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SUBLETHAL EFFECTS OF CADMIUM ON PREY CHOICE AND CAPTURE EFFICIENCY IN JUVENILE BROOK TROUT (*SALVELINUS FONTINALIS*)

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Abstract—Prey choice in juvenile brook trout (*Salvelinus fontinalis*) was investigated under sublethal Cd stress in the presence of alternative prey types. Following 30-d exposures to either 0, 0.5, or 5.0 μg/L Cd, individual fish held in artificial stream channels were presented with both motile (*Baetis tricaudatus*) and nonmotile (*Chironomus tentans*) prey items and their foraging behavior and capture success was observed. The Cd-exposed trout were found to express a significant preference for *C. tentans* larvae as alternative prey to *B. tricaudatus* nymphs. Nevertheless, these preliminary findings indicate that, irrespective of prey choice, the capture efficiency of Cd-stressed trout declined by 20 to 55% with increasing Cd concentration when compared with control fish, and the activity of individual trout increased by 25% over controls, although these responses were not statistically significant. Cadmium significantly affected fish condition factors: The condition factor of control fish increased by 34% over the 30-d period, and Cd-exposed fish declined in condition by 12 to 18%. It is hypothesized that such a switch by fish to feeding on benthic prey under natural exposure conditions and their proximity to contaminated sediment may further exacerbate the sublethal effects of Cd on these individuals by intensifying or prolonging Cd exposure through a combination of trophic transfer and altered foraging behavior.

Keywords—Salmonid Foraging behavior Sublethal effects Cadmium

INTRODUCTION

Using the long-term rate of net energy intake as an indirect indicator of fitness, optimal foraging models suggest that those individuals exhibiting behaviors that maximize net energy intake possess a selective advantage [1]. Such individuals are hypothesized to allocate a greater contribution of energy to aspects of survival and fecundity while minimizing developmental time [2].

Due to this close association between energy budgets and fitness, any changes in net energy intake, even relatively subtle ones, may have far-reaching effects on populations in the field. Foraging behavior has been identified [3] as being a sensitive indicator of toxicant stress, easily quantifiable, and ecologically relevant, determining the scope for growth [4] both of individuals and structuring communities.

Fish predator–prey systems are particularly well-suited to examine predictions from optimal foraging models. Fish diet directly influences growth rate, and fecundity is related to body size [5,6]. Thus, a fish with higher net energy intake simultaneously will decrease developmental time and increase fecundity.

To date, relatively few studies have been published on the effects of Cd on fish behavior (e.g., [7–9]), and fewer still on foraging effects [10–12]. Research by Riddell et al. [13] revealed that sublethal concentrations of Cd can modify the net energy available to juvenile brook trout (*Salvelinus fontinalis*) by altering both the rates of energy intake (reduced capture efficiency) and energy expenditure (increased activity) of individuals. Because juvenile brook trout had been shown [13] to experience poor capture success with motile prey items (*Baetis tricaudatus* nymphs), the aim of the current study was to investigate any change in prey preference by juvenile brook trout under Cd stress in the presence of alternative prey types commonly encountered in the environment.

By presenting trout with both motile, drifting, *B. tricaudatus* nymphs and nonmotile, benthic, *Chironomus tentans* larvae, the current study attempted to determine whether trout under varying degrees of Cd stress would switch from foraging on drifting mayflies to benthic chironomids in order to compensate for their poor capture success with motile prey items. In a companion group of experiments of similar design, the prey, rather than the predator, were pre-exposed to the range of Cd concentrations. This second group of experiments was devised to determine whether exposure of the prey species to Cd affected their palatability to trout predators.

METHODS

Sources of test organisms

Baetis tricaudatus nymphs (0.4–0.5 cm in length, excluding cerci) were collected from Big Hill Springs, a pristine, spring-fed, first-order foothills stream located 30 km northwest of Calgary, Alberta, Canada. *Baetis tricaudatus* are the numerically dominant mayfly species at the site and Cd levels here are negligible (<0.1 μg/L). Organisms were sampled using a U-shaped net sampler (0.25-mm mesh size; see Scrimgeour et al. [14]). Uninjured nymphs of the required size were transferred quickly via pipette to aerated stream water in a 10-L cooler. No mortalities occurred during transportation to the laboratory, and nymphs were acclimated over a 3- to 4-d period to designated laboratory temperature (12 ± 1°C) and water (dechlorinated City of Saskatoon tap water: Hardness = 156 mg/L $CaCO_3$, <0.1 μg/L Cd) conditions. Laboratory photoperiod was maintained at 16:8 h light:dark. Nymphs then were

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maintained under these conditions for an additional 48 h before exposure to Cd solutions.

Chironomus tentans cultures were initiated with egg cases obtained from Environmental Consulting & Testing (Superior, WI, USA) and cultured following the protocols described by Sadler [15]. Each of the 3 × 76–L stock tanks possessed 1.5 cm even depth of washed silica sand substrate (250–425 μm; Brock White Canada, Saskatoon, SK). A water volume of 35 L was maintained in each tank using a flow-through system to help maintain water quality. Stock water was stored in a 950-L polypropylene cylinder and allowed to acclimate to room temperature during constant water exchange (5 ml/min). Water source and laboratory conditions were identical to those described for *B. tricaudatus*, except ambient temperature was maintained at 20 ± 1°C. These stock cultures provided an average of 330 surviving second to third instar larvae per egg case to be used in experiments.

Juvenile *S. fontinalis* (6–7–cm fork length, condition factor 1.04–1.11) were obtained from Fort Qu'Appelle Hatchery (Fort Qu'Appelle, Saskatchewan, Canada) where Cd levels are negligible (<0.1 μg/L). Collected individuals were transported to the laboratory in 20-L coolers containing aerated hatchery water. No mortalities occurred during transportation, and individuals were acclimated over a 3- to 4-d period to laboratory conditions identical to those described previously for *B. tricaudatus* nymphs. Fish then were maintained under these conditions for an additional 48 h before exposure to Cd solutions.

Food sources

Baetis tricaudatus nymphs were maintained on laboratory-cultured *Nitzschia* sp. diatom mats (strain F110; Department of Fisheries and Oceans, Winnipeg, MB, Canada) at a rate of one mat/eight mayflies/day. Diatom batch cultures were maintained in exponential growth phase and subcultured onto ceramic tiles (6.25 cm^2) to form uniform, single-species diatom mats within 6 to 8 d. All cultures were grown in S-diatom medium [16] at 18 ± 1°C, under a 16:8-h light:dark photoperiod.

Each *C. tentans* stock tank was fed every second day using 5 to 20 ml of TetraMin® (Tetra, Blacksburg, VA, USA) slurry depending on hunger level. This slurry was prepared by blending 100 g of TetraMin in 1 L of water for 30 s. The slurry then was transferred into a series of 50-ml polypropylene centrifuge tubes and stored at −4°C until required.

Salvelinus fontinalis were fed at a rate of 2% body weight/aquarium/day of commercial starter trout pellets, with live prey organisms (field-collected *B. tricaudatus* nymphs and/or laboratory-cultured *C. tentans* larvae) being substituted as live food items every 3 to 4 d.

Cadmium solutions and exposure regime

Cadmium concentrations of 0.5 and 5.0 μg/L were used as treatments. These concentrations are within environmentally realistic concentrations (≤5 μg/L) measured in North American surface waters [17] and are relevant to current Canadian water quality guidelines [18].

Cadmium exposure solutions were prepared by the dilution of a 10-mg/L stock solution ($CdCl_2 0.2^1/_2 H_2O$; Sigma Chemical, St Louis, MO, USA) with synthetic test water [19]. Stock solutions were renewed every 3 d and stored at 4°C.

Following acclimation to laboratory conditions, *B. tricaudatus* nymphs were distributed between 3 × 21–L glass aquaria each containing 5 L of dechlorinated city water and a nominal Cd concentration of either 0 (control), 0.5, or 5.0 μg/L. Each aquarium was aerated vigorously. Typically, the density of organisms per tank was 100 to 150 mayflies. Organisms remained in the exposure media for 7 d before an experiment. During this time, the media were not replaced, but any dead individuals (<1% mortality across all treatments) and exuviae were removed. The feeding regime was maintained on a daily basis until 24 h before an experiment, when the organisms were starved to standardize hunger level.

In a similar fashion, acclimated fish of similar length and condition were distributed between 3 × 76–L glass aquaria each containing 60 L of dechlorinated city water and a nominal Cd concentration of either 0 (control), 0.5, or 5.0 μg/L. Each aquarium was aerated vigorously. The density of organisms was six fish per tank. A static-renewal procedure was adopted where 20 L of aquaria water were replaced with fresh dechlorinated city water on a daily basis. Each 20-L volume of replacement water was made up to the Cd concentration specific to each aquarium and was delivered from separate, labeled carboys. Fish waste and uneaten food were removed using a hand-pump siphon before each water exchange. Fish were checked at least once daily. Water temperature, dissolved oxygen, and pH were monitored following each water exchange to ensure and maintain consistent experimental conditions. Organisms were held under these conditions for a period of 30 d (no mortalities occurred), after which time they were employed in experimental trials. The feeding regime was maintained on a daily basis until a 48-h period before an experiment, when the organisms were starved to standardize hunger level.

For *C. tentans* larvae, 3 × 39–L aquaria were used in place of the larger 76-L stock tanks. Each aquarium was designated to receive a nominal Cd concentration of either 0, 0.5, or 5.0 μg/L. Three 76-L reservoirs (one per aquarium) were set up to deliver a particular Cd solution to its respective aquarium using a flow-through system. Over a 48-h period before the introduction of larvae, the silica sand substrate in each aquarium was stirred by hand for a 2-min period, three times a day, to help mix the substrate with the overlying Cd solution. Once complete, 300 × second-instar larvae then were introduced into each aquarium. After an exposure period lasting 7 d (as for *B. tricaudatus* nymphs) these individuals had entered third instar (~1.5 cm in length) and were ready to be used in experiments. Water flow and temperature, airflow, and drains were checked for each aquarium on a daily basis. Dissolved oxygen, pH, and ammonia were measured once a week.

Occasional water samples were obtained from all aquaria for Cd analysis (Perkin-Elmer 5000 [Norwalk, CT, USA] atomic adsorption spectrophotometer). Diatom mats were exposed to the required Cd concentration for 48 h before an experiment.

Artificial stream channels

Behavioral tests were conducted in artificial stream channels [13]. Each experimental unit consisted of a long, rectangular Plexiglas® (Röhm, Darmstadt, Germany) flume (170 × 27 × 17 cm) with semicircular ends. A white plastic central divider served to split the stream in half as well as to provide a background against which predator and prey behaviors could be observed clearly. A current speed of 4 cm/s was maintained using a diaphragm-pump system. A series of submerged airlines fitted at opposing ends of the stream forced the water to flow around the flume in a loop, in addition to providing aeration. Screen partitions fronted with coarse Nitex® (Sefar, Heiden, Switzerland) netting were placed between the central di-

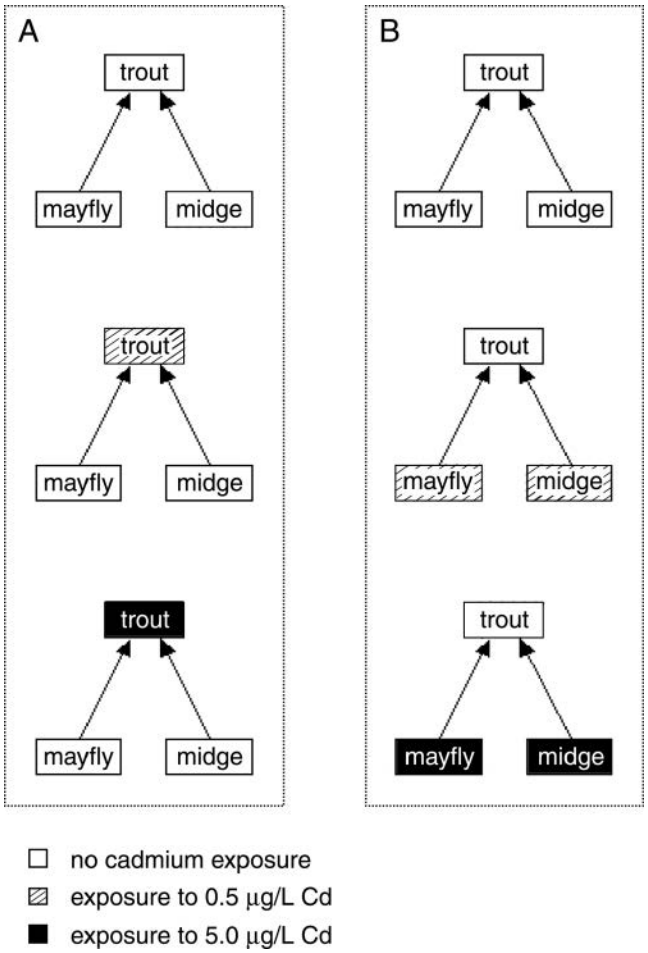

Fig. 1. Design of the prey-choice experiments. See text for details.

vider and the outer wall of the flume. These helped to compartmentalize the flume into three sections (a testing arena subdivided into predator-holding and prey-presentation sections, and a prey-holding section) while still allowing relatively unimpeded water flow. Each stream received 20 L of dechlorinated city water.

Experimental design and procedure

The food web under investigation in the current series of experiments used the following elements: *Nitzschia sp.* + *B. tricaudatus* + *C. tentans* + *S. fontinalis*.

The design of the experiments is outlined in Figure 1. For experiment A, nine brook trout were selected randomly, three trout per treatment, following the 30-d pre-exposure to either 0, 0.5, or 5.0 µg/L Cd. The behavior of individual trout then was investigated in an uncontaminated environment in the presence of uncontaminated food web elements. Experiment B had a similar structure. However, in this case, both prey species (*B. tricaudatus* nymphs and *C. tentans* larvae) and diatom mats were pre-exposed to the range of Cd concentrations. The foraging behavior of unexposed trout then was investigated in the presence of these contaminated food web elements, again in an uncontaminated environment.

Experiments were conducted in a constant-temperature room (12 ± 1°C, 16:8-h light:dark photoperiod) using artificial stream channels, with one channel per treatment. Channels were replicated (three per treatment) in time rather than space, due to limitations in both space and stream channel numbers.

Each test channel required one fish, 12 mayfly nymphs, and 12 chironomid larvae. Individual fish were transferred using a fine-mesh net into the predator-holding section of each stream. Using wide-tipped tongs, eight cultured diatom mats then were placed randomly throughout the testing arena along with 80 glass beads (4 mm diameter; Fisher Scientific, Fair Lawn, NJ, USA). These beads served as prey refuges from predators while still allowing the prey species to be observed. Using a wide-bore pipette, 12 mayfly nymphs and 12 chironomid larvae then were introduced into the prey-presentation section. An additional number of nymphs and larvae were placed into the prey-holding section.

After a 15-min acclimation period, the screen partition separating predator and prey was removed and the organisms allowed to interact for 20 min, during which time the testing arena was videotaped (Sony® [Tokyo, Japan] DCR-TRV900 digital camcorder). Any prey that were consumed during this observation period were replaced with individuals from the prey-holding section to maintain constant numbers.

An experiment was terminated at the end of the observation period and the test organisms were sampled for Cd analysis (see *Sampling for cadmium analysis* section). These procedures were repeated for all replicates across all Cd treatments.

Behavioral observations

During review of the videotapes, behavioral observations were made for both *S. fontinalis* and *B. tricaudatus*. Although the experiments were designed to investigate the effects of Cd on prey choice and the capture efficiency of trout specifically, other behavioral measures, such as reaction distance and active and handling times, also were investigated for trout in order to provide a more complete picture of the consequences of Cd contamination.

Reaction distance was defined as the distance between predator and prey at the beginning of an attack. Attack initiation was recorded when the predator rapidly oriented itself toward the prey.

Capture efficiency (*CE*) was defined as

$$CE = \frac{C}{A_t} \tag{1}$$

where C = total successful attacks (i.e., captures without reemergence of prey item) and A_t = total attacks.

Handling time began with initiation of an attack and ended when prey escaped or were swallowed. Proportion of the foraging bout spent handling prey items (*HTP*) was defined as

$$HTP = \frac{T_{ht}}{T_T} \tag{2}$$

where T_{ht} = total handling time and T_T = total foraging time.

Proportion of the foraging bout spent active (*ATP*) was defined as:

$$ATP = \frac{T_T - T_{xt}}{T_T} \tag{3}$$

where T_{xt} = total resting time.

In addition, the attack ratio, an index of the number of attacks by trout on mayflies versus attacks on chironomids, was measured. This ratio enabled any prey preference by trout to be estimated. Drift rate (the number of mayflies leaving substrate and drifting during an observation period: See [13]) was measured for *B. tricaudatus* nymphs, but no behavioral investigations were made for *C. tentans* larvae, because they

remained inactive throughout the observation periods. Additional definitions of fish and mayfly behaviors are provided in Riddell et al. [13].

Measurement of S. fontinalis *condition factor*

The condition factor (K) of a fish was determined from the length and weight data of each individual by using the Fulton's condition factor equation [20]:

$$K = (W \times L^{-3}) \times 100 \quad (4)$$

where W is wet body weight (g) and L is total length (cm).

The condition factor of each fish was measured before Cd exposure and again at the end. This required identification of each individual. Because dye-marking poses a risk of injury to small fish [21], a digital photograph was taken of the vermiculations-marbled patterns on the back and on the dorsal and tail fins, specific to each fish. This enabled individual fish to be identified successfully because these patterns changed little over the 30-d exposure period. A similar procedure is adopted by herpetologists and permits discrimination among several hundred individuals [22].

Sampling for cadmium analysis

Following completion of the experiments, food web elements and exposure aquaria water, food, and substrate samples were prepared for Cd analysis (see [23] for analytical procedures). Cadmium results for water and diatom samples were reported as μg/L and μg/g dry weight, respectively.

Samples of TetraMin fish food slurry and sand substrate were obtained from each *C. tentans* exposure aquarium and placed in separate, labeled (date, sample type, Cd-exposure concentration) centrifuge tubes. Samples were centrifuged at 3,600 rpm for 45 min before acidification so that particulate matter formed a pellet at the bottom of the centrifuge tube. The supernatant then was decanted and the pellet used for Cd analysis following the digestion procedure detailed in [23]. Results were reported as μg/g dry weight.

Invertebrate species were sampled by first transferring individuals into carbonated water to anesthetize them and then removing them to dry, labeled (date, species, Cd-exposure concentration) centrifuge tubes to be placed in a −70°C freezer for 4 h. Tube contents then were freeze-dried (LABCONCO® Freeze Dry System, Kansas City, MO, USA) and analyzed for Cd. Cadmium results were reported as μg/g dry weight.

Due to time constraints, fish were not analyzed for Cd in this series of experiments. However, because the holding conditions, source, and size range of individuals were identical to those of previous experiments [13], tissue concentrations in these fish were expected to be similar. From [13]: (gill) $y = 0.260 + 0.680x$, $r^2 = 0.954$; (liver) $y = 0.129 + 0.332x$, $r^2 = 0.911$; (gut) $y = 0.106 + 0.324x$, $r^2 = 0.630$; (muscle) $y = 0.094 + 0.349x$, $r^2 = 0.370$.

Statistical analyses

All analyses were performed using the StatView statistics package (Ver 5.0.1, SAS Institute, Cary, NC, USA). Data sets were checked for normality (Kolmogorov-Smirnov test) and homogeneity of variance (Levene's test) before statistical analysis.

Baetis tricaudatus drift rate was analyzed using one-way analysis of variance. The factor tested was treatment, which represented Cd concentration (levels: 0, 0.5, and 5.0 μg/L). The element of the food web exposed to the treatment differed between experiments A and B; only trout were exposed in experiment A, whereas all food web elements except trout were exposed in experiment B (Fig. 1).

For trout, because more than one behavioral variable (attack ratio, capture efficiency, reaction distance, and active and handling times) was measured once per individual, behavioral data were analyzed using multivariate analyses of variance. Again, the factor tested was treatment. If a test statistic rejected H_0, univariate analyses of variance were performed on each of the variables, to test for differences among means for each variable separately [24]. Such a procedure ignores any relationships among the variables, but this was not considered important (in a biological sense) due to the nature of the questions being asked.

Because condition factor measurements were obtained for individual trout at the beginning and end of the 30-d Cd exposure period, the resulting data were analyzed using repeated-measures analyses of variance. Factors (and levels) tested were Cd concentration (0, 0.5, 5.0 μg/L) and time (before exposure, after exposure). Post hoc tests were not applied to the means of within subjects factors, because repeated observations on an individual, and therefore the means based on these groupings, are correlated. The significance level for all tests was $\alpha = 0.05$.

RESULTS

B. tricaudatus *behavior*

No significant differences in *B. tricaudatus* drift rate were observed in either experiment ($p > 0.05$); drift rate remained the same (mean = 14 drift events per observation period, standard deviation = 1) irrespective of whether trout or mayflies had been subject to Cd exposure.

S. fontinalis *behavior*

Experiment A: Exposed predator, unexposed prey. The results of the multivariate analyses of variance revealed a significant effect of Cd on only the mayfly:midge attack ratio of juvenile *S. fontinalis* ($p < 0.01$). Figure 2A shows that unexposed trout expressed a slight preference for mayfly nymphs, whereas the majority of attacks performed by Cd-exposed trout primarily focused on chironomids. Also, the data suggest a trend to increased preference of *C. tentans* larvae by trout as Cd concentration increases, although this response is variable and requires further testing.

Cadmium failed to produce significant effects on other aspects of *S. fontinalis* behavior ($p > 0.05$), although there does appear to be a trend toward decreased capture efficiency and increased activity with increasing Cd concentration (Fig. 2A).

Experiment B: Unexposed predator, exposed prey. In experiment B, no significant effect of Cd-exposed prey on any aspect of *S. fontinalis* foraging behavior was found ($p > 0.05$). However, there does appear to be a trend toward a decreased capture efficiency of Cd-contaminated prey items as Cd concentration increases (Fig. 2B). The proportion of the observation period spent active by juvenile *S. fontinalis* tended to increase in the presence of Cd-exposed prey (Fig. 2B). No attack ratio value is present for prey species exposed to 0.5 μg/L Cd because trout performed no attacks on both mayflies and chironomids during the same observation period in this treatment. However, of the six attack attempts recorded, each was targeted at mayfly nymphs.

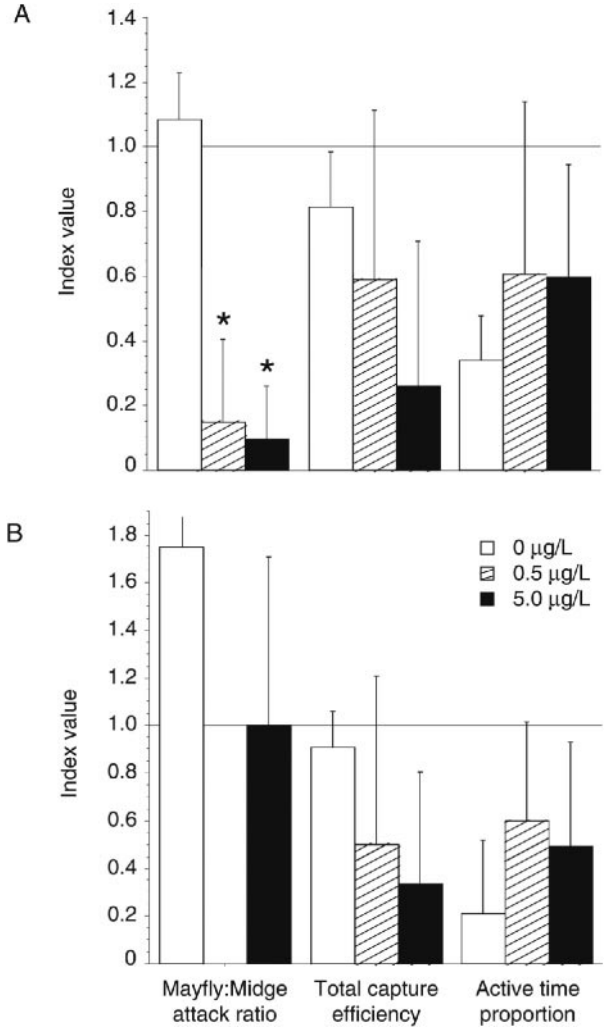

Fig. 2. Attack ratios of (**A**) Cd-exposed *Salvelinus fontinalis* and unexposed invertebrate prey, and (**B**) unexposed *S. fontinalis* and Cd-exposed invertebrate prey. Capture efficiencies for both prey types combined and *S. fontinalis* active time proportions also are illustrated. The horizontal lines represent unity. Means ± standard deviation. An * indicates significantly different responses to controls.

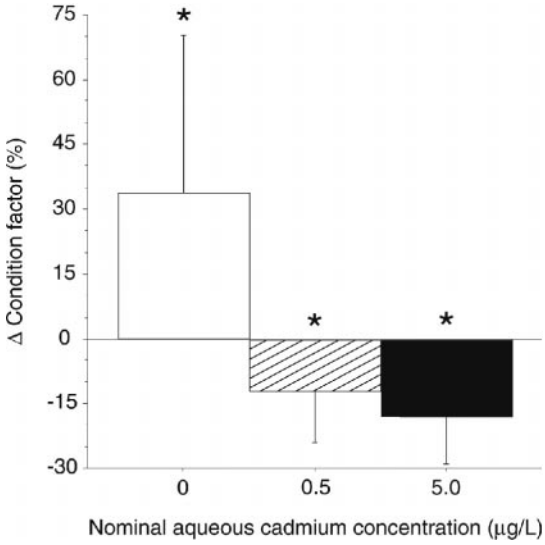

Fig. 3. Change in condition factor of juvenile *Salvelinus fontinalis* following the 30-d exposure to the range of Cd concentrations. Means ± standard deviation. An * indicates significantly different responses to initial values.

S. fontinalis *condition factor*

The 30-d exposure to Cd resulted in impaired condition factor in fish exposed to 0.5 and 5.0 µg/L (Fig. 3), while the condition factor of control fish improved. Differences in condition factor for both control and Cd-exposed fish were significant ($p < 0.01$).

Cadmium analyses

Cadmium concentrations were linear functions of exposure concentration for invertebrate food and sand substrate (Fig. 4A) and prey species (Fig. 4B). The regression models explained 97 to 99% of the variability in uptake by invertebrate food, with TetraMin slurry tending to accumulate almost twice as much Cd per gram of dry weight than *Nitzschia* sp. diatom mats (Fig. 4A). Uptake by the sand substrate was poor, failing to accumulate more than approximately 0.05 µg/g even at the highest (5.0 µg/L) aqueous concentration.

Uptake of Cd by *B. tricaudatus* nymphs was similar to results obtained from previous experiments [13]. Mayfly nymphs tended to accumulate more Cd per gram of dry weight than *C. tentans* larvae (Fig. 4B).

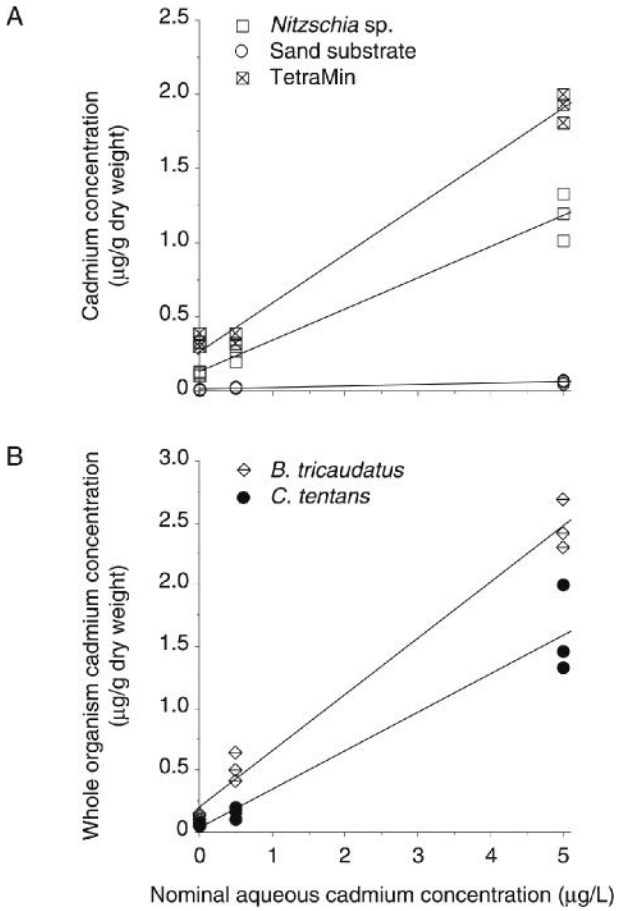

Fig. 4. Linear regression of Cd uptake by (**A**) *Nitzschia* sp. diatom mats, aquarium sand substrate, and TetraMin® aquarium fish food (Tetra, Blacksburg, VA, USA) and (**B**) *Baetis tricaudatus* nymphs and *Chironomus tentans* larvae over the concentration range used in the study. (TetraMin: $y = 0.263 + 0.329x$, $r^2 = 0.986$; *Nitzschia* sp.: $y = 0.134 + 0.210x$, $r^2 = 0.971$; Sand substrate: $y = 0.018 + 0.009x$, $r^2 = 0.893$; *B. tricaudatus*: $y = 0.199 + 0.456x$, $r^2 = 0.984$; *C. tentans*: $y = 0.036 + 0.312x$, $r^2 = 0.944$).

The relationship between nominal versus measured aqueous cadmium concentrations in aquaria is described by y (measured) = 0.020 + 0.752x (nominal), $r^2 = 0.982$.

DISCUSSION

Prey choice by S. fontinalis

Whether prey behavior affects encounter rates in fish will depend in part on the type of sensory system used by the individual to detect prey. Such systems include vision [25], olfaction [26], lateral line [27], and hearing [28]. Trout often are described as visual predators (e.g., [29]) and, due to their predominantly drift-feeding behavior in lotic systems [29,30] and general morphology [31], likely rely on this sense more than any other to detect prey.

The current study found *B. tricaudatus* drift rate to remain unaltered irrespective of whether trout or mayflies had been subject to Cd exposure. These results are similar to those obtained in previous experiments where, in the presence of a trout predator, *B. tricaudatus* drift rate varied only slightly with the addition of Cd to the system [13]. Thus, compared to *C. tentans* larvae, the higher exposure and activity levels of *B. tricaudatus* nymphs likely would result in a greater number of encounters between trout and mayflies if trout were foraging visually.

The behavioral response of trout to the two prey types was expected to differ, due to both the differences in activity between the prey species and the more benthic nature of chironomids. The two prey types also differ in their escape responses; *B. tricaudatus* nymphs enter the drift or retreat to refugia under predation risk, whereas *C. tentans* larvae either withdraw into the substrate or show little response [32]. Once encountered, however, chironomids escape less frequently than mayflies (personal observation, D. Riddell). Whether trout more frequently consume mayflies or chironomids will depend on the trade-offs between encounter and capture efficiency.

The results of the current study found that trout, in the absence of a Cd treatment, exhibited both a high (80–90% success) overall capture efficiency and a preference for mayfly prey (Fig. 2A and B). Because handling time of trout foraging on either mayflies or chironomids was similar (<5 sec, likely because both prey types were within the gape size of trout), the difference in profitability between prey types should be determined largely by their difference in energy content [33]. The energy content per gram wet weight of baetid mayflies is approximately 2× that of chironomids (1,124 and 656 Cal, respectively [34]). Thus, a dietary preference for mayflies is of greater energetic benefit to trout.

It would be advantageous for trout to specialize on *B. tricaudatus* nymphs if the net energy obtained by foraging exclusively on mayflies was greater than that gained by including both mayflies and chironomids in the diet. However, due to the short handling times for both prey types, the probability of a trout missing an encounter with a mayfly while handling a chironomid is low. Thus, although mayflies are a more energy-rich prey type, trout should consume both prey types when encountered, and not exclude the less profitable chironomids from their diet.

Because the densities of both prey types used in the current study were identical, the encounter rate with a particular prey type depended more on the behaviors adopted by both the prey species and the predator.

Effects of cadmium

The results of the current study revealed that Cd-stressed trout exhibited a preference for *C. tentans* larvae over *B. tricaudatus* nymphs as prey items. Thus, when foraging for chironomids, trout would be expected to rely less on vision and more on olfaction. Therefore, one would expect to observe a corresponding increase in *S. fontinalis* rooting behavior as individuals probed the substrate while foraging for prey items. This was not observed, possibly because the nature of the provided substrate (glass beads) prevented *C. tentans* larvae from completely being concealed and inaccessible to a trout predator. Also, the red pigmentation of the larvae may have acted as a visual stimulus, as was found for three-spined sticklebacks and their *Tubifex* sp. prey [35]. Under such circumstances, trout required little foraging effort to pick chironomid prey from off the floor of the test arena. In nature, however, one would expect an increase in rooting behavior by trout to ensure capture success of chironomids in silty or sandy substrates. Whether this is indeed the case will be the subject of future papers.

Although not significant, exposure to Cd tended both to increase active time proportion and decrease overall capture efficiency in trout, similar to results obtained in the previous experiments [13]. Probable reasons for increased activity in fish exposed to Cd, such as excess mucus production, irritation, and nervous system effects, are discussed in a previous paper [13].

Unexposed trout feeding on contaminated prey also tended to experience reduced capture efficiency. Because the trout themselves were not Cd-stressed in this instance, the results suggest that, irrespective of prey type, individual fish were rejecting unpalatable Cd-contaminated prey. Investigating the components of handling behavior (see Riddell et al. [13]) of these individuals lends weight to this conclusion, in that the number of attacks did not differ greatly from those of control fish, but their capture success (i.e., retention of prey leading to ingestion) was compromised.

Reasons for the trend to increased activity in trout presented with Cd-contaminated prey are unclear. It is possible that such observed increases in active time resulted from increased searching effort by trout seeking palatable food items. However, further experiments that include both contaminated and uncontaminated prey items in the test arena would have to be undertaken before such a hypothesis could be tested.

Brook trout exposed for 30 d to 0.5 and 5.0 μg/L Cd experienced a decline in condition factor at both concentrations in the current study. A decrease in condition factor usually is interpreted as depletion of energy reserves stored as liver glycogen or body fat. Declines in condition factor may be related to responses, behavioral or otherwise, to certain stressors, such as changes in feeding patterns (e.g., [36]) or an increase in metabolic rate [37]. As the 30-d exposure period progressed, individuals in the treatment holding tanks were observed to consume less food than controls (personal observation). These visual estimates were not verified quantitatively, although these changes in feeding patterns/energy intake (or energy expenditure due to increased activity levels) likely have contributed to the lower condition factor of Cd-exposed fish.

Cadmium uptake

Results of Cd analyses revealed linear uptake of the metal by invertebrate food, sand substrate, and prey species. TetraMin slurry was found to accumulate almost twice as much

Cd per gram of dry weight than *Nitzschia* sp. diatom mats. Because the TetraMin slurry remained in suspension for a period of time following introduction into aquaria, more of its surface area was available for Cd adsorption, unlike the diatom mats where the rate of adsorption would be limited by mat thickness [38].

Uptake by the sand substrate was poor, failing to accumulate more than approximately 0.05 μg/g Cd even at the highest (5.0 μg/L) aqueous concentration. The absence of any organic material, typical of natural sediment, may have limited the adsorption capacity of the substrate. Natural sediments can act as a sink for aquatic contaminants and, as such, often contain higher contaminant concentrations than those in the aqueous phase [39]. Thus, one would expect a higher metal body burden in *C. tentans* larvae rather than *B. tricaudatus* nymphs under natural exposure conditions. The opposite was true in the current experiments, probably due to the dearth of Cd in the immediate environment of cultured chironomids. Because *C. tentans* larvae potentially were obtaining more Cd through their diet than *B. tricaudatus* nymphs, it is likely that differences in environmental Cd concentrations and invertebrate surface-area–to–volume ratios [13] contributed to the observed differences in metal burden between prey types.

CONCLUSION

Juvenile salmonids primarily feed on drifting invertebrates [29,30]. However, the results of this preliminary study strongly suggested that, following exposure to Cd, trout expressed a preference for nonmotile, benthic, *C. tentans* larvae as alternative prey to motile, drifting, *B. tricaudatus* nymphs. This switch was made by Cd-stressed trout as a likely consequence of requiring to meet certain energy demands while compensating for their poor capture success with motile prey items [13]. Nevertheless, the capture efficiency of Cd-stressed trout tended to decline with increasing Cd concentration, irrespective of prey choice, and the activity of individual trout increased, further compromising the energy budget of these fish and revealed in decreased condition factor when compared with controls. By decreasing the amount of energy available for the survival, growth, and reproduction of an organism, individual fitness is reduced. Furthermore, a switch by fish to feeding on benthic prey under natural exposure conditions and their proximity to contaminated sediments may further exacerbate the sublethal effects of Cd on these individuals by intensifying or prolonging Cd exposure through trophic transfer or foraging behavior.

When presented with Cd-exposed prey, unexposed *S. fontinalis* showed no preference for one prey type over another. However, the total capture efficiency of *S. fontinalis* under these conditions tended to decrease, although results were not statistically significant.

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