered by *Chaoborus* larvae at various depths and in various sea-

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Table 1. Location of lakes from which we collected water or final-instar *Chaoborus* larvae or both for the uptake and loss experiments. Also given is lakewater pH as well as mean larval and total dissolved Cd concentrations (±SD, $n = 10$ except for lake Caron where $n = 5$).

				Chaoborus	
Lake (region)	Location	pH	[Cd] (nM)	Species	Cd concentration (μg g^{-1} ± SD)
Low Cd lakes					
Bertrand (Quebec City)	46°58′N, 72°01′W	4.8	0.35 ± 0.09	*americanus*	1.14 ± 0.19
Hélène (Rouyn-Noranda)	48°13′N, 79°10′W	8.0	0.09 ± 0.02	*punctipennis*	0.05 ± 0.04
Laberge (Quebec City)	46°35′N, 71°20′W	8.2	0.24 ± 0.12	(not found)	—
Laflamme (Quebec City)	47°19′N, 71°07′W	6.0	0.26 ± 0.07	*flavicans*	0.29 ± 0.12
High Cd lakes					
Caron (Rouyn-Noranda)	47°56′N, 78°58′W	6.8	0.93 ± 0.05	*flavicans*	6.01 ± 1.04
Marlon (Rouyn-Noranda)	48°16′N, 79°04′W	7.2	1.10 ± 0.05	*punctipennis*	4.93 ± 1.85
Turcotte (Rouyn-Noranda)	48°18′N, 79°04′W	5.1	16.2 ± 1.1	*americanus*	14.4 ± 1.01

sons. Results for 14 and 22°C are described herein and compared with those reported previously at 5°C (Croteau et al. 2001). Because larvae used in our experiments at 14 and 22°C were collected from lakes in the spring, just prior to adult emergence, whereas those studied at 5°C were collected in autumn (Croteau et al. 2001), the latter were smaller and younger than the former. Although differences in the temperature and feeding histories of insects collected from various lakes in different seasons can influence their responses to temperature (Ward and Stanford 1982), such influences were unlikely to have had a major influence on our experiments. First, migratory *Chaoborus* larvae would have been exposed to a wide range of temperatures on a daily basis in all of our source lakes and, second, prey used in our experiments (copepods) were also the major microcrustacean in the plankton of all source lakes (M.-N. Croteau, unpubl. data).

We identified *Chaoborus* species using the keys in Saether (1972) and selected final (fourth) instar larvae on the basis of head capsule lengths as given in Larow and Marzolf (1970, *C. punctipennis*), Fedorenko and Swift (1972, *C. americanus*), and Parma (1971, *C. flavicans*). Collection of *C. americanus* yielded two body sizes of fourth instar larvae; we selected only the smaller of the two sizes for our experiments both to minimize emergence during experimentation and to ensure that larvae of all species were of similar age (<1 yr, Carter and Kwik 1977).

Collection of water and invertebrates—For our Cd-uptake experiments, we collected larvae of the three *Chaoborus* species in late May 1999 from three low-Cd lakes, two of which were located near Québec City (Lakes Bertrand and Laflamme) and one in the Rouyn-Noranda region (Lake Hélène) upwind from a metal smelter (Table 1). For our Cd loss experiments, we collected larvae of the same *Chaoborus* species in early June 1999 from three high-Cd lakes located in the Rouyn-Noranda region downwind from the smelter (Lakes Caron, Marlon, and Turcotte, Table 1). Larvae for these experiments were collected after sunset by hauling a 250-μm plankton net horizontally in the water column.

Water samples were collected using in situ diffusion samplers (peepers) similar to those described by Croteau et al. (1998). These Plexiglas samplers comprise eight compartments of 4 ml each that were filled with ultrapure water (Milli-Q, > 18 MΩ cm) and separated from lake water by a 0.2-μm polysulfone membrane (Gelman HT-200). After preparation, each sampler was sealed in a clean plastic bag prior to its placement in a lake. Two diffusion samplers were suspended about 1 m above the bottom in the epilimnion of each lake and retrieved after a 3-d equilibration period. Samples (4 ml) for Cd analyses were removed from five compartments in each dialysis sampler by piercing the membrane with a pipette fitted with an acid-cleaned tip. These samples were injected into preacidified (53 μl of 1.35 N Anachemia HNO_3) high-density polyethylene bottles (HDPE, 4-ml capacity). On installation and retrieval dates, we measured pH in water samples collected with a van Dorn bottle at the depth of the diffusion samplers using a portable pH meter (Hanna instruments, Microprocessor model HI9024/HI9025).

We also collected *C. punctipennis* larvae and their potential copepod prey in the spring (May–June) of 1997 (most lakes) and 1998 (Lake Hélène) from a series of eight additional lakes for measurement of Cd concentrations and comparison to model predictions (Table 2). These animals were selected under a microscope from several nighttime horizontal plankton hauls in each lake. Pooled samples of 3–15 depurated *Chaoborus* larvae (single individuals from Lake Hélène) or 100–150 copepods were placed on preweighed acid-washed Teflon sheeting then frozen until analysis.

Cd kinetics experiments—Larvae of the three *Chaoborus* species were held individually in 30-ml HDPE bottles filled with filtered (64 μm) lake water for up to 14 d in the dark at either 14 or 22°C. In the Cd-uptake experiment, Cd-poor larvae of each *Chaoborus* species were exposed to Cd-rich prey and water from Lake Marlon, whereas in the Cd-efflux experiment Cd-rich larvae of each species were exposed to Cd-poor prey and water from Lake Laberge (Table 1). In the Cd-efflux experiment, bulk zooplankton (mainly copepods) were offered in excess, whereas in the Cd-uptake experiment prey offered were the calanoid copepods *Skistodiaptomus oregonensis* Lilljeborg (≈40%) and *Epischura lacustris* Forbes (≈60%). These copepods were composed mainly of

Table 2. Location of lakes from which we collected final-instar *C. punctipennis* larvae and copepod prey for comparison with model predictions. Cadmium concentrations in invertebrates (μg g^{-1} dry weight) are means ($\pm$SD) of several samples (n = 1–5) of pooled individuals.

Lake	Location	Cd concentration (μg g^{-1} $\pm$ SD)	
		C. punctipennis	Copepods
Bousquet	48°14′N, 78°34′W	2.0 ± 0.2	0.99 ± 0.1
d'Alembert	48°23′N, 79°01′W	2.3	3.1 ± 0.4
Duprat	48°20′N, 79°07′W	1.4 ± 0.1	1.6 ± 0.1
Flavrian	48°18′N, 79°11′W	1.3 ± 0.1*	2.0
Forest	46°23′N, 81°00′W	8.3 ± 0.4	1.4 ± 0.04
Hélène	48°14′N, 78°34′W	0.13 ± 0.02	1.1 ± 0.2
La Bruère	48°10′N, 78°57′W	1.7 ± 0.1	2.9 ± 0.5
Vaudray	48°07′N, 78°42′W	2.9 ± 0.1	5.8 ± 0.2

* *Chaoborus albatus.*

adults (≈45%) and copepodite v's (≈55%), both of which should be eaten by all of the *Chaoborus* species because their mean body width (0.32 ± 0.07 [SD] mm) is less than the mouth size of the smallest study species (0.45 mm for fourth instar *C. punctipennis*; Moore 1988). In the Cd-uptake experiment, each *Chaoborus* larva was offered either 20 (for the small-bodied *C. punctipennis*) or 25 (for the large-bodied *C. americanus* and *C. flavicans*) fresh copepods daily, which is in excess of its needs (larvae consumed 20 to 80% of prey offered). We used naturally contaminated prey so that Cd accumulation by the predator would be representative of that which occurs in the field; the availability of Cd from food is reported to depend on the exposure history of the food particles (Wallace and Lopez 1996). Three samples of prey for Cd measurements were collected each day and stored on preweighed pieces of acid-washed Teflon sheeting in microcentrifuge tubes at −4°C until analysis.

Both filtered lake water and prey were renewed daily by transferring each larva to a new bottle filled with freshly collected filtered lake water and prey. In the Cd-uptake experiment, we preserved uneaten copepods in 5% formalin for later counting to determine daily ingestion rates for each *Chaoborus* larva. At each sampling time, five undepurated larvae of each *Chaoborus* species were frozen individually on pieces of preweighed acid-washed Teflon sheeting. Larvae were not given time to eliminate their gut contents because a preliminary experiment conducted at 22°C showed that there was no significant difference in Cd concentrations between *Chaoborus* larvae that were allowed to eliminate their gut contents for 1 d and those that were not (*t*-test, $P > 0.05$, data not shown). The duration of the experiments at 22°C was generally shorter than those at 14°C because of larval pupation at the higher temperature. Larval mortality rates were very low in all of our experiments (<3%) and larvae consumed prey on all days, suggesting that they were not overly stressed by the experimental conditions.

Analyses—To minimize inadvertent trace metal contamination, labware, water-sampling materials, vials, and Teflon sheeting were soaked in 15% nitric acid and rinsed in ultrapure water prior to use. Total dissolved Cd concentrations were measured by flameless atomic-absorption spectrophotometry (AAS) (Perkin-Elmer model SIMAA 6000). Certified reference riverine water samples (National Research Council of Canada; SLRS-4, 1643d) were analyzed for Cd during each analytical run, and measured trace metal concentrations were within the certified range. *Chaoborus* larvae and zooplankton samples were freeze-dried (FTS Systems™), weighed (Mettler ME30 electronic microbalance) and digested in concentrated nitric acid (Aristar grade). For invertebrate samples collected in 1997, digestions were carried out in thick-walled, screw-cap Teflon vials in an autoclave at 120°C for 3 h. Cooled digested samples were diluted to volume with ultrapure water. All other samples were digested at room temperature in 4-ml HDPE vials with concentrated nitric acid (100 μl mg^{-1} dry weight [d.w.]) for 7 d. Hydrogen peroxide (40 μl mg^{-1} d.w.) was added 24 h prior to final dilution with ultrapure water (760 μl mg^{-1} d.w.). Samples of similar weight of a certified reference material (lobster hepatopancreas, TORT-1, NRCC) were submitted to the same digestion procedure during each run. Cadmium concentrations in animals were analyzed by flameless AAS (Varian Spectra AA-30). Cadmium 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

Cadmium bioaccumulation model—We fit our experimental data to a bioaccumulation model to estimate the efficiency with which a species assimilated Cd, the rate at which it lost Cd, as well as the rate at which larvae grew at each temperature. We treat larvae as a single compartment for the accumulation of Cd and assume that their Cd uptake from water is negligible (Munger and Hare 1997; Munger et al. 1999). We then express the rate of change in larval Cd concentrations as the difference between Cd entering and leaving larvae provided that we take into account Cd dilution due to animal growth (Thomann 1981), that is,

$$\frac{d[\mathrm{Cd}]_{Chaoborus}}{dt} = \underbrace{(\mathrm{AE} \times \mathrm{IR} \times [\mathrm{Cd}]_{\mathrm{Food}})}_{\text{Cd uptake from food}} - \underbrace{(k_e[\mathrm{Cd}]_{Chaoborus})}_{\text{Cd loss by efflux}} - \underbrace{(k_g[\mathrm{Cd}]_{Chaoborus})}_{\text{Cd dilution by growth}} \quad (1)$$

where AE is the Cd assimilation efficiency (g Cd retained g^{-1} Cd ingested), IR is the ingestion rate (g prey g^{-1} predator d^{-1}), $[\mathrm{Cd}]_{\mathrm{Food}}$ and $[\mathrm{Cd}]_{Chaoborus}$ (μg Cd g^{-1} d.w.) are the Cd concentrations in prey and in *Chaoborus* larvae, respectively, and k_e and k_g (d^{-1}) are the rate constants for Cd efflux and animal growth, respectively.

Furthermore, we assumed that larval growth can be represented by the exponential function (Spacie and Hamelink 1985),

$$W = W_0 e^{k_g t} \quad (2)$$

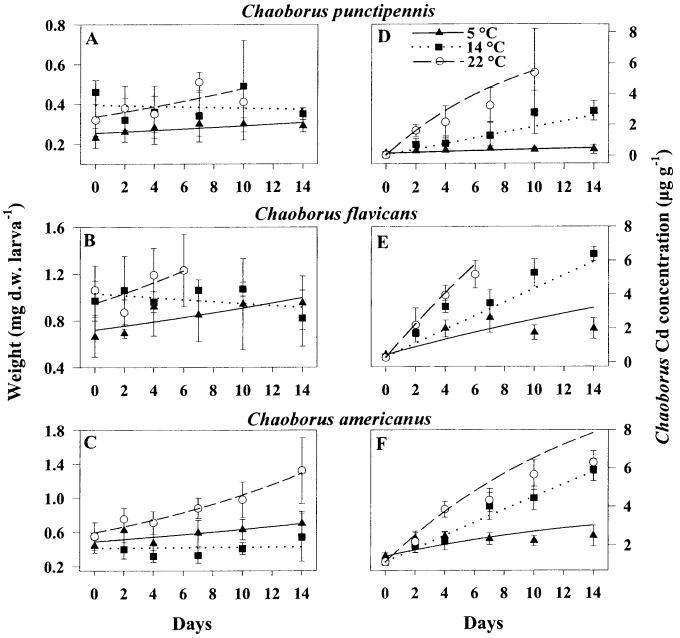

Fig. 1. Temporal changes in (A, B, and C) mean (±SD) dry weight and (D, E, and F) mean (±SD) Cd concentration of low-Cd *Chaoborus* species larvae that were exposed for from 6 to 14 d to water and copepods (ad libidum) from a Cd-rich lake. Experimental data are represented by symbols, whereas lines represent model curves obtained to describe either (A, B, and C) changes in larval weight, using Eq. 2 and the parameters W_0 and k_g given in Table 3, or (D, E, and F) changes in larval Cd concentration using Eq. 4 and the parameters AE, IR, W_0, k_g, k_e, and $[Cd]^0_{Chaoborus}$ given in Tables 3 and 4.

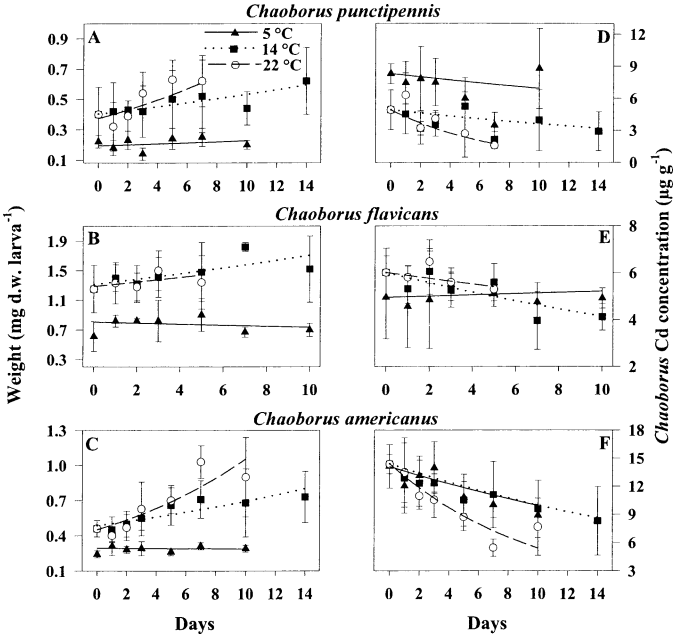

Fig. 2. Temporal changes (mean ± SD) in (A, B, and C) dry weights and (D, E, and F) Cd concentrations of high-Cd *Chaoborus* larvae that were exposed for 7 to 10 d to water and bulk zooplankton (ad libidum) from a low-Cd lake. Experimental data are represented by symbols, whereas lines represent model curves obtained to describe either changes in larval weight (A, B, and C), using Eq. 2 and the parameters W_{0*} and k_{g*} given in Table 4, or changes in larval Cd concentration (D, E, and F) using Eq. 3 and the parameters k_e, k_{g*}, and $[Cd]^0_{Chaoborus*}$ given in Tables 3 and 4.

where W_0 is the initial weight (mg d.w. larva^{-1}) and t is time (d). We then used Eq. 2 and the integrated form of Eq. 1 to estimate for each *Chaoborus* species at each temperature the rate constants k_e and k_g as well as the Cd assimilation efficiency, as described below.

First, we used Eq. 2 and our measurements of changes in larval mass during both the Cd uptake (Fig. 1A–C) and loss experiments (Fig. 2A–C) to estimate, by nonlinear regression, values of W_0 and the growth rate constants k_g (uptake experiment, Table 3) and k_{g*} (loss experiment, Table 4). Second, to estimate values of the Cd loss rate constant k_e, we assumed that Cd uptake was negligible during our Cd loss experiment. This assumption is reasonable because we fed high-Cd *Chaoborus* larvae low-Cd prey; Cd concentrations in prey offered during the Cd loss experiment ($[Cd]_{Food*}$, Table 4) were 10 to 19 times lower that those offered during the Cd-uptake experiment ($[Cd]_{Food}$, Table 3). This assumption allowed us to simplify Eq. 1, which in its integrated form becomes

$$[Cd]_{Chaoborus} = [Cd]^0_{Chaoborus*} e^{-(k_{g*}+k_e)t} \quad (3)$$

where $[Cd]^0_{Chaoborus*}$ is the Cd concentration in larvae (μg Cd g^{-1} d.w.) at the beginning of the Cd loss experiment. Using our measurements of Cd concentrations in *Chaoborus* during the Cd loss experiment (Fig. 2D–F) and the k_{g*} values from Table 4, we estimated the loss rate constant k_e by nonlinear regression (Eq. 3). Most of our k_e values (Table 4) fall in the range reported for *Chaoborus* larvae (0.003 to 0.037 d^{-1}; Munger et al. 1999; Croteau et al. 2001) and soil arthropods (0.007 to 0.202 d^{-1}; Janssen and Bergema 1991; Crommentuijn et al. 1994).

Third, using the values of k_g (Table 3) and k_e (Table 4), the ingestion rates calculated daily for each *Chaoborus* larva of each species, as well as the mean daily Cd concentration measured in food offered during the uptake experiment, we estimated the efficiency with which the various *Chaoborus* species assimilated Cd (AE, Table 3) at each temperature by fitting our data points (Fig. 1D–F) to the integrated form of Eq. 1, that is,

$$[Cd]_{Chaoborus} = \frac{AE \times IR \times [Cd]_{Food}}{k_g + k_e}(1 - e^{-(k_g+k_e)t}) + [Cd]^0_{Chaoborus} e^{-(k_g+k_e)t} \quad (4)$$

where we assume that AE, IR, and $[Cd]_{Food}$ are constant for each experiment. Cadmium concentrations in prey (9.5–14.5 μg g^{-1}, Table 3) were higher than the highest Cd concentration that we measured in *Chaoborus* at the end of the uptake experiment conducted at 22°C (i.e., 6.3 μg g^{-1} for *C. americanus*). Dilution of Cd along food chains is reported to be common in nature (Hare 1992; Chen et al. 2000*a*).

Cadmium exchange rates—To obtain Eq. 3, we assumed that Cd uptake by *Chaoborus* larvae during our Cd loss experiment was negligible. We tested this assumption by in-

Table 3. Mean values for the three *Chaoborus* species of model parameters measured (±95% CI) or estimated (±SE) from our Cd uptake experiments. Significant differences among temperatures ($P < 0.05$; *t*-test) are indicated by different superscript letters. Values for 5°C are from Croteau et al. (2001).

Parameter	Abbreviation or symbol	Species	Temperature		
			5°C	14°C	22°C
Initial *Chaoborus* weight (mg larva^{-1}) (± 95% CI)	W_0	*C. punctipennis*	0.23 ± 0.04^a (n = 5)	0.46 ± 0.06^b (n = 5)	0.32 ± 0.07^c (n = 5)
		C. flavicans	0.66 ± 0.15^a (n = 5)	0.97 ± 0.15^b (n = 5)	1.06 ± 0.21^b (n = 4)
		C. americanus	0.44 ± 0.07^a (n = 5)	0.55 ± 0.14^a (n = 5)	0.55 ± 0.14^a (n = 5)
Final *Chaoborus* weight (mg larva^{-1}) (± 95% CI)	W_{Final}	*C. punctipennis*	0.29 ± 0.03^a (n = 5)	0.35 ± 0.03^b (n = 5)	0.41 ± 0.09^b (n = 3)
		C. flavicans	0.95 ± 0.20^a (n = 5)	0.82 ± 0.23^a (n = 4)	1.23 ± 0.35^a (n = 3)
		C. americanus	0.70 ± 0.12^a (n = 5)	0.54 ± 0.27^a (n = 4)	1.34 ± 0.58^b (n = 3)
Initial *Chaoborus* Cd concentration (μg g^{-1}) (±95% CI)	$[Cd]^0_{Chaoborus}$	*C. punctipennis*	0.18 ± 0.04^a (n = 5)	0.07 ± 0.04^b (n = 5)	0.05 ± 0.03^b (n = 5)
		C. flavicans	0.46 ± 0.02^a (n = 5)	0.33 ± 0.08^b (n = 5)	0.29 ± 0.12^b (n = 4)
		C. americanus	1.44 ± 0.15^a (n = 5)	1.14 ± 0.16^b (n = 5)	1.14 ± 0.16^b (n = 5)
Final *Chaoborus* Cd concentration (μg g^{-1}) (±95% CI)	$[Cd]^{Final}_{Chaoborus}$	*C. punctipennis*	0.41 ± 0.25^a (n = 5)	2.89 ± 0.55^b (n = 5)	5.35 ± 3.22^b (n = 3)
		C. flavicans	1.98 ± 0.53^a (n = 5)	6.38 ± 0.41^b (n = 4)	5.18 ± 0.92^b (n = 3)
		C. americanus	2.48 ± 0.46^a (n = 5)	5.91 ± 0.57^b (n = 4)	6.29 ± 0.83^b (n = 3)
Prey Cd concentration (μg g^{-1}) (±95% CI)	$[Cd]_{Food}$	*C. punctipennis*	10.6 ± 0.3^a (n = 49)	14.5 ± 1.0^b (n = 42)	10.5 ± 0.6^a (n = 30)
		C. flavicans	10.6 ± 0.3^a (n = 49)	14.5 ± 1.0^b (n = 42)	9.5 ± 0.2^a (n = 18)
		C. americanus	10.6 ± 0.3^a (n = 49)	14.5 ± 1.0^b (n = 42)	12.5 ± 1.1^b (n = 42)
Ingestion rate (g prey g^{-1} predator d^{-1}) (± 95% CI)	IR	*C. punctipennis*	0.052 ± 0.009^a (n = 25)	0.103 ± 0.018^b (n = 23)	0.216 ± 0.038^c (n = 18)
		C. flavicans	0.057 ± 0.008^a (n = 25)	0.108 ± 0.012^b (n = 21)	0.147 ± 0.030^c (n = 13)
		C. americanus	0.046 ± 0.007^a (n = 25)	0.133 ± 0.013^b (n = 24)	0.165 ± 0.014^c (n = 22)
Growth rate constant (d^{-1}) (±SE)	k_g	*C. punctipennis*	0.0134 ± 0.0082^a (n = 25)	−0.0039 ± 0.0134^a (n = 28)	0.0352 ± 0.0081^b (n = 23)
		C. flavicans	0.0232 ± 0.0058^a (n = 25)	−0.0088 ± 0.0054^b (n = 26)	0.0429 ± 0.0249^a (n = 17)
		C. americanus	0.0253 ± 0.0046^a (n = 25)	0.0030 ± 0.0153^b (n = 29)	0.0557 ± 0.0041^c (n = 29)
Cd assimilation efficiency (%) (±SE)	AE	*C. punctipennis*	5.7 ± 1^a (n = 30)	12 ± 1^b (n = 28)	39 ± 3^c (n = 23)
		C. flavicans	45 ± 4^a (n = 30)	26 ± 2^b (n = 26)	75 ± 2^c (n = 17)
		C. americanus	58 ± 4^a (n = 30)	18 ± 1^b (n = 29)	40 ± 2^c (n = 27)

Table 4. Mean values for the three *Chaoborus* species of model parameters measured (±95% CI) or estimated (±SE) from our Cd loss experiments. Significant differences among temperatures ($P < 0.05$; *t*-test) are indicated by different superscript letters. Values for 5°C are from Croteau et al. (2001).

Parameter	Abbreviation or symbol	Species	Temperature		
			5°C	14°C	22°C
Initial *Chaoborus* weight (mg larva^{-1}) (±95% CI)	W_{0*}	*C. punctipennis*	0.22 ± 0.04^{a} (n = 5)	0.40 ± 0.18^{b} (n = 4)	0.40 ± 0.18^{b} (n = 4)
		C. flavicans	0.61 ± 0.18^{a} (n = 5)	1.25 ± 0.36^{b} (n = 3)	1.25 ± 0.36^{b} (n = 3)
		C. americanus	0.24 ± 0.03^{a} (n = 5)	0.46 ± 0.06^{b} (n = 5)	0.46 ± 0.06^{b} (n = 5)
Final *Chaoborus* weight (mg larva^{-1}) (±95% CI)	$W_{\mathrm{Final}*}$	*C. punctipennis*	0.20 ± 0.03^{a} (n = 5)	0.62 ± 0.22^{b} (n = 4)	0.62 ± 0.17^{b} (n = 4)
		C. flavicans	0.70 ± 0.08^{a} (n = 5)	1.52 ± 0.62^{b} (n = 2)	1.34 ± 0.49^{b} (n = 2)
		C. americanus	0.29 ± 0.03^{a} (n = 5)	0.73 ± 0.25^{b} (n = 3)	0.90 ± 0.38^{b} (n = 3)
Initial *Chaoborus* Cd concentration (μg g^{-1}) (±95% CI)	$[\mathrm{Cd}]^{0}_{Chaoborus*}$	*C. punctipennis*	8.29 ± 0.81^{a} (n = 5)	4.93 ± 1.81^{b} (n = 4)	4.93 ± 1.81^{b} (n = 4)
		C. flavicans	4.95 ± 1.55^{a} (n = 5)	6.01 ± 1.18^{a} (n = 3)	6.01 ± 1.18^{a} (n = 3)
		C. americanus	14.1 ± 2.05^{a} (n = 5)	14.4 ± 0.89^{a} (n = 5)	14.4 ± 0.89^{a} (n = 5)
Final *Chaoborus* Cd concentration (μg g^{-1}) (±95% CI)	$[\mathrm{Cd}]^{\mathrm{Final}}_{Chaoborus*}$	*C. punctipennis*	8.78 ± 3.29^{a} (n = 5)	2.91 ± 1.78^{b} (n = 4)	1.63 ± 0.36^{b} (n = 4)
		C. flavicans	4.92 ± 0.38^{ab} (n = 5)	4.12 ± 0.79^{a} (n = 2)	5.30 ± 0.21^{b} (n = 2)
		C. americanus	8.90 ± 1.03^{a} (n = 5)	8.30 ± 4.13^{a} (n = 3)	7.67 ± 3.44^{a} (n = 3)
Prey Cd concentration (μg g^{-1}) (±95% CI)	$[\mathrm{Cd}]_{\mathrm{Food}*}$	*C. punctipennis*	1.1 ± 0.1^{a} (n = 36)	0.66 ± 0.02^{b} (n = 42)	0.62 ± 0.03^{b} (n = 21)
		C. flavicans	1.1 ± 0.1^{a} (n = 36)	0.63 ± 0.02^{b} (n = 30)	0.61 ± 0.02^{b} (n = 15)
		C. americanus	1.1 ± 0.1^{a} (n = 36)	0.66 ± 0.02^{b} (n = 42)	0.63 ± 0.02^{b} (n = 30)
Growth rate constant (d^{-1}) (±SE)	k_{g*}	*C. punctipennis*	0.0150 ± 0.0118^{a} (n = 55)	0.0276 ± 0.0078^{ab} (n = 31)	0.0700 ± 0.0270^{b} (n = 22)
		C. flavicans	−0.0091 ± 0.0112^{a} (n = 55)	0.0261 ± 0.0074^{b} (n = 27)	0.0226 ± 0.0301^{ab} (n = 18)
		C. americanus	−0.0019 ± 0.0091^{a} (n = 55)	0.0359 ± 0.0055^{b} (n = 38)	0.0850 ± 0.0075^{c} (n = 32)
Loss rate constant (d^{-1}) (±SE)	k_{e}	*C. punctipennis*	0.0029 ± 0.0164^{a} (n = 55)	0.0031 ± 0.0151^{a} (n = 31)	0.0760 ± 0.0510^{a} (n = 22)
		C. flavicans	0.0038 ± 0.0090^{a} (n = 55)	0.0111 ± 0.0083^{a} (n = 27)	−0.0014 ± 0.0198^{a} (n = 18)
		C. americanus	0.0368 ± 0.0085^{a} (n = 55)	0.0007 ± 0.0099^{b} (n = 38)	0.0134 ± 0.0158^{ab} (n = 32)

Table 5. Cadmium exchange rates during our Cd loss experiments calculated using Eq. 1 and the model parameters AE, IR, $[Cd]_{Food}$, and k_g (Table 3), as well as k_e (Table 4) at either the beginning (t_0) or the end (t_{final}) of our experiments. The duration of each experiment is given in parentheses. Values for 5°C are from Croteau et al. (2001).

Cd exchange rate (ng Cd g *Chaoborus*$^{-1}$ d^{-1})	Temperature	*C. punctipennis*		*C. flavicans*		*C. americanus*	
		t_0	t_{final}	t_0	t_{final}	t_0	t_{final}
Cd uptake rate	5°C	3	3	28	28	29	29
Cd loss rate		154	163 (10 d)	−26	−26 (10 d)	493	344 (10 d)
Cd uptake rate	14°C	8	8	18	18	16	16
Cd loss rate		151	89 (14 d)	224	153 (10 d)	526	304 (14 d)
Cd uptake rate	22°C	52	52	67	67	42	42
Cd loss rate		720	238 (7 d)	127	112 (5 d)	1413	755 (10 d)

serting in Eq. 1 the values for AE and IR (Table 3), as well as those for $[Cd]_{Food*}$, k_e, k_{g*}, and $[Cd]_{Chaoborus*}$ (Table 4), to estimate Cd uptake and loss rates at the beginning and end of the Cd loss experiments. With the exception of *C. flavicans* (at 5 and 22°C), Cd-uptake rates were lower than Cd loss rates by approximately 5 to 50 times (Table 5). This result confirms that Cd uptake was negligible compared to Cd loss during most of our Cd loss experiments. The negative Cd loss rate for *C. flavicans* at 5°C is due to the combination of a very low k_e value and weight gain by this species during the Cd loss experiment (Fig. 2B). Because the Cd-uptake rates given in Table 5 suggest that all *Chaoborus* species accumulated some Cd during our Cd loss experiments, actual Cd loss rates could be slightly higher than those given in this table.

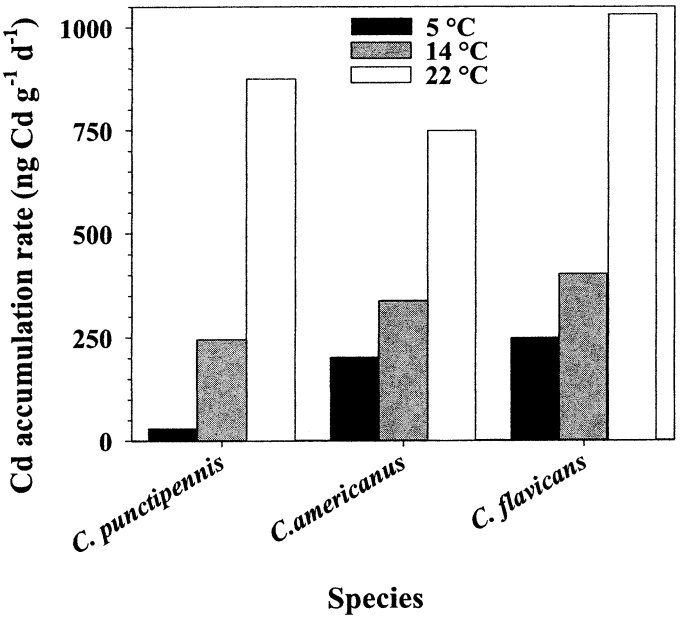

Fig. 3. Changes in initial cadmium accumulation rates as a function of temperature for the three *Chaoborus* species. Values were calculated for the beginning of the uptake experiments (t = 0) using Eq. 1 and the parameters AE, IR, $[Cd]_{Food}$, and $[Cd]^0_{Chaoborus}$ given in Table 3 as well as k_e given in Table 4.

Discussion

Influence of temperature on Cd bioaccumulation rate—The initial rate at which a given *Chaoborus* species accumulated Cd was directly related to the temperature at which it consumed its Cd-rich prey (Fig. 3), as were predator Cd concentrations at the end of our uptake experiments (Fig. 1D–F). Most metabolic, physiological, and behavioral processes in insects (e.g., oxygen consumption, locomotion) show an approximately exponential dependency on temperature within the range tolerated by the animal (Hoffmann 1985). Likewise, metal concentrations in invertebrates are reported to increase with increasing temperature (Douben 1989; Janssen and Bergema 1991; Van Hattum et al. 1993; Bervoets et al. 1996), although the reasons for such trends are usually unknown. Possible explanations for such temperature-controlled increases in metal content include declines in animal weight or metal efflux rate or increases in metal ingestion rate and assimilation efficiency. Below, we examine each of these possibilities to determine whether they could explain the differences that we measured in the rate at which *Chaoborus* larvae accumulated Cd at various temperatures.

First, mean values of the growth rate constant k_g were higher at 22°C than at the lower temperatures, and these differences were significant for both *C. punctipennis* and *C. americanus* (*t*-test, $P < 0.05$, Table 3). Temperature is known to play a major role in regulating seasonal changes in the growth rates of aquatic insects (Ward and Stanford 1982). Because a higher growth rate would dilute accumulated Cd and thus, taken alone, would lead to a reduction rather than an increase in the rate of Cd accumulation by *Chaoborus*, this variable cannot explain the increase that we observed in the rate of larval Cd accumulation with increasing temperature (Fig. 3). The generally lower k_g values for larvae held at 14°C compared to those held at 5°C (k_g, Table 3) were unexpected because larvae at 14°C ingested more prey than did those at 5°C (IR, Table 3). The explanation for this apparent anomaly could lie in differences between larvae in their developmental state (Ward and Stanford 1982). Larvae exposed at 5°C were collected in the autumn, whereas those exposed at 14°C were collected in the spring just prior to pupation and emergence. *Chaoborus* larvae

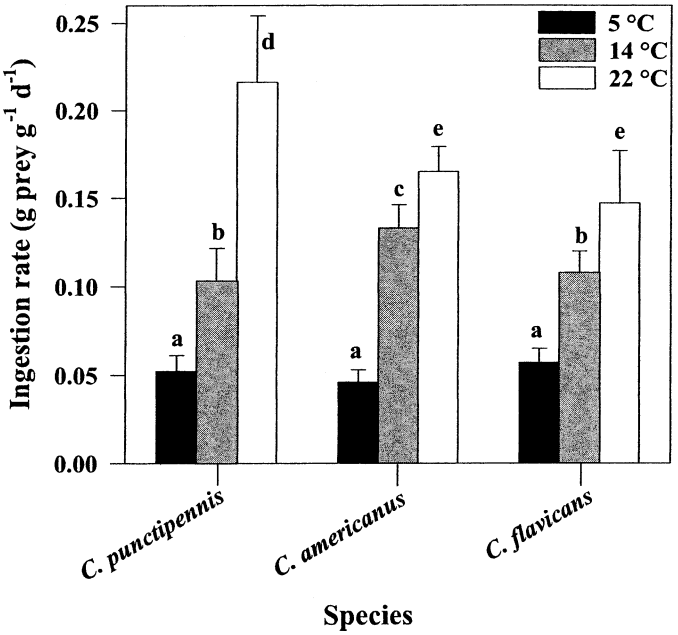

Fig. 4. Ingestion rates (mean ± 95% CI) as a function of temperature for the three *Chaoborus* species during our Cd-uptake experiments. Significant differences both among temperatures and *Chaoborus* species ($P < 0.05$, *t*-tests) are indicated by different letters.

close to emergence are reported to be able to retard their rate of development if there is a small drop in ambient temperature, thereby reducing their risk of emerging during unfavorable conditions (Bradshaw 1973). In our study, larvae exposed to Cd in prey at 14°C were collected from lakes in which the temperature of the epilimnion exceeded 14°C at the time of our experiments.

Second, the Cd loss rate constants for our three *Chaoborus* species did not vary significantly with temperature ($P > 0.05$, Table 4). Thus, the greater Cd bioaccumulation rate that we observed with increasing temperature (Fig. 3) cannot be ascribed to a reduction in Cd losses at higher temperatures (Eq. 1). The similarity of the Cd loss rates among the three *Chaoborus* species suggests that their Cd is likely bound at the cellular level in a similar manner (Croteau et al. in press). Cadmium loss rates for aquatic isopods (Van Hattum et al. 1993) and soil mites (Janssen and Bergema 1991) are also reported to remain constant over a range of temperatures. In contrast, Cd loss rates have been observed to increase with increasing temperature in some fish (Douben 1989) and terrestrial collembolans (Janssen and Bergema 1991).

Third, the rate at which larvae of each *Chaoborus* species ingested prey during our Cd-uptake experiments showed a significant increase with increasing temperature ($P < 0.05$, Fig. 4). Several previous studies have shown that invertebrates ingest more food at higher than at lower temperatures (Heiman and Knight 1975; Ward and Stanford 1982). Thus for all *Chaoborus* species, an increase in prey ingestion explains in part their increased rate of Cd accumulation at higher temperatures.

Finally, *C. punctipennis*, the smallest of our study species (the weight of sympatric larvae at pupation is consistently in the order *C. americanus* > *C. flavicans* > *C. punctipennis*), assimilated Cd with greater efficiency at higher temperatures (Table 3), suggesting that this variable explains in part the increase in this species' Cd accumulation rate with rising temperature (Fig. 3). Increases in the efficiency of digestive processes, for example, enzyme activity (Mayer et al. 1996; Chen et al. 2000*b*) or the transfer rate of Cd across the gut membrane (Bervoets et al. 1996) or both, could explain an increase in metal assimilation efficiency at higher temperatures. In contrast, Cd assimilation efficiencies of the large-bodied species *C. flavicans* and *C. americanus* did not show a consistent increase with temperature (Table 3). Cadmium assimilation efficiencies of the small-bodied species were significantly less ($P < 0.05$, *t*-tests) than those of the two large-bodied species for five of the six species-temperature combinations (Table 3). Likewise, in our earlier study (Croteau et al. 2001), the Cd assimilation efficiencies of another small-bodied species (*Chaoborus albatus*) were lower than those of the large-bodied species studied herein. Suggested explanations for these differences among *Chaoborus* species were differences in the residence time of gut contents (Decho and Luoma 1991), enzyme efficiencies (Mayer et al. 1996; Chen et al. 2000*b*), and the number and nature of Cd-uptake sites in the gut (Hare 1992).

Overall, our experimental results suggest that increases in both the rate of prey ingestion and the efficiency with which Cd was assimilated by larvae combined to produce the higher Cd accumulation rates that we measured with increasing temperature for all *Chaoborus* species. In contrast, our experimental results suggest that neither the rate of larval growth nor the rate at which larvae lose Cd is influenced by temperature.

Predicting Cd accumulation in Chaoborus *populations in the field*—Because conditions in the laboratory differ from those in the field and because the feeding and temperature histories of insects can influence their responses in experiments (Ward and Stanford 1982), we compared predictions based on the model parameters extracted from our experimental data to measurements of steady state Cd concentrations in *Chaoborus* larvae, $[Cd_{Chaoborus}]_{ss}$, collected from a variety of lakes. When $d[Cd]_{Chaoborus}/dt$ equals zero, Eq. 1 becomes

$$[Cd_{Chaoborus}]_{ss} = \frac{AE \times IR \times [Cd]_{Food}}{k_e + k_g} \quad (5)$$

Using the values of AE, IR, $[Cd]_{Food}$ and k_g from the Cd-uptake experiment (Table 3) as well as those of k_e from the Cd loss experiment (Table 4), we estimated steady state values for the three *Chaoborus* species at 5 and 22°C. Steady state values at 14°C were not estimated because we doubt the accuracy of the k_g values for this experiment (as discussed above). Estimated steady state Cd concentrations ($\mu g\ Cd\ g^{-1}$) for larvae feeding on prey used in our experiments increased between 5 and 22°C for all *Chaoborus* species, that is, 2 and 8 for *C. punctipennis*, 4.5 and 12 for *C. americanus*, and 10 and 15 for *C. flavicans*, respectively. Cadmium concentrations measured in *C. punctipennis* larvae exposed to these and other prey in nature (5 $\mu g\ g^{-1}$ for larvae from Lake Marlon; epilimnion at 15°C) fall within the range predicted for this species (2–8 $\mu g\ Cd\ g^{-1}$). Predicted steady state Cd concentrations were consistently ordered among species such that at a given

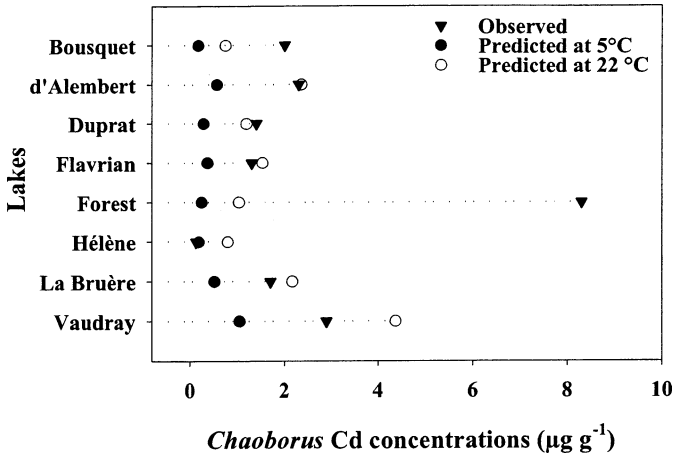

Fig. 5. Measured Cd concentrations in final instar larvae of *Chaoborus punctipennis* from eight Canadian Shield lakes compared with values predicted at 5 and 22°C that were obtained using Eq. 5 and the parameters AE, IR, k_g (Tables 3), and k_e (Table 4) from our experiments and measurements of Cd in copepods from these lakes (Table 2). Temperatures in the epilimnion of the eight lakes were between 5 and 22°C at the time of sampling. Data for Lake Flavrian are for the closely related *Chaoborus albatus.*

temperature those of *C. punctipennis* should be lowest and those of *C. flavicans* should be highest in lakes where these larvae consume the same types and densities of prey that we used in our experiments.

We can further test the reliability of model predictions by using, in Eq. 5, measurements of Cd concentrations in copepods collected from other lakes (Table 2) to determine whether the Cd concentrations measured in *C. punctipennis* larvae from these lakes fall within the expected range. Measured Cd values in larvae fell within the range expected in six of eight lakes (Fig. 5), suggesting that the model adequately represents reality in field populations feeding on a variety of prey types. For the two lakes where model predictions fell outside of the expected range, it is likely that the predator feeds on prey different from those that we collected in these lakes. This supposition is supported by the fact that Cd concentrations in *Chaoborus* larvae from these lakes greatly exceeded those in sympatric copepods (Table 2), in spite of the fact that concentrations of this metal generally decline at higher levels in aquatic food chains (Hare 1992; Chen et al. 2000*a*).

On the one hand, if we extrapolate the direct effect of temperature on Cd bioaccumulation that we observed in the laboratory to insects in a given lake, we might expect that larvae spending the summer in the epilimnion, for example, *C. americanus,* would accumulate more Cd than larvae such as *C. punctipennis* and *C. flavicans* that spend the day in cooler deeper waters and move into warmer surface waters only at night to feed on zooplankton. On the other hand, our results also suggest that such comparisons among sympatric *Chaoborus* species should take into account larval body size because Cd assimilation efficiency appears to differ between small- and large-sized species. Furthermore, because *Chaoborus* species differ in the types of prey that they consume (Hare and Carter 1987), and prey types can differ in their Cd content (Yan et al. 1990; Chen et al. 2000*a*), these factors also likely have to be considered to accurately predict Cd in larvae of various sympatric *Chaoborus* species (for example, Lakes Forest and Bousquet in Fig. 5).

Over time in a given lake, both temperature and the types and densities of prey available to *Chaoborus* larvae vary (Goldman and Horne 1983; Yan et al. 1990). The Cd content of organisms in the food web leading to *Chaoborus* will also vary because of seasonal changes in Cd bioavailability due, for example, to changes in lake water pH during snowmelt (Croteau et al. unpubl. data). The result of such temporal changes, including temperature, are likely to be seasonal variations in *Chaoborus* Cd concentrations, as have been reported for larvae of *C. punctipennis* (Hare and Campbell 1992). Among insect generations, lake warming due to longer term fluctuations in weather (Yan et al. 1996) or climate also could influence animal metal concentrations (Moore et al. 1997).

Comparing among lakes, our laboratory results suggest that larvae inhabiting warm, shallow lakes should accumulate more Cd than those inhabiting deeper, colder lakes. However, because prey types and densities also vary among lakes of different temperature and depth (Auclair et al. 1993), such variables might also have to be considered to predict Cd in a given *Chaoborus* species. In spite of such potential complexity, measurements made in the spring in 23 lakes situated over a large geographical area indicated that Cd concentrations in *C. punctipennis* larvae can be predicted with a fair degree of certainty from Cd concentrations in lake water (Hare and Tessier 1996, 1998). This relationship allows *Chaoborus* larvae to be used as a biomonitor to estimate biologically meaningful Cd concentrations in lakes. However, some uncertainty remains in the relationship between *Chaoborus* and lake water Cd that could potentially be resolved by taking into account differences in the temperature (this study) and prey populations (M.-N. Croteau unpubl. data) among lakes.

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