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Pelagic Food Chain Structure in Ontario Lakes: A Determinant of Mercury Levels in Lake Trout (*Salvelinus namaycush*)

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The trophic structure of pelagic communities in glaciated regions is highly variable due to restricted dispersal of glacial relict taxa and recent species introduction. Much of the between-lake variation in Hg in lake trout (*Salvelinus namaycush*) flesh from the St. Lawrence system (non-point-source contaminated lakes), which spans more than two orders of magnitude (0.03–3.96 µg/g), results from differences in the length of pelagic food chains. Hg levels from the longest food chains where pelagic forage fish and the crustacean *Mysis relicta* were present were about 3.6-fold higher than those from the shortest food chains where these last two trophic components were missing. A lack of correlation between Hg levels in small-mouth bass (*Micropterus dolomieu*), which do not exploit the pelagic food chain, and the length of the pelagic food chain confirmed that the positive relationship observed in lake trout could not be attributed to the confounding effect of some physicochemical factors covarying with our pelagic food chain classification. Our results confirmed that the food chain biomagnification model developed by Rasmussen et al. (1990. *Can. J. Fish. Aquat. Sci.* 47: 2030–2038) to predict PCB levels in lake trout can also be applied to Hg biomagnification.

La structure trophique des communautés pélagiques dans les régions de glaciation est extrêmement variable à cause de la dispersion restreinte de taxons reliques de l'ère glaciaire et de l'introduction d'espèces récentes. Une bonne partie de la variation entre les lacs de la concentration de Hg dans la chair du touladi (*Salvelinus namaycush*) dans le réseau du Saint-Laurent (lacs qui ne sont pas soumis à des sources ponctuelles de pollution), qui couvre plus de deux ordres de grandeur (0,03–3,96 µg/g) provient de différences dans la longueur des chaînes trophiques pélagiques. Les concentrations de Hg dans les chaînes les plus longues, où étaient présents des poissons fourrages pélagiques et le crustacé *Mysis relicta*, étaient environ 3,6 fois plus élevées que celles des chaînes plus courtes où manquaient au moins deux composantes trophiques. L'absence de corrélation entre les teneurs de Hg de l'achigan à petite bouche (*Micropterus dolomieu*), qui n'exploite pas la chaîne trophique pélagique, et la longueur de la chaîne pélagique confirme que la relation positive observée chez le touladi ne peut être attribuée à l'effet trompeur de certains facteurs physico-chimiques qui varient en même temps que notre classification de la chaîne trophique pélagique. Notre résultat a confirmé que le modèle de bioamplification de la chaîne trophique mis au point par Rasmussen et al. (1990. *J. can. sci. halieut. aquat.* 47 : 2030–2038) pour prédire les concentrations de BPC chez le touladi peuvent aussi s'appliquer à la bioamplification du Hg.

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Uptake from food and water have been shown to be two complementary routes through which contaminants such as heavy metals and organic chemicals accumulate in aquatic organisms (reviewed by Biddinger and Gloss 1984). While bioconcentration from water appears to be the predominant pathway for bioaccumulation of a large number of chemicals (Biddinger and Gloss 1984), uptake from food has also been shown to be important for a number of persistent compounds (e.g., DDT: Macek and Korn 1970; PCBs: Thomann 1981; Sodergren 1984; selenium; Sandholm et al. 1973; Bertram and Brooks 1986; Hg:

Boudou et al. 1979). The bioaccumulation of these often toxic substances from food implies that they become biomagnified along the food chain, reaching high concentrations in top consumers such as large predators, including man. While this popular concept is by no means recent (Woodwell et al. 1967; Macek and Korn 1970), some problems have so far limited its role in the development of a predictive theory of the ecological fate of biomagnifying contaminants (but see Thomann 1981).

For example, predators generally have higher contaminant concentrations than their potential prey, as predicted

by the biomagnification hypothesis (e.g., PCBs: Niethammer et al. 1984; Hg: Ratkowsy et al. 1975; Philips et al. 1980; Akielaszek and Haines 1981; Wren et al. 1983). However, it has been suggested that other confounding factors, such as differences in size, age, or metabolic rate between predator and prey, may well be causing this apparent biomagnification (Moriarty 1975; Biddinger and Gloss 1984).

A further complication resides in the inherent difficulty in defining concepts such as "food chain" and "trophic level" in measurable terms (Peters 1991). This last problem becomes more apparent when one is concerned with intraspecific variation in trophic level rather than interspecific predator/prey comparisons. For example, while it can be safely argued that adult pike and zooplankton differ in trophic level, it is much more difficult to establish that pike in one lake occupy a trophic level higher than in another lake.

Rasmussen et al. (1990) attempted to overcome these problems in their study of PCB concentration in lake trout (*Salvelinus namaycush*) from 81 Canadian Precambrian Shield lakes. They showed that intraspecific biogeographical variation in the length of the food chain leading to these pelagic predators determined their white muscle PCB concentration. Trophic level of lake trout was operationally defined by the presence or absence of intermediate species (the crustacean *Mysis relicta* and pelagic forage fish such as smelt and coregonids) trophically linking lake trout to small zooplankton. PCB concentrations were found to approximately triple with each additional intermediate trophic step (from lakes free of *Mysis* and pelagic forage fish, through *Mysis*-free lakes containing pelagic forage fish, to lakes containing both *Mysis* and pelagic forage fish).

In principle, this predictive model of the fate of PCBs in lake communities based on a simplified description of the pelagic food chain should be applicable to other potentially biomagnifying persistent chemicals. Here, we test the Rasmussen et al. (1990) model using Hg concentrations in lake trout from Ontario lakes not subjected to point-source contamination. We predict that Hg concentration in lake trout should parallel that of PCBs, increasing from lakes where lake trout are mostly limited to eating zooplankton to lakes with the longest food chains (lakes containing both *Mysis* and pelagic forage fish).

Smallmouth bass (*Micropterus dolomieu*) can be found in the three trophic classes of lakes we investigated and is a predominantly littoral species feeding mainly on crayfish and cyprinids (Scott and Crossman 1973). Being essentially "disconnected" from the pelagic food chain, smallmouth bass represent a good control for the effect of some physicochemical variable(s) influencing Hg levels in fish independently of food chain length. Lack of a relationship between the length of the pelagic food chain and Hg in smallmouth bass, in conjunction with a positive relationship in lake trout, would, therefore, further support the importance of food chain biomagnification per se in explaining variation in Hg in fish. It would also weaken the possibility that a positive relationship between Hg concentration and trophic level in lake trout could be attributed to the spurious effect of some lake characteristic(s) covarying with the length of the pelagic food chain.

Physicochemical variables related to lake morphometry (maximum depth: Wren and McCrimmon 1983; lake area: Wren et al. 1991) and water chemistry (e.g., pH: Wren and McCrimmon 1983; Suns and Hitchins 1990; McMurtry et al.

1989; Wren et al. 1991; calcium: Wren et al. 1991; alkalinity: Swain and Helwig 1989) have been shown to influence Hg levels in freshwater fish. Such factors could either obscure trophic level effects on Hg in fish or create a spurious relationship between trophic level and Hg concentration in fish by covarying with fish trophic level. Here, we examined potential effects of lake area and maximum depth, Secchi depth, pH, and conductivity on Hg concentration in lake trout and smallmouth bass.

Methods

The fish Hg database was obtained from the Sports Fish Contaminants Monitoring Program of the Water Resources Branch, Ontario Ministry of the Environment (MOE). Total Hg was analyzed by flameless atomic absorption spectrophotometry with a minimum detection limit of 0.01 ppm (MOE 1981). Recent work (Grieb et al. 1990) has shown that in fish, practically all Hg is in the form of methyl mercury and therefore, total Hg essentially measures methyl mercury. Fish were homogenized followed by oxidation with hydrogen peroxide and digestion with a solution of 2:1 sulfuric acid at 60°C. Further technical details pertaining to sample handling are in MOE (1981). We set an arbitrary minimum sample size of 10 individuals before including any species in the study. Fish Hg measurements were reported over the period 1975–84 and data were pooled in the few cases where information from more than one year was available.

Data on lake morphometry and physicochemical variables were obtained from the computerized data inventory of the Ontario Ministry of Natural Resources (MNR), the Ontario Acid Sensitivity Database (MOE) (Neary et al. 1990), and Dadswell (1974).

The food chain classification was based on the presence or absence of pelagic forage fish species (smelt, ciscoes, lake and round whitefish, alewife, and ninespine stickleback) as determined from a published database (MNR). The presence or absence of *Mysis* was determined from Dadswell's (1974) extensive monograph. In those lakes not studied by Dadswell, the presence/absence of *Mysis* was determined from a map showing the maximum extent of glacial lakes (Douglas 1970). Dadswell found *Mysis* to be absent from only about 10% of lakes situated within the glacial-lake boundaries in Ontario. Thus, there is a slight chance of classification error among the lakes classified as *Mysis* positive on the basis of glacial lake maps. He also never found *Mysis* in southern Ontario lakes shallower than 18 m (maximum depth), and we accordingly classified such lakes as *Mysis* free.

Following Rasmussen et al. (1990), lakes were classified according to the number of intermediate trophic levels linking zooplankton to lake trout. These intermediates include the opossum shrimp *M. relicta* and pelagic fish such as coregonids (*C. artedi* and *C. rotundiformis*), rainbow smelt, alewife, and ninespine stickleback. We refer to lakes without *Mysis* or pelagic forage fish as Class 1, lakes with pelagic forage fish but no *Mysis* as Class 2, and lakes with both *Mysis* and pelagic forage fish as Class 3. While we do not claim to know the exact trophic relationships within the pelagic communities of individual lakes, a number of studies on feeding relationships in lakes have supported this classification. Studies on adult lake trout from Class 3 lakes

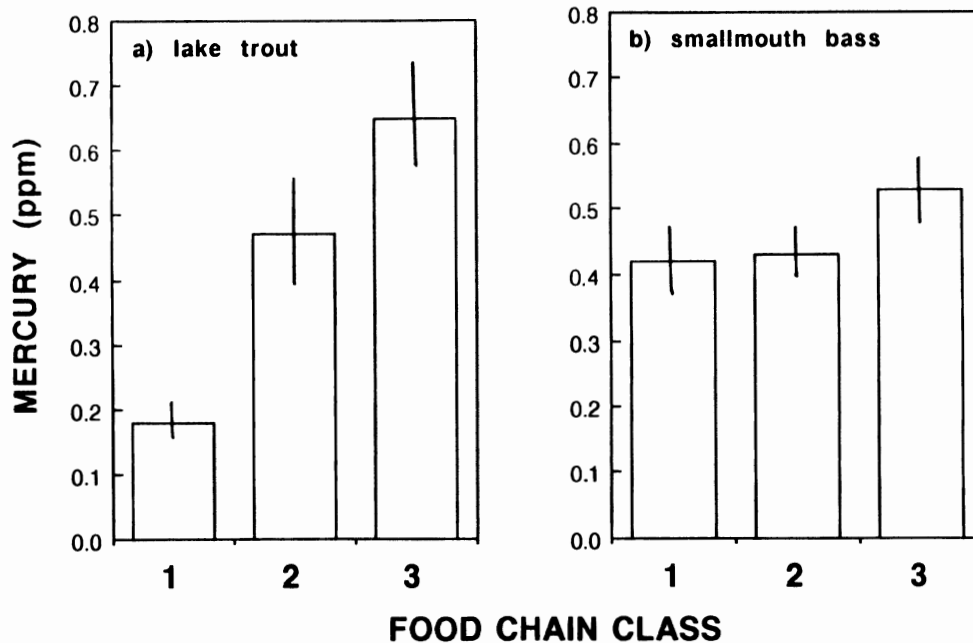


FIG. 1. Geometric mean (± 1 SE) concentration in the muscle (a) lake trout and (b) smallmouth bass in relation to the trophic structure of the pelagic community. Class 1 lakes contain no *Mysis* or pelagic forage fish; Class 2 lakes contain pelagic forage fish but no *Mysis*; Class 3 lakes contain both *Mysis* and pelagic forage fish.

have shown them to be piscivorous, feeding mainly on smelt, ciscoes, alewife, and whitefish (Dymond 1928, Rawson 1930, 1951, 1961; Van Oosten and Deason 1937; Dryer et al. 1965; Scott and Crossman 1973; McCrimmon et al. 1983). The pelagic forage fish eaten by lake trout in these lakes (mainly smelt, coregonids, and alewife) feed heavily on *Mysis* (Rawson 1951; Wells 1968; Scott and Crossman 1973), and *Mysis* prey on zooplankton and some large phytoplankton (Carpenter et al. 1974; Martinez and Bergersen 1989). When *Mysis* is absent (Class 2 lakes), the pelagic forage fish utilize mostly zooplankton (Price 1963).

If both *Mysis* and pelagic forage fish are absent (Class 1 lakes), lake trout feed exclusively on zooplankton and benthic invertebrates for a large part of the year because for most of their growing season, they are isolated from inshore forage fish by a thermal barrier (Martin 1954, 1966; Monroe and Hicks 1984). We hypothesized that if variation in food chain length is responsible for much of the variation in lake trout Hg levels, the lowest Hg concentration should be found where *Mysis* and pelagic forage fish are absent (Class 1) and the highest levels where both trophic links are present (Class 3).

In contrast with lake trout, smallmouth bass is a littoral species that feeds very little, if at all, on pelagic coregonids and smelt (Doan 1940; Westman and Westman 1949; Emery 1975). We therefore used smallmouth bass as a control for the potential confounding effect of some physicochemical factors influencing Hg levels in fish that could also fortuitously covary with the length of the pelagic food chain. While we did not expect to see an effect of pelagic food chain structure on Hg levels in bass, we did expect to find some correspondence between Hg levels in lake trout and bass, reflecting the extent to which the two species are influenced by lake-specific variation in the overall exposure to Hg. Thus, this two-species analysis will allow us to, in effect, partition the variation in lake trout Hg level explained by food

chain structure from the variation associated with lake-specific contamination factors, even though the latter factors are not yet explicitly modelled.

All statistical analyses were based on lake averages of mercury concentration and fish weight. We investigated the effects fish weight, trophic level, and physicochemical variables (such as area and maximum depth, pH, conductivity, and Secchi depth) on Hg in lake trout and smallmouth bass through multiple regression and analysis of variance (ANOVA) (Draper and Smith 1981). Logarithmic transformations were used for all these variables (except pH) to normalize the data and reduce heteroscedasticity. The statistical significance of each parameter in a multiple regression model was tested using *t*-tests.

Results

Hg levels in Ontario lake trout increased with the length of the pelagic food chain (ANOVA, $P < 0.001$) (Table 1; Fig. 1a). Trout from lakes with the shortest food chains (Class 1 lakes) had the lowest Hg levels (geometric mean Hg = 0.18 $\mu\text{g/g}$), followed by lakes with food chains of intermediate length (Class 2 lakes; geometric mean Hg = 0.47 $\mu\text{g/g}$). Trout from lakes with the longest food chains (Class 3 lakes) had the highest Hg levels (geometric mean Hg = 0.65 $\mu\text{g/g}$). The relative increase in Hg levels attributed to the presence of forage fish in the pelagic food chain (Class 2/Class 1: 2.6-fold biomagnification factor) was therefore about twice as important as that attributed to the presence of *Mysis* in food chains containing pelagic forage fish (Class 3/Class 2: 1.4-fold biomagnification).

Multiple regression showed that three variables, average body weight, food chain class, and maximum lake depth, were found to explain a significant (*t*-test, $P < 0.05$) proportion of the total variance in Hg in lake trout. Other variables tested were not significant when subsequently added and

TABLE 1. Hg content of lake trout and smallmouth bass from Ontario Lakes with different pelagic communities. For each lake, the following physicochemical variables are listed: latitude (lat), longitude (long), lake area, maximum depth (Z_{max}), pH, conductivity (cond.), and Secchi depth.

Lake trout												
Lake	Lat.	Long.	Area (ha)	Z_{max} (m)	pH	Cond. (μ S/cm)	Secchi (m)	<i>Mysis</i> ^a	Forage fish ^b	Weight (g)	Hg (μ g/g)	<i>n</i>
<i>Class 1 (Mysis and pelagic forage fish absent)</i>												
Bear	45°20'	78°42'	95	36.6	6.1	34	7.9	—*	—	402	0.28	22
Beaver	46°57'	80°51'			6.9	58		—*	—	109	0.05	49
Big Porcupine	45°27'	78°37'	235	31.7	6.0	27	7.6	—*	—	410	0.18	24
Blue	49°10'	81°15'						—*	—	744	0.06	14
Blue Chalk	45°12'	78°56'	50	22.0	6.9	29	6.4	—*	—	1309	0.24	19
Bluesucker	47°10'	80°37'	144	21.4	5.1	36	8.8	—*	—	1275	0.23	18
Bonnechere	45°28'	78°35'	104	22.0	5.6	27	6.7	—*	—	542	0.33	26
Camp	45°26'	78°55'	189	42.7	6.2	32	6.2	—	—	396	0.15	21
Canisbay	45°34'	78°35'	152	25.9	6.3	34	6.4	—*	—	1440	0.64	11
Centre	45°01'	78°03'	144	17.7			3.1	—*	—	1325	0.49	10
Eels	44°54'	78°08'	945	29.9	6.7		3.3	—	—	488	0.09	13
Fletcher	45°21'	78°47'	256	23.2	6.1	34	3.9	—*	—	860	0.25	21
Iron	47°04'	79°55'	72	27.0	5.7	42	10.3	—*	—	426	0.03	44
Kimball	45°21'	78°41'	212	67.1	6.3	30	9.1	—*	—	690	0.32	36
Kukagami	46°44'	80°33'			5.8	59		—*	—	779	0.05	24
Laundrie	47°07'	80°52'	374	20.4	5.2	33	9.3	—*	—	324	0.14	109
Livingstone	45°22'	78°43'	189	36.6	6.5	37	4.6	—	—	1392	0.38	22
Louisa	45°28'	78°29'	490	61.0	6.1	32	7.7	—	—	540	0.44	30
McCraney	45°34'	78°54'	361	61.3				—*	—	505	0.35	16
McFadden	45°20'	78°51'	54	30.5	6.5	37	7.2	—*	—	901	0.18	22
McGarvey	45°26'	78°34'	70	20.0	5.9	23	3.6	—*	—	2533	0.35	12
Miskwabi	45°03'	78°19'	264	44.2				—*	—	867	0.13	20
Nunikani	45°12'	78°44'	116	24.1	6.2	29	7.2	—*	—	670	0.17	23
Pedro	46°55'	80°32'	64	11.0	5.9	39	5.3	—*	—	782	0.03	58
Percy	45°12'	78°22'	596		7.4	47	3.0	—*	—	502	0.39	14
Pilgrim	47°11'	80°41'	123	25.0	5.2	32	8.0	—*	—	383	0.06	38
Red Chalk	45°11'	78°57'	58	32.0		30	6.1	—*	—	1195	0.22	20
RedPine	45°12'	78°42'	380	41.5	6.4	32	7.5	—*	—	805	0.18	18
Regan	47°14'	80°50'	122	38.0	6.2	43		—*	—	463	0.04	36
Round Island	45°44'	78°12'	156	17.0	6.4	35	4.5	—*	—	973	0.54	15
Saymo	46°59'	83°31'			6.7	38		—*	—	833	0.39	13
Seagram	47°06'	80°32'	102	19.0	5.1	36	6.5	—*	—	706	0.15	15
Silent	44°55'	78°04'	115	23.1	6.9	33	5.4	—*	—	1018	0.24	15
Slipper	45°17'	78°42'		34.0	6.4	28		—*	—	387	0.15	20
St.-Peter	45°19'	78°02'						—*	—	858	0.43	17
Geometric mean										686.1	0.18	
<i>Class 2 (no Mysis, pelagic forage fish present)</i>												
Bark	45°27'	77°51'	3792	87.5	6.6	45		—	W, S	2788	1.53	30
Bella	45°26'	79°02'	328	40.0	6.8		3.3	—	W, S	3532	0.55	31
Bending	49°19'	92°08'	1137	45.8	7.0	29	4.6	—*	W, C	1565	0.67	20
Caribou	45°56'	80°04'	529	59.5				—	C	1488	0.51	17
Carson/Stubb	45°30'	77°45'						—	W	1636	0.57	15
Como	47°55'	83°30'	1596	26.0	7.0	76	4.7	—*	SB	3797	1.29	15
Drag	45°04'	78°23'	912	55.0	6.9	73	5.5	—	C, W	367	0.14	11
Fernow	49°55'	86°05'	688	38.0				—*	S, W, P	1364	0.39	21
Greenwater	48°34'	90°26'	3340	54.9	7.7	64	4.4	—*	C, W	1216	0.34	24
Harp	45°23'	79°07'	72	33.0	6.7	35	3.7	—	C	621	0.88	18
Kamanisseg	45°25'	77°41'	2909	40.0	6.7	50		—	S, W, C	3613	0.96	10
Kawagama	45°18'	78°45'	2819	73.2	6.5		8.4	—	C, W	485	0.17	29
Koshlong	44°58'	78°29'	401	42.7	6.3	36	7.0	—	S, C	1818	0.91	30
Lamuir	45°50'	78°35'	757	39.3				—*	W	2028	0.50	11
Lavieille	45°51'	78°14'	2428	48.8	6.6	48	4.7	—	C, W	2273	1.04	11
Limerick	44°53'	77°37'	829	30.0	8.5		5.3	—	RW	1922	0.63	19
Littlehawk	45°09'	78°43'	343	93.0	6.2	32	6.9	—	C, SB	931	0.33	15
McKay	49°37'	86°25'	139	48.8	5.6	26	3.4	—*	C, W	1234	0.41	16

TABLE 1. (Continued)

Lake trout												
Lake	Lat.	Long.	Area (ha)	Z _{max} (m)	pH	Cond. (µS/cm)	Secchi (m)	Mysis ^a	Forage fish ^b	Weight (g)	Hg (µg/g)	n
Opeongo	45°42'	78°23'	5158	49.4	6.5	43	5.5	—	W, C	1107	0.50	16
Oxtongue	45°22'	78°55'	250	26.8	6.2	35	4.4	—	S, W, C	2812	1.61	19
Papineau	45°21'	77°49'	792	61.0	6.5	94	5.6	—	C, W	583	0.51	11
Peshu	46°58'	83°08'	389	50.6	7.3	43	6.1	—*	W	72	0.16	13
Pedstone	45°11'	78°42'	1194	82.4	6.4	38	8.1	—	W	567	0.24	16
Round	45°38'	77°30'	3069	54.9	7.7	66		—*	W	2578	1.40	39
Shakwa	46°46'	81°59'	649	27.5	6.5	33	5.9	—*	W	75	0.04	41
Sherborne	45°11'	78°47'	252	35.1	5.7	31	9.2	—	S	5907.7	0.19	20
Smoke	45°31'	78°41'	608	54.9	6.5	35	6.7	—	RW	1011.1	0.30	41
Treeby	47°52'	84°51'	130		6.9	73	3.8	—*	C, W	1498.7	0.76	10
Geometric mean										1213.2	0.47	
<i>Class 3 (Mysis and pelagic forage fish present)</i>												
Aegean	50°49'	94°48'	482	59.0	6.7	25	4.8	+*	W	1913	1.32	18
Bear	46°12'	81°27'	683	36.6	7.0	60	8.3	+*	C	2001	0.23	16
Bernard	45°45'	79°23'	2058	47.9	6.7		3.9	+	S, W	2423	0.67	32
Boshkung	45°04'	78°44'	716	71.1	7.1		6.0	+	S, W, C	1161	0.44	20
Charleston	44°32'	76°00'	2519	91.5	8.5		3.7	+	A, W, C	966	0.36	15
Delaney	50°05'	94°03'	1282	81.4				+*	W	1880	0.27	31
Eden	50°40'	94°59'	489	24.6				+*	C, W	1343	0.33	39
Fairy	45°20'	79°11'	712	69.5	6.5		3.6	+	S, W, C	4163	2.68	28
Gillies	45°12'	81°21'	228	34.0			8.3	+*	C, W	170	0.17	16
Gooseneck	50°02'	94°48'	172	29.9			4.3	+*	C	2126	0.73	31
Hawley	54°30'	84°39'	1235	54.0				+*	C, W, P	1081	0.38	15
Joseph	45°10'	79°44'	4268	90.0	6.7		9.6	+	S, W	2205	0.35	25
Kioskokwi	46°05'	78°53'	1127	45.8				+	C, W	1173	1.25	10
Lake of Bays	45°15'	79°04'	6105	53.0	6.5		4.2	+	S, W, C	3280	1.07	58
Larder	48°05'	79°38'	3704	33.5				+	C, W	1351	0.35	10
Loughborough	44°27'	76°25'	1066	34.0			4.8	+	C, W, S, A	2821	0.36	26
Mazinaw	44°50'	77°12'	1572	135.0	7.3		6.0	+	C, W	1591	1.22	21
McCarroll	46°26'	83°56'	198	33.6	7.1	45	5.0	+*	C	1242	0.56	12
Miskokway	45°39'	80°14'	238	41.2				+*	C	787	0.72	28
Muskoka	45°00'	79°30'	12215	66.5	6.7	46	4.9	+	C, W, S	2947	1.97	83
Muskrat	45°40'	76°55'	1202	64.0	8.4		1.5	+	S	2617	0.58	19
Quetico	48°34'	91°55'	4265	61.0	6.9	23	3.4	+*	C, W	1632	0.67	17
Raven	48°03'	79°33'	617	46.9	6.9		2.9	+	W	1381	0.62	12
Rosseau	45°10'	79°35'	6374	90.0				+	C, W, S	2027	0.86	44
Snook	50°12'	94°41'	263	37.2	6.7	33	1.8	+*	C	1316	0.80	71
Sutton	54°15'	84°44'	3764	82.0				+*	C, W, P	1403	1.00	15
Trout	45°35'	80°10'	290	37.2	6.0	28	2.4	+*	C	1349	0.36	21
Trout	46°18'	79°20'	1675	69.2	7.1	78	3.8	+	S, W, RW, C	5331	0.96	22
Trout	46°13'	80°35'	930	36.6	6.6	45	3.2	+	C	1932	0.55	11
Trout	50°14'	94°54'	110	34.8			4.6	+*	C	2152	0.65	16
Twelve Mile	45°01'	78°43'	337	27.5	6.8	52	4.1	+	S	740	0.36	20
Vernon	45°20'	79°17'	1506	37.5	6.1		3.1	+	S, W	3129	3.94	36
Wilson	50°30'	95°02'	312	42.7			1.5	+*	C, W	912	0.90	13
Geometric mean										1614.9	0.65	

were dropped from the regression model. Even though there was a large amount of overlap in maximum depth between the three classes of lakes (Table 1), there was a significant increase in maximum depth from Class 1 to Class 3 lakes (ANOVA, $P < 0.001$). This raised the possibility that the significant positive regression coefficient between Hg and maximum depth could simply be the result of a collinearity between the length of the pelagic food chain and maximum depth, as was observed by Dadswell (1974). Alternatively, maximum depth could truly represent the effect of some

physicochemical factor(s) influencing Hg concentration in lake trout, independent of the trophic structure of the lake. However, even though maximum depth varied greatly within food chain class (Table 1), it was not retained in the multiple regression when the analysis was performed within food chain classes (t -test, Class 1: $P > 0.10$; Class 2: $P > 0.45$; Class 3: $P > 0.14$). This shows that the significant regression coefficient of maximum depth in the multiple regression model was due to a collinearity with the length of the pelagic food chain rather than an independent effect of maximum

TABLE 1. (Continued)

Smallmouth bass												
Lake	Lat.	Long.	Area (ha)	Z _{max} (m)	pH	Cond. (μS/cm)	Secchi (m)	Mysis ^a	Forage fish ^b	Weight (g)	Hg (μg/g)	n
<i>Class 1 (Mysis and pelagic forage fish absent)</i>												
Bear	45°20'	78°42'	95	36.6	6.1	34.0	7.9	—*	—	615	0.48	18
Centre	45°01'	78°03'	144	17.7			3.9	—*	—	282	0.71	14
Kimball	45°21'	78°41'	213	67.1	6.3	30.0	9.1	—*	—	472	0.72	29
Lower Hay	45°24'	78°12'	420	32.3			1.9	—*	—	216	0.38	10
McKenzie	45°22'	78°01'	312	27.8	6.5	46.0	3.8	—*	—	363	0.44	16
Miskwabi	45°03'	78°19'						—*	—	402	0.35	17
Nunikami	45°12'	78°44'	116	24.1	6.2	29.0	7.2	—*	—	88	0.23	37
Redpine	45°12'	78°42'	380	38.7	7.3	32.0	7.5	—	—	285	0.28	23
Silent	44°55'	78°04'	115	23.1	6.9	33.0	5.4	—*	—	357	0.41	15
Geometric mean										305.2	0.42	
<i>Class 2 (no Mysis, pelagic forage fish present)</i>												
Baptiste	45°07'	78°03'	1952	31.0				—	W, C	903	0.84	12
Bella	45°26'	79°02'	337	35.0	6.8		3.3	—	W, S	745	0.37	20
Calabogie	45°16'	76°45'	1316	31.1	7.7			—*	W	601	0.59	39
Eagle	45°50'	79°30'	991	22.0	6.4	36.0	5.0	—	W, S	800	0.33	18
Galeairy	45°30'	78°17'	889	22.9	6.4	36.0	4.3	—	W	222	0.41	16
Jack	44°42'	78°02'	1237	51.2			3.6	—	C	678	0.40	21
Kamanisseg	45°25'	77°41'	2909	40.0	6.7	50.0		—	S, W, C	264	0.25	11
Kashagawigamog	44°59'	78°36'	818	39.7	7.1	79.0	5.2	—*	W, C	391	0.24	16
Koshlong	44°58'	78°29'	401	42.7	6.3	36.0	7.0	—	S, C	1003	0.91	12
Limerick	44°53'	77°37'	744	29.0			5.3	—	RW	452	0.52	20
Littlehawk	45°09'	78°43'	343	86.9	6.2	32.0	6.9	—	C, SB	705	0.56	20
Opeongo	45°42'	78°23'	6000	45.0	6.5		3.6	—	W, C	325	0.37	46
Oxtongue	45°22'	78°55'	246	27.0	6.1		2.2	—	S, W, C	266	0.50	32
Paudash	44°58'	78°03'	755	46.4	7.0	110.0	5.2	—	C	525	0.36	22
Smoke	45°31'	78°41'	607	54.9	6.5	35.0	6.7	—	RW	293	0.31	11
Sydemham	44°25'	76°33'	451	36.6			3.7	—	C	439	0.42	10
Windermere	47°58'	83°47'	3832	30.0			4.8	—*	W	1059	0.37	11
Geometric mean										507.8	0.43	
<i>Class 3 (Mysis and pelagic forage fish present)</i>												
Bay	45°30'	79°12'	133	31.1	6.5		6.2	+	W, S	592	0.61	21
Bernard	45°45'	79°23'	2058	47.9	6.7		3.9	+	S, W	403	0.41	20
Boshkung	45°04'	78°44'	716	71.1	7.1		6.0	+	S, W, C	784	0.50	16
Brandy	45°06'	79°31'	105	7.5				+	C	421	0.93	10
Caribou	45°56'	80°04'	529	59.5				+	C	615	0.48	19
Cecebe	45°38'	79°33'	770	19.5				+	W, C, S	613	0.59	19
Delaney	50°05'	94°03'	1282	81.4				+	S	668	0.27	24
Fairy	45°20'	79°11'	667	74.0	6.5		3.6	+	S, W, C	353	1.14	40
Falls	46°17'	83°02'	169	10.1				+	W, C, S	293	0.29	15
Gloucester Pool	44°51'	79°42'	1378	30.5	7.9			+	W, C, A	1139	0.57	13
Gooseneck	50°02'	94°48'	172	29.9			4.3	+	C	983	0.96	40
Haines	45°21'	79°56'	112	19.2	6.1	45.0	3.2	+	C	130	0.57	12
Joseph	45°10'	79°44'	4268	90.0	6.7		9.6	+	S, W	1015	0.58	21
Kagawong	45°49'	82°18'	5556	33.5				+	S	395	0.39	15
Lake of Bays	45°15'	79°04'	6105	53.0	6.5		4.2	+	S, W, C	940	0.80	33
Lang	46°10'	81°40'	597	21.0	7.2	70.4	6.3	+	W, C	161	0.30	15
Mackie	45°05'	76°59'	157	22.9				+	W	391	0.32	14
Mazinaw	44°50'	77°12'	1572	135.0				+	C, W	972	0.78	12
Mill	45°22'	80°00'	619	40.9	7.0		2.1	+	W, C	459	0.80	16
Miskokway	45°39'	80°14'	238	41.2				+	C	152	0.14	24
Muskoka	45°00'	79°25'	12215	66.5	6.7	46.0	4.9	+	C, W, S	426	0.99	40
Oliver	45°31'	79°48'	52	15.0				+	C	414	0.31	14
Peninsula	45°20'	79°11'	650	33.0	6.8		5.2	+	S	539	0.46	31
Rainy	45°32'	79°30'	259	9.2				+	C	321	0.49	20
Rousseau	45°10'	79°35'	6374	90.0				+	C, W, S	822	0.78	15

TABLE 1. (Concluded)

Smallmouth bass												
Lake	Lat.	Long.	Area (ha)	Z _{max} (m)	pH	Cond. (μS/cm)	Secchi (m)	Mysis ^a	Forage fish ^b	Weight (g)	Hg (μg/g)	n
Tomiko	46°32'	79°49'	1542	24.0	6.1		3.3	+	W	547	0.94	16
Trout	46°13'	80°35'	930	36.6	6.6	45.0	3.2	+	C	647	0.37	15
Twelve Mile	45°01'	78°43'	337	27.5	6.8	52.0	4.1	+	S	639	0.30	20
Vernon	45°20'	79°17'	1506	37.5	6.1		3.3	+	S, W	364	0.98	49
Geometric mean										489.2	0.53	

^aPresence or absence for lakes marked with an asterisk was predicted from the distribution of proglacial lake sediments.

^bA = alewife (*Alosa pseudoharengus*); C = lake cisco (*Coregonus artedii*); W = lake whitefish (*Coregonus clupeaformis*); RW = round whitefish (*Prosopium cylindraceum*); S = rainbow smelt (*Osmerus mordax*); P = ninespine stickleback (*Pungitius pungitius*).

depth on Hg bioaccumulation. Removing maximum depth from the multiple regression, the final model for lake trout was

$$(1) \log \text{Hg } (\mu\text{g/g wet}) = -2.72 + 0.21 (\pm 0.04) \text{ no. of trophic levels (1, 2, or 3)} + 0.61 \log \text{ weight (g)} (\pm 0.09);$$

$$\text{SE}_{\text{est}} = 0.28, R^2 = 0.56, n = 96.$$

Both predictor variables were highly significant (*t*-test, $P < 0.0001$). The number of trophic levels represents the lake Class number, i.e., the number of trophic levels above zooplankton.

Hg levels in smallmouth bass were not related to the length of the pelagic food chain ($r = 0.22$, $n = 55$, $P > 0.05$) (Fig. 1b). Power analysis (Cohen 1969, table 3.3.5) showed that the probability of wrongly accepting the null hypothesis of no effect of food chain class on Hg concentration in smallmouth bass (type II error), when the true correlation between these two variables would have been the same as that found in lake trout ($r = 0.59$), was less than 1%. The lack of a relationship between Hg concentration in smallmouth bass and the classification of the pelagic food chain cannot therefore be ascribed to the somewhat smaller number of lakes in the bass data set. The best model to predict Hg concentration in smallmouth bass included only body weight ($P < 0.05$); the other morphometric and chemical variables did not enter into the model ($P > 0.05$):

$$(2) \log \text{Hg } (\mu\text{g/g wet}) = -2.50 + 0.65 \log \text{ weight (g)} (\pm 0.08); \text{SE}_{\text{est}} = 0.33, R^2 = 0.34, n = 55.$$

Discussion

Our results support previous observations that the Hg concentration in top predators such as lake trout and northern pike (*Esox lucius*) is greatly influenced by the presence or absence of certain species representing important trophic links between these species and zooplankton (Akielaszek and Haines 1981; Bjorklund et al. 1984; Meili 1991; Rask and Metala 1991). This study extends that of Rasmussen et al. (1990) by showing that a simple food chain classification based on the presence/absence of well-known pelagic taxa can be used to predict the concentration in fish of two chemically unrelated compounds, Hg and PCBs. Indeed, PCB levels in lake trout obtained from Rasmussen et al. (1990) were significantly correlated ($P < 0.0001$) with Hg levels in the lake trout in the lakes for which information about both contaminants is available (Fig. 2). Patterns observed

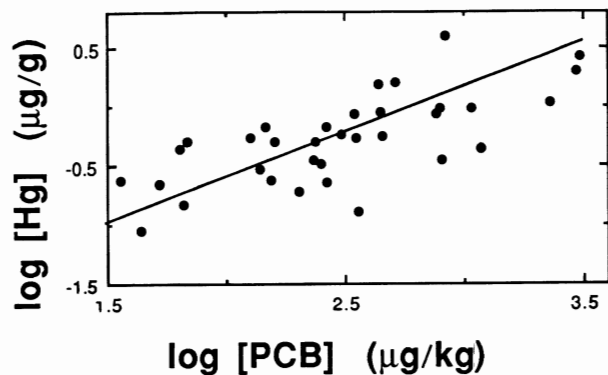


FIG. 2. Relationship between the levels of Hg in the muscle and the levels of PCBs (wet weight) in lake trout in 34 Ontario lakes. PCB data were obtained from table 1 in Rasmussen et al. (1990); Hg data are from this study (Table 1). The geometric mean regression line is shown.

in the distribution of Hg in this study paralleled those observed by Rasmussen et al. (1990) for PCBs in similar communities: contaminant concentration in pelagic species, such as lake trout, was related to the length of the pelagic food chain and contaminant concentration in littoral species, such as smallmouth bass, could not be predicted from the length of the pelagic food chain. Taken together, these two results suggest that pelagic food chains in these Ontario lakes are essentially disconnected from littoral food chains. This has several important consequences for our understanding and prediction of the distribution of biomagnifying compounds in freshwater lakes.

Contaminant concentration in species positioned in different, disconnected food chains within the same lake will show little or no covariation across lakes. For example, Wren et al. (1991) found a statistically significant but only moderate correlation ($r^2 = 0.60$) between Hg in pike and walleye (*Stizostedion vitreum*) in 79 Ontario lakes. While these species usually feed on similar prey (Scott and Crossman 1973), their diets diverge considerably in some lakes. For example, in some lakes, walleye, but not pike, feed extensively on pelagic fish such as smelt (Mathers and Johansen 1985), and the relatively large amount of between-lake variation in walleye Hg concentration (40%), unexplained by Hg concentration in pike, might be due to between-lake variation in the walleye's position along the littoral/pelagic gradient. Species more trophically isolated, as in the case of lake trout and smallmouth bass, will be

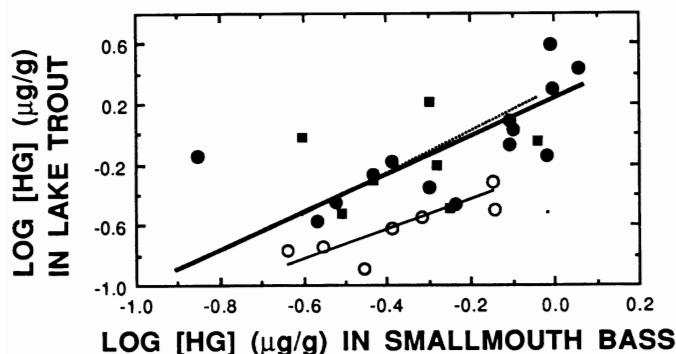


FIG. 3. Relationship between Hg levels in lake trout and smallmouth bass in 29 Ontario lakes. Class 1, 2, and 3 lakes are represented by open circles, solid squares, and solid circles, respectively. The geometric regression lines for each lake trout trophic level class are shown (t -test, Class 1 (fine solid line): $P < 0.01$; Class 2 (broken line): $P < 0.05$; Class 3 (bold lines): $P < 0.001$).

expected to show even weaker correlations. Indeed, Hg levels in these two species in lakes where both species were represented in our data set were poorly (but significantly, $P < 0.01$) correlated with each other ($r^2 = 0.34$, $n = 29$) (Fig. 3). This correlation was essentially unchanged ($r^2 = 0.31$, relationship not shown) when the residuals from the Hg/body weight relationships were used instead of the simple mean Hg levels. An analysis of covariance including Hg in bass as a covariate and lake trout trophic class as an effect accounted for 61% of the total variation in Hg in lake trout. This increase in predictive power from the simple two-species relationship indicates that the effect of variation in a common environment, which is reflected by the relationships between the two species within trophic level class, is approximately equal to the effect of trophic level variation in lake trout. Thus, food chain effects on Hg level in lake trout appear to be as important as the effects of between-lake variation in methyl mercury exposure. Results from monitoring only one species as a means to assess the general level of Hg contamination in fish (e.g., Hakanson et al. 1990) should therefore be interpreted with caution before they are applied to other fish species or to the general contamination status of a lake.

The failure of the model to explain bioaccumulation of both PCBs (Rasmussen et al. 1990) and Hg (this study) in littoral species suggests that lakes are heterogeneous environments with regard to processes leading to the bioaccumulation of contaminants in fish. Apart from food chain biomagnification, these processes could also include spatial and temporal variation in Hg bioavailability at the base of the food chain. There is no systematic way to classify complex littoral food webs, and it is therefore difficult to separate variation in biomagnification through food chains of variable length from variation in bioavailability at the base of the food chain.

Our study echoes Rasmussen et al.'s (1990) warning about the introduction of pelagic forage species such as *Mysis*, smelt, or coregonids as a source of fish food in lakes previously devoid of them. This practice, which has been favored in the past (e.g., *Mysis*: Martinez and Bergersen 1989), will likely result in increases in the concentration of Hg (this study) and PCBs (Rasmussen et al. 1990) in the salmonids situated at the top of the pelagic food chain.

Reports of increased Hg concentration toward the top of aquatic food chains have almost always dealt with comparisons of species that differ not only taxonomically (e.g., fish, invertebrates, zooplankton, and phytoplankton) but also in body size and physiology (e.g., Boudou et al. 1979; Philips et al. 1980; Ribeyre et al. 1980). The interpretation of this increase in Hg upward through the food chain as being the result of transfer via food uptake has been criticized by Huckabee et al. (1979) who suggested that factors such as differences in longevity (duration of exposure to Hg), growth rates, uptake, and depuration rates among species belonging to different trophic levels could well be as important as food chain transfer. Here, we have related between-lake variation in Hg concentration within a single species (lake trout) to the length of the pelagic food chain leading to this top predator. While the selection of a single species should minimize the effects of the confounding factors discussed by Huckabee et al. (1979), some of the objections raised against the interspecific comparisons of Hg concentrations could also apply to between-population studies such as the present one. For example, differences in age of the specimens, potentially related to demographic differences between Class 1 and 3 lake trout, could explain our results if Class 3 trout were generally found to be older than Class 1 fish. In addition, as pointed out by deFreitas (1974), faster growth rates resulting in a growth dilution and therefore lower Hg concentration can also be a confounding factor in interspecific studies. This raises the possibility of a growth rate artifact in our study if Class 1 trout generally grow faster than Class 3 trout, leading to higher growth dilution and lower Hg concentration in Class 1 populations. However, both the age and growth rate explanations appear to be ruled out in our study because piscivorous populations of lake trout (Classes 2 and 3) have been shown to grow faster than planktivorous (Class 1) populations (Martin 1966). When body size is statistically held constant, as was done in our final model (eq. 1), Class 3 fish are younger than Class 1 fish, since they grow faster and have therefore been exposed to Hg for less time. If there is any importance to factors such as age and growth dilution, these would help obscure rather than favor the trends observed in the present study. Consequently, the importance of biomagnification up through the food chain from Class 1 to Class 3 populations may well be more important than revealed by the differences in mean Hg concentrations across the three food chain classes. This could explain the difference between our estimate of the average biomagnification factor per trophic level (1.95) and the higher value of 3.33 obtained by Meili (1991) for the water/seston-zooplankton-roach/perch-pike food chain.

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