

# Organochlorine transfer in the food web of subalpine Bow Lake, Banff National Park

Linda M. Campbell, David W. Schindler, Derek C.G. Muir, David B. Donald, and Karen A. Kidd

**Abstract:** Lake trout (*Salvelinus namaycush*) from subalpine Bow Lake, near the Continental Divide in Banff National Park, have been reported to have higher concentrations of toxaphene than other lake trout populations of the Rocky Mountains. Our original hypothesis was that unusually high biomagnification via a long food chain was responsible for elevated levels of toxaphene and other persistent organochlorines in the lake trout. This hypothesis was refuted by the analyses of stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios in lake biota. Stable nitrogen isotope analyses demonstrated that the food chain length in Bow Lake was short. The sources of carbon (pelagic or benthic), as indicated by stable carbon isotope values, were highly correlated with organochlorine concentrations in the food web. Lake trout with more pelagic carbon signatures had higher organochlorine concentrations than littoral-feeding mountain whitefish (*Prosopium williamsoni*) and lake trout. The pelagic copepod *Hesperodiaptomus arcticus* had higher organochlorine concentrations (wet weight basis) than any other organism, including the fish. This was attributed to the high lipid content of copepods and possibly their ingestion of suspended solids, including glacial silt or direct absorption from solution in glacial inflows.

**Résumé :** Les touladis du lac Bow, lac subalpin du parc national Banff situé près de la ligne de partage des eaux, semblent présenter des concentrations de toxaphène plus élevées que d'autres populations de touladis des montagnes Rocheuses. Nous sommes partis de l'hypothèse qu'une bioamplification anormalement forte le long d'une chaîne trophique très longue était responsable des teneurs élevées en toxaphène et en d'autres organochlorés persistants chez les touladis. Cette hypothèse a été réfutée après l'analyse des rapports des isotopes stables du carbone ( $\delta^{13}\text{C}$ ) et de l'azote ( $\delta^{15}\text{N}$ ) dans le biote du lac. D'après les analyses des isotopes stables de l'azote, nous avons établi que le réseau trophique du lac Bow est raccourci. Les sources de carbone (pélagiques ou benthiques), d'après les valeurs des isotopes stables du carbone, étaient fortement corrélées aux concentrations d'organochlorés dans le réseau trophique. Les touladis présentant de plus fortes signatures de carbone pélagique avaient des concentrations plus élevées d'organochlorés que les ménominis de montagnes et les touladis qui se nourrissaient sur le littoral. Le copépode pélagique *Hesperodiaptomus arcticus* présentait des concentrations d'organochlorés plus élevées (poids humide) que tout autre organisme, poissons y compris. Ce phénomène est attribuable à la forte teneur en lipides des copépodes, et peut-être au fait qu'ils ingèrent des solides en suspension, notamment du silt glaciaire, ou qu'ils absorbent directement des composés en solution dans l'eau d'origine glaciaire.

[Traduit par la Rédaction]

## Introduction

In a survey conducted in 1991–1992, persistent organochlorine compounds (toxaphene, total dichlorodiphenyltrichloroethane ( $\Sigma\text{DDT}$ ), total polychlorinated biphenyls ( $\Sigma\text{PCB}$ ), and other compounds) were detected in lake trout (*Salvelinus namaycush*) from 14 lakes in the Canadian Rocky Mountains (Donald et al. 1993). Lake trout from sub-

alpine Bow Lake in Banff National Park contained some of the highest toxaphene (chlorobornanes) concentrations in the study, leading to concern about the presence of persistent organochlorine (OC) contaminants in the Rocky Mountain area. Concentrations of toxaphene in lake trout from Bow Lake were up to 10–20 times higher than in fish populations from other nearby lakes (Donald et al. 1998). There was no record of any direct addition of toxaphene or other OCs to

Received July 5, 1999. Accepted March 21, 2000.  
J15236

**L.M. Campbell<sup>1</sup>** and **D.W. Schindler<sup>2</sup>** Department of Biological Sciences, University of Alberta, Edmonton, AB T6G 2E9, Canada.

**D.C.G. Muir.** Environment Canada, National Water Research Institute, 867 Lakeshore Road, P.O. Box 5050, Burlington, ON L7R 4A6, Canada.

**D.B. Donald.** Environment Canada, Room 300 Park Plaza, 2365 Albert Street, Regina, SK S4P 4K1, Canada.

**K.A. Kidd.** Department of Fisheries and Oceans, Freshwater Institute, 501 University Crescent, Winnipeg, MB R3T 2N6, Canada.

<sup>1</sup>Present address: Department of Biology, University of Waterloo, Waterloo, ON N2L 3GT, Canada.

<sup>2</sup>Author to whom all correspondence should be addressed. e-mail: d.schindler@ualberta.ca

Bow Lake or surrounding areas (Donald et al. 1993), which suggested an atmospheric source. A recent mass-balance study of persistent OCs suggests that Bow Lake may be receiving much of its OCs from glacial water flowing into the lake and from precipitation at high altitudes (Dr. J. Blais, Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada, personal communication).

In contaminated aquatic ecosystems, there is usually an increase in OC concentrations with each trophic level in a food web (Evans et al. 1991). In an earlier study of Lake Laberge, Yukon Territory, unusually high concentrations of toxaphene and other contaminants in predatory fish were explained by the presence of longer food chains than found in other nearby lakes (Kidd et al. 1998b). We hypothesised that Bow Lake might also have a longer food chain than other Rocky Mountain lakes, contributing to the high concentrations in fish.

Stable nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) isotope ratios of biota can be invaluable in characterising food web structure and trophic interactions (Peterson and Fry 1987). Stable carbon and nitrogen isotope ratios integrate long-term dietary patterns, especially in cold-water fish that have slow tissue turnover rates (Hesslein et al. 1993). Stable isotope analyses complement taxonomic data obtained from stomach contents because both long-term and short-term trophic behaviour can be evaluated for individual animals.

$^{14}\text{N}$  is selectively eliminated by organisms and  $^{15}\text{N}$  incorporated in body tissues, so that with each successive trophic level,  $\delta^{15}\text{N}$  ( $^{15}\text{N}:^{14}\text{N}$ ) values in the tissue of biota increase. Freshwater studies indicate that the average  $\delta^{15}\text{N}$  difference between trophic levels is between 3.2 and 3.4‰ (Peterson and Fry 1987). Kidd et al. (1995) demonstrated that contaminant uptake by fish and other organisms in Yukon aquatic food chains could be reliably predicted by using stable isotopes of nitrogen to measure trophic positioning. Similar positive significant relationships between OCs and stable nitrogen isotope ratios were observed in Lake Ontario in southern Ontario (Kiriluk et al. 1995), Lake Baikal in Russia (Kucklick et al. 1996), and Peter Lake in Northwest Territories (Kidd et al. 1998a).

In contrast, stable carbon isotopes fractionate very little during transfer between trophic levels, with less than 1‰ enrichment in  $\delta^{13}\text{C}$  ( $^{13}\text{C}:^{12}\text{C}$ ) per trophic level (Peterson and Fry 1987). Because of low fractionation rates, the stable carbon isotope values of organisms reflect the average  $\delta^{13}\text{C}$  of their diets. Differences in  $\delta^{13}\text{C}$  between pelagic, benthic, and terrestrial sources are transferred up the food chain, revealing the importance of different sources of primary production to organisms (Rau and Anderson 1981; Hecky and Hesslein 1995). The differences in  $\delta^{13}\text{C}$  between pelagic and benthic consumers can be used in conjunction with OC measurements to determine the relative contribution of these carbon sources to the biomass of any consumer within the food web as well as to contaminant burdens.

This study had two objectives. The first was to determine the food web structure in Bow Lake by using  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  to characterise trophic level and carbon sources, respectively. The second was to test the hypothesis that the food web structure and (or) lipid content determine persistent OC concentrations in biota.

## Methods

### Study area

Bow Lake is an ultraoligotrophic subalpine lake located in northern Banff National Park (51°45'N, 116°30'W) (Table 1). The Icefields Parkway, a major tourist thoroughfare, runs along the eastern side of Bow Lake. The majority of the inflow to Bow Lake comes from the Bow Glacier, a tongue of the Wapta Icefields that straddles the Continental Divide. The lake discharges to the Bow River, which flows southeast through the park, becoming part of the Saskatchewan River system. The current fish community consists of lake trout (*Salvelinus namaycush*) and mountain whitefish (*Prosopium williamsoni*). The large calanoid copepod *Hesperodiaptomus arcticus* is the most abundant zooplankton species, followed by *Daphnia middendorffiana*. Campbell (1997) provides a detailed review of the limnology, fish stocking history, and the environment of Bow Lake.

### Field methods and analyses of fish stomach contents

Lake trout and mountain whitefish were captured using gill nets (June 1994) or fish traps (August 1994) set in the littoral zone. Fish stomachs were removed upon capture and were either frozen for stable isotope analyses or preserved in sugar formalin for taxonomic analyses. Sixteen lake trout (1019 ± 411 g, 9.6 ± 2.1 years old) and 12 mountain whitefish (250 ± 238 g, 7.3 ± 4.6 years old) were submitted for OC and stable isotope analyses. All fish and fish stomachs were wrapped in solvent-cleaned aluminium foil, stored on dry ice in the field, and then stored at -60°C in the laboratory. Otoliths were removed from fish in the field and stored in glycerin-alcohol solution. The ages of fish were later determined by counting annuli on otoliths using Calcified Structure Analysis software at the Glenora Fisheries Station (Ontario).

The contents of fish stomachs were examined under a dissecting microscope. Many stomachs contained highly digested material, which precluded accurate weight estimates of the individual taxa. The percent frequency of occurrence of each prey was calculated for lake trout and mountain whitefish (excluding empty stomachs). Mountain whitefish fry, adult Ephemeroptera, and Plecoptera found in lake trout stomachs were included in stable isotope analyses. Additional data for Bow Lake fish dietary habits were obtained from an Environment Canada database for the years of 1984, 1991, and 1993 and from published mountain whitefish studies from the 1930s (Rawson 1939; McHugh 1940). The presence of plerocercoid larval cysts of *Diphyllobothrium ditremum* on the surface of fish stomachs was noted, as it provides an indirect measure of zooplanktivory. *Diphyllobothrium ditremum* is transmitted to fish by feeding upon copepods or infected fish (Anthony 1967). We did not determine the frequency and duration of the plerocercoid infection in fish from Bow Lake.

Zooplankton were collected throughout the summers of 1994 and 1995 by towing a 64-µm-mesh Wisconsin-style net of 1-m diameter through the entire water column and then along the surface for about 5 m to maximise the amount collected. Zooplankton were sorted into adult *H. arcticus*, larval *H. arcticus*, and *D. middendorffiana* using 243- and 947-µm screens and hand sorting. In addition, unsorted zooplankton samples (which were taken directly from the net haul without any separation into species or size-classes) and *H. arcticus* samples were processed for OC and stable isotope analyses. However, large *D. middendorffiana* were analysed for stable isotope ratios only. Phytoplankton could not be collected in sufficient amounts for stable isotope or OC analyses. Benthic algae were obtained for stable isotope analyses by scraping rocks from the littoral zone. Benthic invertebrates were collected by sweeping the shoreline with long-handled collecting nets. In addition, burlap sacks (filled with rocks and marked with a float) were set underwater near the shoreline to provide artificial

**Table 1.** Physical and chemical parameters for Bow Lake, Banff National Park.

Variable	Value
Area	2.8 km <sup>2</sup>
Volume	0.64 km <sup>3</sup>
Maximum depth	51 m
Average depth	22.9 m
Elevation	1940 m
Midsummer surface temperature (measured in July 1994 and 1995)	10–12°C
Dissolved organic carbon	0.46±0.12 mg·L <sup>-1</sup>
Total phosphorus	4.6±1.3 µg·L <sup>-1</sup>
Total dissolved phosphorus	2.2±1.2 µg·L <sup>-1</sup>
Total dissolved nitrogen	83.9±5.2 µg·L <sup>-1</sup>
NO <sub>3</sub> + NO <sub>2</sub>	46.4±2.6 µg·L <sup>-1</sup>
Ammonia	3.2±0.9 µg·L <sup>-1</sup>
Chlorophyll <i>a</i>	0.31±0.2 µg·L <sup>-1</sup>
Conductivity	161.8±3.2 µS·cm <sup>-1</sup>
pH	8.1±0.06
Turbidity	2.6 NTU
Dissolved inorganic carbon δ <sup>13</sup> C	-5.86‰
Particulate organic matter + particulate inorganic matter δ <sup>13</sup> C	-16.44‰ (average)
Particulate organic matter δ <sup>15</sup> N	0.51‰
Sediment organochlorine content	3.1%

habitat for benthic invertebrates and were found to be a particularly successful tool for collecting the amphipod *Gammarus lacustris*. All invertebrate species were pooled by major taxa for OC and stable isotope analyses except for *H. arcticus*, *G. lacustris*, and *D. middendorffiana*. Samples were stored at -60°C in solvent-cleaned glass jars until analysis.

## Laboratory methods

### Stable isotope analyses

For stable isotope analyses, skinless dorsal muscle samples were removed from individual fish. All invertebrates were pretreated with 1 N hydrochloric acid to remove carbonates prior to δ<sup>13</sup>C analyses. Prepared non-lipid-extracted samples were combusted in a Carlo Erba NA 1500 elemental analyser using the automated methods detailed in Kidd et al. (1998a). The precision over several years is 0.4 part per mil (2 SD). The ratios of the stable isotopes were measured against the reference standards PeeDee dolomite for δ<sup>13</sup>C and air for δ<sup>15</sup>N using the formula below. The delta notation (δ) is used to indicate the parts per mil (‰, or parts per thousand) difference in the isotopic ratio of the sample from the standard. A working standard of Pharmamedium of known isotopic composition was run with every 10 samples. The formula is

$$\delta^{13}\text{C or } \delta^{15}\text{N} = (R_{\text{sample}} \times R_{\text{standard}}^{-1}) \times 1000$$

where  $R = {}^{13}\text{C}_2/{}^{12}\text{C}_2$  for δ<sup>13</sup>C and  $R = {}^{15}\text{N}_2/{}^{14}\text{N}_2$  for δ<sup>15</sup>N.

### OC extractions and analysis

Six major OC groups were quantified for this study: toxaphene (chlorobornanes), ΣDDT, ΣPCB, total chlordane (ΣCHL), dieldrin, and total hexachlorocyclohexane (ΣHCH). Extraction and processing of samples for OCs follow the same methods outlined in Kidd et al. (1998b). For fish, dorsal muscle samples with skin attached (dissected from the same side of all fish using solvent-cleaned tools) were analysed. Analysis of skin-on fillets may underestimate total OC burdens by as much as 20% but was done to facilitate ef-

ficient processing for both stable isotopes and OC analyses in the laboratory. Fish muscle and invertebrate samples were extracted in 1:1 hexane–dichloromethane for 4 h using a Soxhlet apparatus. One-tenth of the Soxhlet extract was set aside to gravimetrically determine the percent extractable lipids. Invertebrate samples were prefiltered to remove fine particles before determining the percent extractable lipids. Lipids were removed using gel permeation chromatography by eluting through SX-3 Bio-bead columns with 1:1 hexane–dichloromethane.

The Soxhlet extracts were separated on 1.2% deactivated Florisil (8 g) columns into three fractions (F1, F2, and F3). F1 contained all PCB congeners, some DDT and DDT metabolites, some toxaphene congeners, and the PCB 30 internal standard in 100% hexane. F2 contained most of HCH, toxaphene, and CHL congeners, the remaining DDT congeners, and the octachloronaphthalene internal standard in 85:15 hexane–dichloromethane. F3 contained the remaining OC congeners from the column including dieldrin in 1:1 hexane–dichloromethane. Each fraction was analysed on a Varian 3600 gas chromatograph with a <sup>63</sup>Ni electron capture detector. Internal standards (PCB 30 and octachloronaphthalene) were used to monitor extraction efficiency, and samples were not corrected for recoveries. Recoveries of internal standards in all fish samples were 78 ± 10% for F1 and 77 ± 11% for F2. Zooplankton samples had 100% recovery rates for both F1 and F2, while benthic invertebrate sample recoveries were 99.1 ± 1.9% for F1 and 99.4 ± 1.2% for F2. Toxaphene in samples was quantified by analysing combined F1 and F2 with high resolution gas chromatography electron capture negative high-resolution mass spectrometry (Miskimmin et al. 1995). All concentrations are reported as wet weight values.

### Data analyses

Calculations were made with SAS software (version 6.10, SAS Institute Inc., Cary, N.C.). For fish, weight was chosen as the size variable. Nonpaired Student's *t* tests were used to compare the means of stable nitrogen and carbon isotope values between lake trout and mountain whitefish and between zooplankton and benthic invertebrates. Nonparametric statistics were used for OC data analyses because of the small sample sizes (Zar 1984). Nonparametric Spearman rank correlation coefficients (*r<sub>s</sub>*) were used to measure correlations between OC concentrations and percent lipids, δ<sup>15</sup>N, and δ<sup>13</sup>C in biota. The significance of the Spearman coefficients was based on the sample size at a significance level of α = 0.05 and was based on the statistical tables listed in Zar (1984). For fish, weight was chosen as the size variable to examine relationships with OC data.

## Results

### Fish and copepod gut contents and dietary habits

Lake trout in Bow Lake appeared to preferentially feed upon chironomids (44–94%) and *G. lacustris* (43–79%) (Table 2). Fish (9–46%) were often found in trout stomachs, but the frequency varied greatly between years. Trichoptera, Plecoptera, and Ephemeroptera (4–75%) were occasionally found in these stomachs. Among the least common dietary items found in lake trout stomachs were zooplankton (1–15% of lake trout stomachs in 1993–1994 and 1984). However, in 1994, more than 60% of the lake trout captured had plerocercoid larval cysts of *D. ditremum* on their stomachs, indicating some zooplanktivory.

In Bow Lake, mountain whitefish diets were primarily benthic (Table 2). In 1994, Trichoptera were the dominant prey item (50% of mountain whitefish stomachs), along with

Lymnaeidae (33%). No chironomids were found in 1994 mountain whitefish stomachs, but McHugh (1940) and Rawson (1939) found mostly chironomids ( $\geq 20\%$ ) in mountain whitefish collected from Bow Lake earlier this century (Table 2). Ephemeroptera nymphs were found in a significant number of mountain whitefish from the 1930s, although not in the mountain whitefish from 1994. *Gammarus lacustris* and Plecoptera were found in low numbers for mountain whitefish in all years. Mountain whitefish also have been found with *D. ditremum* plerocercoid larval cysts (Rawson 1939).

The guts of individual *H. arcticus* collected in 1995 were full of glacial silt, which appeared to be ingested along with diatoms, algae, or other small zooplankton. Diatom shell fragments were observed in some individual gut contents. Glacial silt is very fine suspended sediment (grain size 2–4  $\mu\text{m}$ ) derived from rocks and sediment beneath glaciers.

### Stable nitrogen isotopes

According to the  $\delta^{15}\text{N}$  data, all adult fish of both species fed at a similar trophic level (Table 2; Fig. 1). Lake trout values ( $\delta^{15}\text{N}$  of 5.8–7.6‰) and adult mountain whitefish values ( $\delta^{15}\text{N}$  of 6.1–7.8‰) were not significantly different, varying within 2‰ of each other (Student's *t* test,  $t = 1.43$ ,  $p = 0.175$ ) (Fig. 1). Mountain whitefish fry had a  $\delta^{15}\text{N}$  value (4.3‰) intermediate between  $\delta^{15}\text{N}$  values for adult mountain whitefish and invertebrates. The average difference between the  $\delta^{15}\text{N}$  values of Bow Lake invertebrates (excluding the exceptions outlined below) and fish was about 4‰ (Fig. 2), indicating that both lake trout and mountain whitefish were located only one trophic level above invertebrates, with no intermediate fish prey.

$\delta^{15}\text{N}$  values for zooplankton and benthic invertebrates (1.3–2.9‰) were not significantly different (Student's *t* test,  $t = 0.853$ ,  $p = 0.216$ ), indicating that most invertebrates occupied a similar trophic level (Table 2; Fig. 1). In Bow Lake, *H. arcticus* and Plecoptera had  $\delta^{15}\text{N}$  values similar to those of lake trout in 1994 (5.6‰), but *H. arcticus* and Plecoptera had lower  $\delta^{15}\text{N}$  values in 1995 ( $2.5 \pm 0.3$  and  $3.6\text{--}4.2\%$ , respectively). Another shift in stable nitrogen isotopes was found with the 1994 Ephemeroptera samples: the adult mayfly sample had a higher  $\delta^{15}\text{N}$  ratio (4.9‰) than mayfly nymphs ( $1.7 \pm 0.3\%$ ). Nitrogen signatures of benthic algae were variable, with one sample having a very low  $\delta^{15}\text{N}$  (–1.34‰) and another sample having a  $\delta^{15}\text{N}$  value (1.27‰) comparable with that of some benthic invertebrates (Fig. 2; Table 1). The range of  $\delta^{15}\text{N}$  values between algae, invertebrates, and fish suggests that there were only three isotopically distinct trophic levels in Bow Lake.

### Stable carbon isotopes

The pelagic and benthic carbon signals at the base of the food web were isotopically distinct, with benthic invertebrates such as *G. lacustris* having significantly heavier  $\delta^{13}\text{C}$  values (–25.8 to –24.2‰) than pelagic zooplankton (–33.9 to –31.1‰) (Student's *t* test,  $t = 11.2$ ,  $p < 0.001$ ) (Fig. 2; Table 2). One Ephemeroptera nymph had a  $\delta^{13}\text{C}$  value similar to that of zooplankton (–30.5‰). The two benthic algae samples had different  $\delta^{13}\text{C}$  values (–24.05 and –17.98‰). Mountain whitefish adults and fry had carbon signatures

similar to those of benthic invertebrates (–25.6 to –20.3‰). Lake trout  $\delta^{13}\text{C}$  values (–30.7 to –24.8‰) fell between pelagic and benthic invertebrate  $\delta^{13}\text{C}$  values, indicating a broad dietary range with more pelagic carbon being assimilated than benthic carbon. Mountain whitefish values (–25.6 to –20.3‰) were significantly less negative than those of lake trout (Student's *t* test,  $t = 5.61$ ,  $p < 0.001$ ), indicating that they fed exclusively on benthic invertebrates.

### Lipid content

*Hesperodiaptomus arcticus* had the highest lipid content ( $14.9 \pm 8.6\%$ ) of all Bow Lake biota, including lake trout ( $6.7 \pm 3.1\%$ ). *Gammarus lacustris* had higher proportions ( $7.5 \pm 3.4\%$ ) than mountain whitefish ( $4.3 \pm 2.2\%$ ) (Table 2). The lipid content in biota did not increase with trophic level, as indicated by a lack of a significant correlation with  $\delta^{15}\text{N}$  ( $r_s = -0.357$ ). However, lipid content in biota significantly increased with more depleted  $\delta^{13}\text{C}$  values ( $r_s = 0.547$ ) (Fig. 2), indicating that pelagic organisms had higher lipid content.

### OCs in the food web

Toxaphene was the major contaminant group detected in all biota. The average concentrations ranged from  $181.5 \pm \text{ng}\cdot\text{g}^{-1}$  wet weight<sup>-1</sup> in *H. arcticus* to  $2.2 \text{ ng}\cdot\text{g}^{-1}$  in Lymnaeidae.  $\Sigma\text{DDT}$  concentrations were generally less than half those of toxaphene, ranging from  $22.5 \pm 9.1 \text{ ng}\cdot\text{g}^{-1}$  in *H. arcticus* to  $0.6 \text{ ng}\cdot\text{g}^{-1}$  in Lymnaeidae.  $\Sigma\text{PCB}$  and  $\Sigma\text{CHL}$  were found at much lower concentrations than toxaphene, ranging from about  $12 \text{ ng}\cdot\text{g}^{-1}$  in *H. arcticus* to about  $0.5 \text{ ng}\cdot\text{g}^{-1}$  in Lymnaeidae.  $\Sigma\text{HCH}$  and dieldrin concentrations were low in all biota, except for zooplankton, which had concentrations comparable with their  $\Sigma\text{PCB}$  and  $\Sigma\text{CHL}$  concentrations.

The highest OC concentrations were found in *H. arcticus*, an omnivore, and in lake trout, the top predator. Toxaphene tended to be highest in *H. arcticus*, while  $\Sigma\text{CHL}$  and  $\Sigma\text{HCH}$  concentration values for the two species overlapped (Table 3; Figs. 3–5).  $\Sigma\text{DDT}$ ,  $\Sigma\text{PCB}$ , and  $\Sigma\text{CHL}$  were higher in lake trout (Table 3; Figs. 3–5). Mixed zooplankton and other invertebrates had lower OC concentrations. *Gammarus lacustris* had OC concentrations comparable with those for mountain whitefish.

Lipid concentrations (Fig. 3) and carbon sources (Fig. 4) were better correlated with OC bioaccumulation patterns in Bow Lake biota than trophic position as indicated by  $\delta^{15}\text{N}$  (Fig. 5). Biota with higher lipid content (percent lipids) had significantly higher concentrations of all OC compounds ( $r_s = 0.577$  to  $0.872$ ) (Fig. 3). The consistent and significant negative correlations of  $\delta^{13}\text{C}$  with all OC concentrations in the biota of Bow Lake food web ( $r_s = -0.477$  to  $-0.664$ ) (Fig. 4) indicated that OC bioaccumulation was greater in pelagic organisms, which had more depleted carbon signatures and higher lipid. Correlations between contaminants and  $\delta^{15}\text{N}$  through the food web were nonsignificant ( $r_s = -0.216$  to  $0.486$ ) (Fig. 5). Similarly, in lake trout, toxaphene and  $\Sigma\text{HCH}$  were significantly correlated with lipids ( $r_s = 0.880$  and  $0.726$ , respectively) and with  $\delta^{13}\text{C}$  ( $r_s = -0.698$  and  $-0.726$ , respectively). However, in lake trout,  $\Sigma\text{CHL}$  was

**Table 2.** Stomach content data for mountain whitefish and lake trout from Bow Lake and stable nitrogen and carbon isotope ratios and percent lipid (mean  $\pm$  SD) of biota collected in 1994 and 1995.

	Fish (see codes)								Code	Year	n	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	% lipid
	M	M (<2 years old) <sup>a</sup>	M ( $\geq$ 2 years old) <sup>a</sup>	M <sup>b</sup>	L	L	L	L						
Year fish captured	Aug. 1994	1936–1938	1936–1938	1938	June–Aug. 1994	July 1993	June 1991	June 1984						
Total no. of stomachs (no. empty)	12 (7)	12	35	81	16 (2)	23 (1)	26 (0)	38 (0)						
Lake trout							2		L	1994	19	6.4 $\pm$ 0.5	-27.3 $\pm$ 1.8	6.7 $\pm$ 3.1
Mountain whitefish					4		12	6	M	1994	12	6.7 $\pm$ 0.6	-23.0 $\pm$ 1.5	4.3 $\pm$ 2.2
Mountain whitefish fry									MF	1994	3	4.3	-22.8	
Unidentified fish							5							
Chironomidae		*** <sup>3</sup>	***	***	7	16	18	36	C	1995	1	2.8	-24.5	
Tipulidae									T	1995	2	1.3–1.5	-24.2 to -22.8	2.0–5.5
Other Diptera		*	*											
Hemiptera			*											
Trichoptera	6	*	*	*		3	2	15			2		-26.2	
Plecoptera	1	*	*	*	7	1	2	6	P	1994	1	5.6	-23.8	
									P	1995	2	3.6–4.2	-24.6 to -26.9	
Ephemeroptera (adults)		*			12	7		3	EA	1994	1	4.9	-20.6	
Ephemeroptera (nymphs)	1		**	**		2		2	EN	1994	3	1.7 $\pm$ 0.3	-27.0 $\pm$ 3.0	
<i>G. lacustris</i>	1		*	*	10	10	13	30	G	1994	1	3.77	-23.9	
									G	1995	2	2.7–2.7	-23.9 to -24.1	5.2–9.9
Unidentified Copepoda			*											
<i>H. arcticus</i>					2	1			H	1994	1	5.6	-31.0	
									H	1995	3	2.5 $\pm$ 0.3	-31.2 $\pm$ 4.2	14.9 $\pm$ 8.6
Unidentified Cladocera								6						
<i>Alona</i> sp.		**	*											
<i>D. middendorffiana</i>					1	4			D	1994	1	0.68	-32.3	
Unsorted zooplankton									Z	1995	2	1.8	-31.1	6.5–11.3
Araneae			×					1						
Hydroachnidia		×	×								1		-33.1	
Sphaeriidae (Mollusca)			*	**										
Lymnaeidae (Gastropoda)	4		×		1		1		S	1995	1	1.4	-25.8	0.4
Oligochaeta			*				2		O	1995	1	1.2	-25.2	
Benthic algae									B1	1994	1	-1.34	-17.98	
									B2	1995	1	1.27	-24.05	

**Note:** For each taxon listed, the number of fish stomachs containing that taxon is listed. Occurrence by volume: more than 20% (\*\*\*), 10–20% (\*\*), 1–10% (\*), and less than 1% (×). The mountain whitefish stomach data from the 1930s are given on a volumetric basis. Only the samples analysed for OCs were also analysed for lipid content due to laboratory procedures.

<sup>a</sup>Data from McHugh 1940. The author separated the mountain whitefish into “less than 2 years old” and “2 years and older.”

<sup>b</sup>Data from Rawson (1939).



**Table 3.** Summary data for OC concentrations (ng-g wet weight<sup>-1</sup>) in Bow Lake biota.

Type	n	Toxaphene	ΣDDT <sup>a</sup>	ΣPCB <sup>b</sup>	ΣCHL <sup>c</sup>	Dieldrin	ΣHCH <sup>d</sup>
Lake trout	16	58.4±44.3	22.2±19.1	7.4±5.7	8.1±5.8	2.3±1.8	1.4±0.9
Mountain whitefish	12	13.5±8.4	8.1±6.1	2.8±2.8	2.5±1.8	0.7±0.5	0.6±0.4
<i>H. arcticus</i>	3	181.5±77.1	22.5±9.1	12.9±13.4	12.2±1.9	10.5±12.8	2.0±0.9
Mixed zooplankton	2	21.7–77.0	8.1–20.5	1.9–3.7	7.3–15.5	4.9–19.2	1.9–4.6
<i>G. lacustris</i>	2	44.7–45.3	8.9–9.1	3.7–3.7	4.0–5.5	3.2–4.5	1.1–2.1
Lymnaeidae	1	2.2	0.6	0.5	0.6	0.0	0.03
Tipulidae	2	3.2–9.9	1.8–2.4	2.4–3.5	1.8–2.6	0.0–0.2	0.3–0.5

**Note:** Average values and standard deviations are indicated for all taxa represented by three or more samples. Ranges indicate OC concentrations for taxa represented by two samples.

<sup>a</sup>ΣDDT is the sum of *p,p'*- and *o,p'*-DDT, *p,p'*- and *o,p'*-DDE, and *p,p'*- and *o,p'*-DDD.

<sup>b</sup>ΣPCB is the sum of 4/10, 7, 6, 8/5, 19, 18, 17, 24/27, 16/32, 26, 25, 31, 28, 33, 22, 45, 46, 52, 49, 47, 48, 44, 42, 41/71, 64, 40, 74, 70/76, 66, 95, 56/60, 91, 84/89, 101, 99, 83, 97, 87, 85, 136, 110, 82, 151, 144/135, 149, 118, 134, 114, 131, 146, 153, 132, 105, 141, 130/176, 179, 137, 138, 158, 178/129, 175, 187, 183, 128, 185, 174, 177, 171, 156, 201/157, 172/197, 180, 193, 191, 200, 170, 190, 198, 199, 196/203, 189, 208, 195, 207, 194, 205, 206, and 209.

<sup>c</sup>ΣCHL is the sum of chlordane-related congeners: heptachlor, heptachlor epoxide, *cis*-chlordane, *trans*-chlordane, *cis*-nonachlor, *trans*-nonachlor, nonachlor III, dihydroheptachlor compounds (C, C1, C2, C3), and octachlorane compounds (C4 and C5).

<sup>d</sup>ΣHCH is the sum of  $\alpha$ -HCH,  $\beta$ -HCH, and  $\gamma$ -HCH (lindane).

other invertebrates during the winter, which is up to 8 months long, whereas all fish sampled for stomach analyses were sampled during 2 months of the summer, when high silt concentrations make sight-dependent planktivory ineffective. The presence of copepod-transmitted parasitic cysts on many fish stomachs is further evidence that fish in Bow Lake feed on zooplankton.

In this study the isotopic composition of invertebrates varied over time due to changes in nutrient cycling and also with changes in life stage. For instance, *H. arcticus* apparently occupied different trophic levels in 1994 and 1995, as indicated by very different stable nitrogen isotope ratios (5.6‰ in 1994 and  $2.5 \pm 0.3$ ‰ in 1995). *Hesperodiptomus arcticus* are known to have a varied diet ranging from zooplankton to diatoms, depending on the abundance of prey (Paul and Schindler 1994). In addition, in subarctic lakes, the variation in zooplankton isotopic signals has been linked with seasonal variation in the isotopic signatures of sediment detritus and particulate organic matter (Gu et al. 1994). Another example included the 1994 adult mayfly (Ephemeroptera) sample that had a higher  $\delta^{15}\text{N}$  ratio than the mayfly nymphs. Mihuc and Toetz (1994) reported a similar shift in emerging subalpine chironomids: most species demonstrated heavier  $\delta^{15}\text{N}$  ratios as adults than as pupae or larvae, which was attributed to changing body composition. More stable isotope studies examining variation in aquatic pelagic and benthic invertebrates are needed to determine the extent of and the reasons for seasonal and developmental variations in isotopic signals.

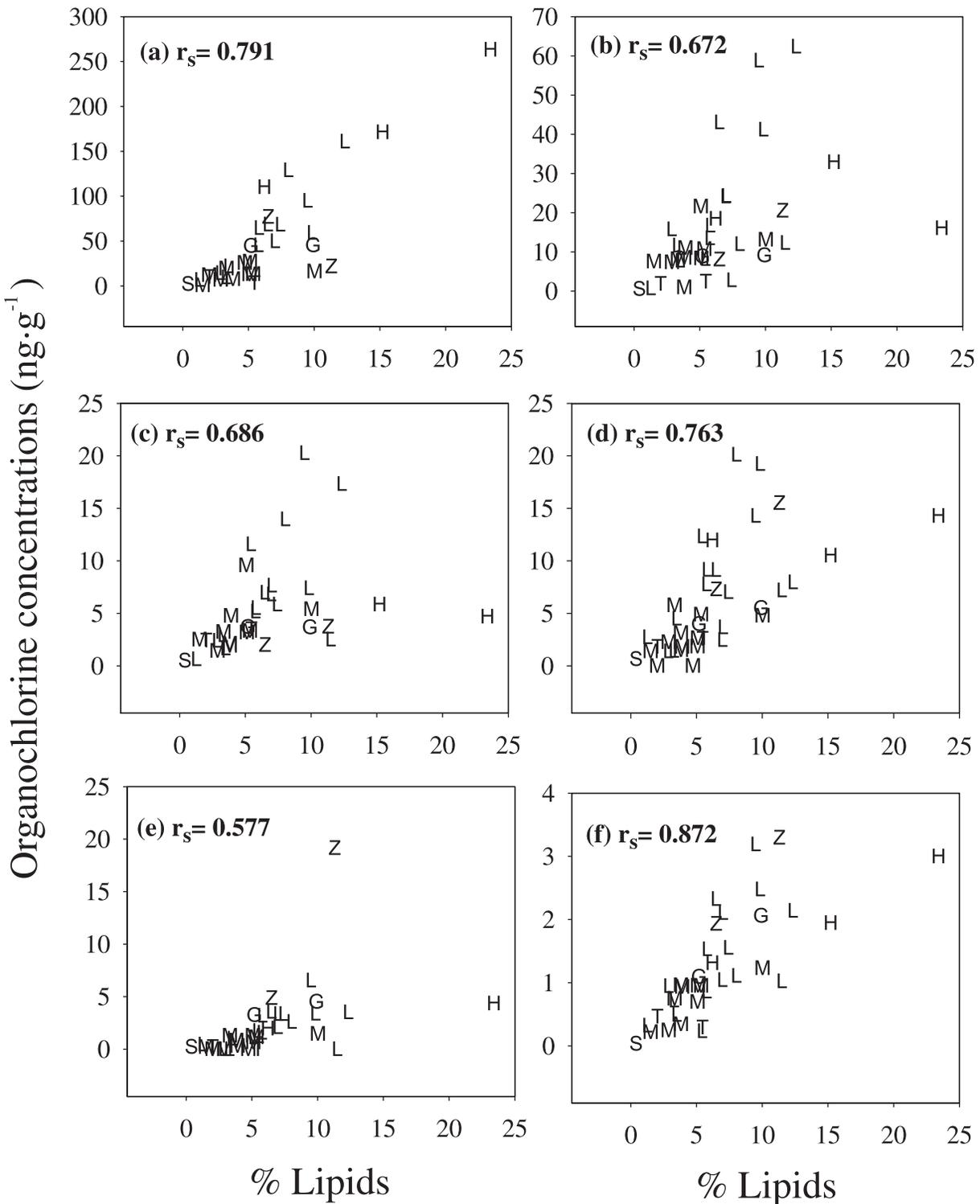
Lighter  $\delta^{13}\text{C}$  values in biota were positively correlated with higher lipid content. Studies have shown that lipid is isotopically lighter in  $\delta^{13}\text{C}$  than protein or carbohydrate, and organisms with higher lipids have lighter  $\delta^{13}\text{C}$  values (DeNiro and Epstein 1977). However, Kling et al. (1992) found little difference between  $\delta^{13}\text{C}$  values of whole and lipid-extracted samples of zooplankton (1.2‰) and salmonids (0.1–0.2‰) collected in an Arctic lake. Similarly, a study in Canadian Shield lakes has shown that  $\delta^{13}\text{C}$  values indicate feeding diversity in aquatic food webs but did not correlate with lipid content (estimated from C:N ratios) within organisms (France 1995). In Bow Lake, lipid content did not alter  $\delta^{13}\text{C}$  values enough to render stable carbon iso-

tope ratios unusable for determining food sources. Even after adjusting  $\delta^{13}\text{C}$  data for lipid effects (the lipid content of *H. arcticus* is  $14.9 \pm 8.6\%$ ), based on values (3% for zooplankton and 2% for other biota and fish) given in Kling et al. (1992), similar food chain relationships remained in Bow Lake. Furthermore, it is notable that while lipid content of *H. arcticus* varied, the  $\delta^{13}\text{C}$  values remained similar, indicating that the present variation in lipid content did not significantly influence the  $\delta^{13}\text{C}$  values of this zooplankton in Bow Lake.

### OCs in the food web

Stable isotope analyses, stomach contents, and the known community structure did not support the hypothesis that a long food chain was responsible for the high OC concentrations in the lake trout in Bow Lake. In addition, OC concentrations in biota were not related to their  $\delta^{15}\text{N}$  values. This finding is unusual because in other aquatic studies,  $\delta^{15}\text{N}$  measurements have been excellent predictors of biomagnification of OCs in food webs (Kidd et al. 1995, 1998b; Kiriluk et al. 1995; Kucklick et al. 1996). However, the aquatic food chains in other bioaccumulation studies were longer than in Bow Lake. Frequently, several species of forage fish and invertebrates provide intermediate steps between primary producers and predatory fish, leading to a wide range of  $\delta^{15}\text{N}$  values within the food web. For example, in the food web of Lake Laberge, Yukon Territory, the top predators, burbot (*Lota lota*) and lake trout, had  $\delta^{15}\text{N}$  values about 8–9‰ above benthic invertebrate values and 6–7‰ above zooplankton values, and there were four forage fish species with intermediate  $\delta^{15}\text{N}$  values (Kidd et al. 1995). In the pelagic food web of Lake Ontario, the  $\delta^{15}\text{N}$  values of lake trout were 6–8‰ higher than zooplankton values or amphipod values, while sculpin and alewife (*Alosa pseudoharengus*) values were 3–5‰ above the invertebrate values (Kiriluk et al. 1995). The pelagic-dominated food web of Lake Baikal (Kucklick et al. 1996) had three sculpin species with values 6‰ higher than zooplankton values, 4‰ higher than pelagic amphipod values, and 2‰ higher than benthic amphipod values. In the abbreviated food web of Bow Lake,  $\delta^{15}\text{N}$  values of fish were only an average of 4‰ higher than invertebrate values. In Bow Lake, other factors

**Fig. 3.** OC concentrations versus lipid content in Bow Lake. (a) Toxaphene; (b)  $\Sigma$ DDT; (c)  $\Sigma$ PCB; (d)  $\Sigma$ CHL; (e) dieldrin; (f)  $\Sigma$ HCH. The Spearman correlation coefficients ( $r_s$ ) are significant, with significance determined at  $\alpha = 0.05$  (Zar 1984). Codes are defined in Table 2.

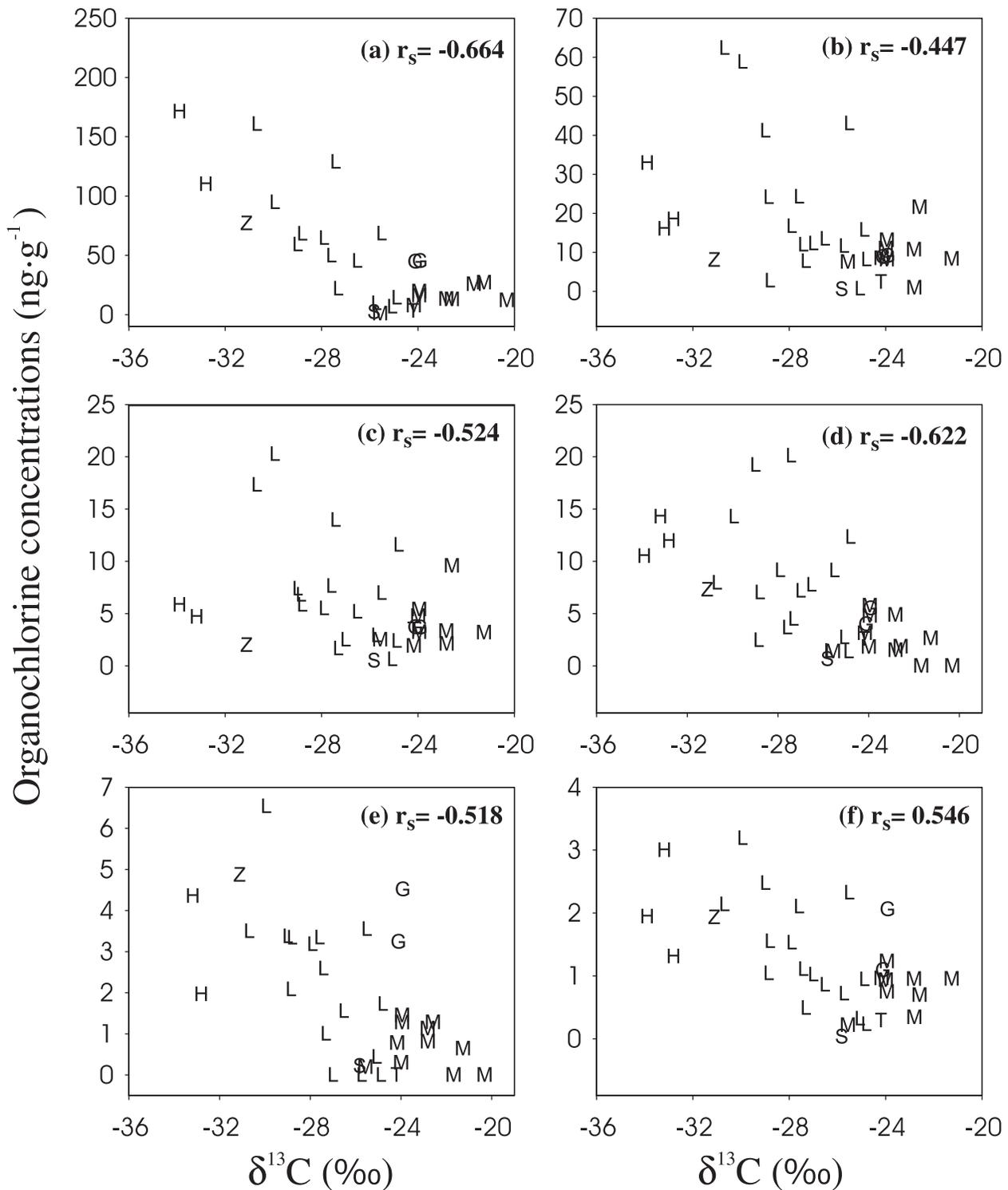


have influenced OC biomagnification to a greater extent because fish at a similar isotopic trophic level have considerably different OC concentrations.

In the Bow Lake food web,  $\delta^{13}\text{C}$  values correlated significantly with OC concentrations. Lake trout and other organ-

isms that had lighter  $\delta^{13}\text{C}$  signatures also had higher OC concentrations. No other published study has reported a significant correlation between  $\delta^{13}\text{C}$  and OC concentrations for a freshwater food web. Despite a 7‰ range in the  $\delta^{13}\text{C}$  values of lake trout from an arctic lake, no relationship between

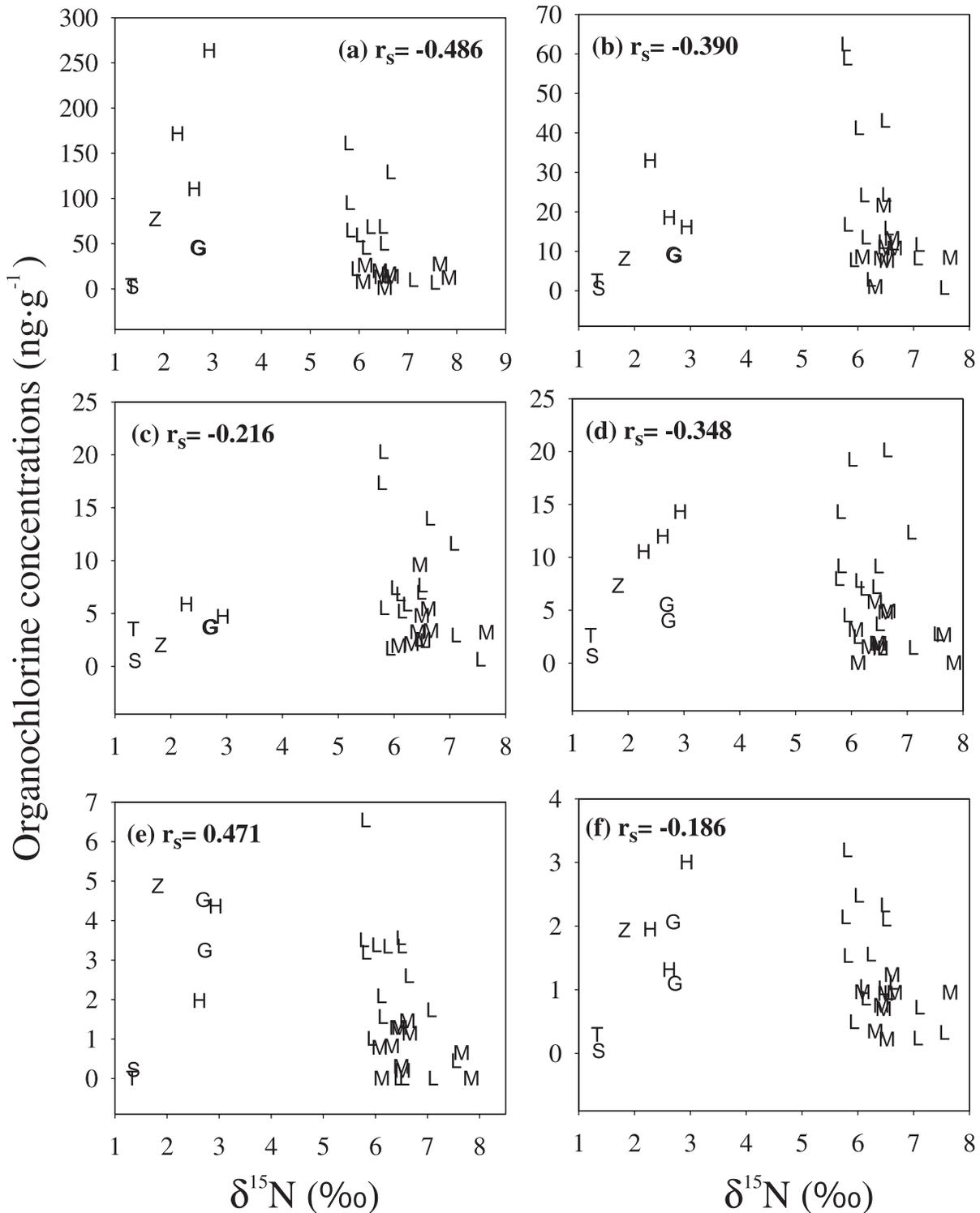
**Fig. 4.** OC concentrations versus  $\delta^{13}\text{C}$  values in Bow Lake biota. (a) Toxaphene; (b)  $\Sigma\text{DDT}$ ; (c)  $\Sigma\text{PCB}$ ; (d)  $\Sigma\text{CHL}$ ; (e) dieldrin; (f)  $\Sigma\text{HCH}$ . The Spearman correlation coefficients ( $r_s$ ) are significant, with significance determined at  $\alpha = 0.05$  (Zar 1984). Codes are defined in Table 2.



OC concentrations and carbon source was observed (Kidd et al. 1998a). Spies et al. (1989), however, reported a positive correlation between average  $\Sigma\text{DDT}$  and  $\delta^{13}\text{C}$  in two offshore marine food webs (southern California) with grouped inver-

tebrates (invertebrate predators and detritivores) and three species of fish. The changes in  $\delta^{13}\text{C}$  values (approximately 2.5‰ difference between the two sampling sites) resulted from more depleted isotopic values in feeding areas contam-

**Fig. 5.** OC concentrations versus  $\delta^{15}\text{N}$  values in Bow Lake biota. (a) Toxaphene; (b)  $\Sigma\text{DDT}$ ; (c)  $\Sigma\text{PCB}$ ; (d)  $\Sigma\text{CHL}$ ; (e) dieldrin; (f)  $\Sigma\text{HCH}$ . The Spearman correlation coefficients ( $r_s$ ) are not significant, with significance determined at  $\alpha = 0.05$  (Zar 1984). Codes are defined in Table 2.



inated by high sewage input. Similarly, the correlation between  $\delta^{13}\text{C}$  values and OC concentrations in the Bow Lake food web is due to resource partitioning, with the lighter carbon isotope signatures indicative of a more pelagic diet for

lake trout when compared with mountain whitefish. As a result, fish in Bow Lake relying on pelagic carbon were more at risk of accumulating OCs than those relying on benthic carbon.

There were some correlations between toxaphene,  $\Sigma$ PCB, and  $\Sigma$ CHL and lake trout age and weight, which suggests that the duration of exposure to these compounds may be important and could contribute towards the increased concentrations in adult lake trout. Similar relationships have been seen in salmonids in other ecosystems (Borgmann and Whittle 1992; Larsson et al. 1996; Kidd et al. 1998a). Significant correlations were also observed between lipids and OC concentrations within lake trout, indicating that both weight and lipid were important in predicting concentrations of these contaminants. Higher lipid content has been linked to pelagic diet (as indicated by  $\delta^{13}\text{C}$ ), so the OC concentrations in lake trout were probably due to the combination of dietary habits and duration of exposure. While age and weight of mountain whitefish were more significantly correlated than in lake trout, concentrations of OCs were not significantly correlated with lipid, size, or age of this species.

In Bow Lake, which receives most of its water from glaciers and is at a relatively high elevation, organisms must contend with an unproductive environment, low nutrients, and cold temperatures year-round (Campbell 1997). Phytoplankton and zooplankton, especially diatoms (Shifrin and Chisholm 1981) and copepods (Schindler et al. 1971), often become more lipid rich in cold surroundings or nutrient-poor environments. This may lead to increased OC burdens at lower trophic levels, particularly in lipid-rich copepods and phytoplankton. In a laboratory experiment, silicon-limited diatoms (*Nitzschia* sp.) exposed to  $^3\text{H}$ -labelled tetrachlorodibenzofurans (TCDF) were shown to have higher lipids and correspondingly higher concentrations of OCs than diatoms grown in nutrient-rich cultures (Kilham 1998). When the TCDF-exposed silicon-limited diatoms were fed to *Daphnia magna*, the zooplankton exhibited higher TCDF concentrations than zooplankton fed non-nutrient-limited diatoms (Kilham 1998), indicating that nutrient limitation at the base of the food web can affect the uptake of contaminants at higher trophic levels. In another recent study, the plankton in an oligotrophic Swedish lake had higher lipid content and higher PCB concentrations than the plankton in a eutrophic lake (Larsson et al. 1998). They also discovered that the highest seasonal PCB concentrations in the plankton from the oligotrophic lake coincided with peak dominance of lipid-rich calanoid copepods in the zooplankton community. The lipid content in biota cannot be ignored when studying the fate of OCs in whole food webs, especially in oligotrophic ecosystems.

The high OC concentrations (especially toxaphene) in the zooplankton *H. arcticus* may be the result of either direct absorption or ingestion. The small body size (<2 mm in length) and high lipid content of *H. arcticus* may increase adsorption of OCs from the surrounding water column. Deposition of OCs increases with higher elevations in the mountains (Blais et al. 1998), and glaciers in the Rocky Mountains have high concentrations of OCs that were deposited in the past when OC compounds were in more widespread use (Donald et al. 1999). Despite their hydrophobic nature, a considerable proportion of OCs in the glacial inflow to Bow Lake are in dissolved form, probably because glacial silt has little affinity for OCs (Dr. J. Blais, Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada, personal communication). Marine copepods exposed to  $^{14}\text{C}$ -

labelled DDT in water had a significant portion (28–80%) of total body burden DDT in their extractable lipids (Harding and Vass 1977). This matter is currently being investigated by our research group.

Alternatively, a more speculative hypothesis is that the copepods are ingesting glacial silt that has sorbed OCs from glacial sources. In Bow Lake, high proportions of glacial silt are found in copepod fecal pellets in bottom sediments (Smith and Syvitski 1982), and *H. arcticus* have been found to be important in the sedimentation processes (Smith and Syvitski 1982). If glacial silt from Bow Glacier is a source of contaminants, then *H. arcticus* may be bioaccumulating OCs to higher than expected concentrations due to their high lipid content and consumption of these particulates.

In the simple aquatic community of Bow Lake, bioaccumulation patterns for OCs in the food web did not follow the patterns of stable isotope/OC studies of more complex food webs. Food chain length alone was insufficient to explain why lake trout had higher toxaphene concentrations than the same species from other nearby lakes. Results suggest that OCs were more efficiently transferred in pelagic than in benthic food chains due to the higher lipid content of pelagic organisms. The highest concentrations of OCs were found in lipid-rich pelagic copepods rather than in fish. Dietary patterns (as indicated by stable carbon isotope ratios) and lipid content were more important than trophic-related biomagnification for explaining OC concentrations in lake trout in the short food web of Bow Lake.

## Acknowledgements

This research was supported by a Natural Sciences and Engineering Research Council of Canada strategic grant to D.W. Schindler, a Canadian Circumpolar/Boreal Research grant to L.M. Campbell and D.W. Schindler, a Friends of Banff National Park grant, and a Natural Sciences and Engineering Research Council of Canada PG-A scholarship to L.M. Campbell. Dr. G. Stern provided the HREC/NIMS toxaphene analyses for this project. We thank B. Rosenberg, B. Ross, and D. Savoie for their technical expertise at the Freshwater Institute (Winnipeg, Man.). R. Crosley and J. Syrgiannis (Environment Canada, Regina, Sask.) assisted with field work in 1994, while M. Campbell, J. Clare, J. Hiebert, S. McNaught, R. Thacker, and F. Wilhelm (University of Alberta, Edmonton, Alta.) provided field assistance in 1995. M. Agbeti (University of Alberta) assisted with the phytoplankton identification and P. Aku (Glenora Fisheries Station, Picton, Ont.) did the fish otolith ageing. A. Shostak (University of Alberta) identified the parasite cysts on lake trout stomachs. R.E. Hecky (Environment Canada, Burlington, Ont.) provided an early review of the manuscript.

## References

- Anthony, D.D. 1967. Taxonomy and ecology of *Diphylllobothrium* in Alberta and British Columbia. Ph.D. thesis, University of Alberta, Edmonton, Alta.
- Blais, J.M., Schindler, D.W., Muir, D.C.G., Kimpe, L.E., Donald, D.B., and Rosenberg, B. 1998. Accumulation of persistent organochlorines in mountains of western Canada. *Nature* (Lond.), **395**: 585–588.

- Borgmann, U., and Whittle, D.M. 1992. Bioenergetics and PCB, DDE, and mercury dynamics in Lake Ontario lake trout (*Salvelinus namaycush*): a model based on surveillance data. *Can. J. Fish. Aquat. Sci.* **49**: 1086–1096.
- Campbell, L.M. 1997. The use of stable isotope ratios to discern organochlorine bioaccumulation patterns in a sub-alpine Rocky Mountain food web. M.Sc. thesis, University of Alberta, Edmonton, Alta. ISBN 0–612–22581-X.
- DeNiro, M.J., and Epstein, S. 1977. Mechanism of carbon isotope fractionation associated with lipid synthesis. *Science (Washington, D.C.)*, **197**: 261–263.
- Donald, D.B. 1987. Assessment of the outcome of eight decades of trout stocking in the mountain national parks, Canada. *N. Am. J. Fish. Manage.* **7**: 545–553.
- Donald, D.B., Bailey, R.C., Crosley, R., Muir, D., Shaw, P., and Syrgiannis, J. 1993. Polychlorinated biphenyls and organochlorine pesticides in the aquatic environments along the Continental Divide region of Alberta and British Columbia. Inland Waters Directorate (Environment Canada) report to Parks Canada, Regina, Sask.
- Donald, D.B., Stern, G.A., Muir, D.C.G., Fowler, B.R., Miskimmin, B.M., and Bailey, R. 1998. Chlorobornanes in water, sediment, and fish from toxaphene treated and untreated lakes in western Canada. *Environ. Sci. Technol.* **32**: 1391–1397.
- Donald, D.B., Syrgiannis, J., Crosley, R.W., Holdsworth, G., Muir, D.C.G., Rosenberg, B., Sole, A., and Schindler, D.W. 1999. Delayed deposition of organochlorine pesticides at a temperate glacier. *Environ. Sci. Technol.* **33**: 1794–1798.
- Evans, M.S., Noguchi, G.E., and Rice, C.P. 1991. The biomagnification of polychlorinated biphenyls, toxaphene and DDT compounds in a Lake Michigan offshore food web. *Arch. Environ. Contam. Toxicol.* **20**: 87–93.
- France, R.L. 1995. Carbon isotopic variability in the composite pelagic foodweb of four oligotrophic lakes: feeding diversity or metabolic fractionations? *J. Plankton Res.* **17**: 1993–1997.
- Gu, B., Schell, D.M., and Alexander, V. 1994. Stable carbon and nitrogen isotopic analysis of the plankton food web in a subarctic lake. *Can. J. Fish. Aquat. Sci.* **51**: 1338–1344.
- Gu, B., Schell, D.M., Huang, X., and Yie, F. 1996. Stable isotope evidence for dietary overlap between two planktivorous fishes in aquaculture ponds. *Can. J. Fish. Aquat. Sci.* **53**: 2814–2818.
- Harding, G.C.H., and Vass, W.P. 1977. Uptake from sea water and clearance of  $^{14}\text{C-p,p'-DDT}$  by the marine copepod *Calanus finmarchicus*. *J. Fish. Res. Board Can.* **34**: 177–182.
- Hecky, R.E., and Hesslein, R.H. 1995. Contributions of benthic algae to lake food webs as revealed by stable isotope analyses. *J. North Am. Benthol. Soc.* **14**: 631–653.
- Hesslein, R.H., Hallard, K.A., and Ramlal, P. 1993. Replacement of sulfur, carbon and nitrogen in tissues of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by  $\delta^{34}\text{S}$ ,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ . *Can. J. Fish. Aquat. Sci.* **50**: 2071–2076.
- Kidd, K.A., Schindler, D.W., Hesslein, R.H., and Muir, D.C.G. 1995. Correlation between stable nitrogen isotope ratios and concentrations of organochlorines in biota from a freshwater food web. *Sci. Total Environ.* **160/161**: 381–390.
- Kidd, K.A., Hesslein, R.H., Ross, B.J., Koczanski, K., Stephens, G.R., and Muir, D.C.G. 1998a. Bioaccumulation of organochlorines through a remote freshwater food web in the Canadian Arctic. *Environ. Pollut.* **102**: 91–103.
- Kidd, K.A., Schindler, D.W., Hesslein, R.H., and Muir, D.C.G. 1998b. Effects of trophic position and lipid on organochlorine concentrations in fishes from subarctic lakes in Yukon Territory. *Can. J. Fish. Aquat. Sci.* **55**: 869–881.
- Kilham, S.S. 1998. Effects of physiological state on the bioaccumulation of toxic chemicals in algae and their transfer to zooplankton. *Verh. Int. Ver. Limnol.* **26**: 1734–1736.
- Kiriluk, R.M., Servos, M.R., Whittle, D.M., Cabana, G., and Rasmussen, J.B. 1995. Using ratios of stable nitrogen and carbon isotopes to characterize the biomagnification of DDE, mirex, and PCB in a Lake Ontario pelagic food web. *Can. J. Fish. Aquat. Sci.* **52**: 2660–2674.
- Kling, G.W., Fry, B., and O'Brien, W.J. 1992. Stable isotopes and planktonic trophic structure in Arctic lakes. *Ecology*, **73**: 561–566.
- Kucklick, J.R., Harvey, H.R., Ostrom, P.H., Ostrom, N.E., and Baker, J.E. 1996. Organochlorine dynamics in the pelagic food web of Lake Baikal. *Environ. Toxicol. Chem.* **15**: 1388–1400.
- Larsson, P., Backe, C., Bremle, G., Eklöv, A., and Okla, L. 1996. Persistent pollutants in a salmon population (*Salmo salar*) of the southern Baltic Sea. *Can. J. Fish. Aquat. Sci.* **53**: 62–69.
- Larsson, P., Okla, L., and Cronberg, G. 1998. Turnover of polychlorinated biphenyls in an oligotrophic and an eutrophic lake in relation to internal lake processes and atmospheric fallout. *Can. J. Fish. Aquat. Sci.* **55**: 1926–1937.
- McHugh, J.L. 1940. Food of the Rocky Mountain whitefish *Prosopium williamsoni* (Girard). *J. Fish. Res. Board Can.* **5**: 131–137.
- Mihuc, T., and Toetz, D. 1994. Determination of diets of alpine aquatic insects using stable isotopes and gut analysis. *Am. Midl. Nat.* **131**: 146–155.
- Miskimmin, B.M., Muir, D.C.G., Schindler, D.W., Stern, G.A., and Grift, N.P. 1995. Chlorobornanes in sediments and fish thirty years after toxaphene treatment of lakes. *Environ. Sci. Technol.* **29**: 2490–2495.
- Paul, A.J., and Schindler, D.W. 1994. Regulation of rotifers by predatory calanoid copepods (subgenus *Hesperodiptomus*) in lakes of the Canadian Rocky Mountains. *Can. J. Fish. Aquat. Sci.* **51**: 2520–2528.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**: 293–320.
- Rau, G.H., and Anderson, N.H. 1981. Use of  $^{13}\text{C}/^{12}\text{C}$  to trace dissolved and particulate organic matter utilization by populations of an aquatic invertebrate. *Oecologia*, **48**: 19–21.
- Rawson, D.S. 1939. A biological survey and recommendations for fisheries management in waters of the Banff National Park. Department of Mines and Resources, National Parks Bureau, Ottawa, Ont.
- Schindler, D.W., Clark, A.S., and Gray, J.R. 1971. Seasonal caloric values of freshwater zooplankton, as determined with a Phillipson bomb calorimeter modified for small samples. *J. Fish. Res. Board Can.* **28**: 559–564.
- Shifrin, N.S., and Chisholm, S.W. 1981. Phytoplankton lipids: interspecific differences and effects of nitrate, silicate and light-dark cycles. *J. Phycol.* **17**: 374–384.
- Smith, N.D., and Syvitiski, J.P.M. 1982. Sedimentation in a glacier-fed lake: the role of pelletization of deposition of fine-grained suspensates. *J. Sediment. Petrol.* **52**: 503–513.
- Spies, R.B., Kruger, H., Ireland, R., and Rice, D.W., Jr. 1989. Stable isotope ratios and contaminant concentrations in a sewage-distorted food web. *Mar. Ecol. Prog. Ser.* **54**: 157–170.
- Zar, J.H. 1984. *Biostatistical analysis*. Simon & Schuster Co., Englewoods Cliffs, N.J.