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THE EFFECT OF LAKE TROPHY ON LIPID CONTENT AND PCB CONCENTRATIONS IN PLANKTONIC FOOD WEBS

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Abstract. We investigated the influence of trophic status on the lipid content and polychlorinated biphenyl (PCB) concentrations in planktonic food webs from 19 lakes in southern Sweden. The lipid content in phytoplankton (10–45 μm), microzooplankton (45–150 μm), and large macrozooplankton (>500 μm) was negatively related to the total phosphorus (Tot-P) concentration in lakes. The lipid content in macrozooplankton (>150 μm) and young-of-the-year roach (*Rutilus rutilus*) was not related to Tot-P in lakes. On a dry mass basis (ng/g dry mass), the sum of PCB concentrations in phytoplankton and microzooplankton was negatively related to Tot-P in lakes. Thus, the PCB concentrations in phytoplankton and microzooplankton were explained by the decreasing lipid content of these fractions with increasing trophic status of lakes; and when normalized to lipid content (ng/g extractable lipid) we found no differences in PCB concentrations among lakes. We conclude that the lipid content of phytoplankton increased with increased nutrient stress, explaining the negative relationship between lake trophy and phytoplankton organochlorine (OC) concentrations on a dry mass basis. The relationship found between lipids and lake trophy in producers was not transferred in the food chain.

Key words: biomass; food web; lipids; phytoplankton; polychlorinated biphenyls (PCBs); Rutilus rutilus; *trophic status; zooplankton.*

INTRODUCTION

Since the restrictions against use of organochlorines (OCs) like polychlorinated biphenyls (PCBs) and DDT in most industrialized countries, the dominating input of these chemicals to aquatic ecosystems is via the atmosphere (Swackhamer and Hites 1988, Muir et al. 1990). The atmospheric fallout of semivolatile compounds such as PCB and DDT to aquatic systems is largely through wet deposition (Mackay 1989). In the air, such pollutants sorb to particles that are scavenged by rain. In addition, the compounds dissolve in airborne water in accordance with Henry's Law constant and are associated in raindrops with colloids and dissolved organic matter (Bidleman 1988). When inflow via the atmosphere is the only source of OCs, it is shown by the relation between atmospheric fallout and uptake in organisms (Larsson et al. 1990); i.e., the similarity between the OC profiles of atmospheric fallout and those of aquatic and terrestrial animals.

When long-range, atmospheric transport and deposition via precipitation dominate OC input to aquatic systems, ecological variables influencing the uptake of OCs in aquatic organisms can be investigated (Larsson and Okla 1989). Aquatic ecosystems of different character will receive approximately the same amount and composition of OCs, and the fate of these may, thus, be compared to elucidate the effects of, for example, differences in ecosystem structure. PCB accumulation by aquatic organisms is influenced by several related factors such as concentration in the surrounding medium (Barron 1990), bioavailability (Hall et al. 1986, Schrap and Opperhuizen 1990, Lores et al. 1993), biomagnification (Rasmussen et al. 1990), lipid content (Larsson et al. 1996, Kucklick and Baker 1998), growth rate (Sijm et al. 1992), and age (Stow and Carpenter 1994).

Earlier studies have demonstrated a negative relationship between trophic status of lakes and uptake of OCs in aquatic biota (Taylor et al. 1991, Larsson et al. 1992). The effects of eutrophication on lake ecosystems, through excessive input of nutrients, is primarily an increase of the overall biomass of plankton communities, especially that of the phytoplankton (Pace 1986, Mazumder et al. 1988). Lower OC concentrations in organisms of eutrophic systems have been recorded and attributed to an increased biomass of these systems (Taylor et al. 1991, Richer and Peters 1993). Taylor et al. (1991) suggested a ''biomass dilution'' responsible for this relationship. Lakes of high trophic status have high plankton biomasses to which the OCs are partitioned, reducing OC concentrations in water, and thereby the bioavailability, giving a lower concentration per mass unit of plankton. Biodilution may also occur under rapid growth conditions when the growth rate of phytoplankton exceeds the partitioning rate of organochlorines between water and phytoplankton, which prevents equilibrium to be reached (Swackhamer and Skoglund 1993). Another hypothesis has suggested that eutrophication may increase the sedimentation rate of

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TABLE 1. Lakes characteristics and limnological variables of the studied lakes.

Lake	Area (km^2)	Max depth (m)	Temp (°C)	Tot-P (μg/L)†	Chl *a* (μg/L)‡	Secchi depth (m)	Biomass (g dm/m^3)	TOC (mg/L)§
Krageholmsjön	2.1	10	22.3	153	38.7	1.1	1.45	7.2
Sövdesjön	2.8	12	22.8	80	105.7	0.5	1.78	11.7
Ringsjön	20	16	24.0	80	61.9	0.7	0.78	9.0
Vombsjön	12.8	16	24.1	80	15.8	1.1	1.92	6.1
Finjasjön	10	13	23.8	70	39.6	1.0	4.79	9.9
Åsnen	150	14	22.4	21	12.9	1.3	0.74	8.7
Västersjön	4.6	13	24.1	16	5.5	3.2	0.19	5.4
Vidöstern	48	35	23.6	15	5.9	2.8	0.18	7.9
Levrasjön	2.6	19	23.3	14	1.3	3.5	0.03	5.1
Kösen	11	22	24.3	12	4.9	3.5	0.20	8.2
Flåren	34	15	23.0	10	3.3	3.4	0.33	7.9
Ivösjön	54	50	24.3	10	3.0	2.5	0.23	6.7
Rottnen	33	18	23.6	10	4.0	3.2	0.19	9.2
Unnen	17	25	25.1	9	2.6	4.3	0.26	6.4
Immeln	24	28	22.0	9	3.8	3.0	0.19	6.2
Madkroken	12	21	21.7	8	5.9	3.1	0.27	7.2
Ånghultasjön	4.4	28	21.2	8	6.4	3.4	0.24	8.4
Örken	23	38	21.2	7	2.6	5.2	0.24	11.9
Mien	20	39	24.0	7	2.6	5.0	0.08	7.5

† Tot-P = total phosphorus.
‡ Chl *a* = chlorophyll *a*.
§ TOC = total organic carbon.

organic matter, thus purging the water column clear from OCs and enhancing sediment contamination (Pavoni et al. 1990, Millard et al. 1993). Other studies suggest a higher lipid content of phytoplankton in oligotrophic lakes as an important mechanism behind the observed relationship. Larsson et al. (1998) attributed the higher PCB concentrations recorded in phytoplankton of an oligotrophic lake than of a eutrophic lake to a higher lipid content of the phytoplankton in the former. Lipid rich phytoplankton in oligotrophic lakes, hence, has a higher accumulation capacity for the lipophilic OCs.

The reported relationships between OCs and trophic status in earlier studies have been either in experimental setups (Richer and Peters 1993, Gunnarsson and Rosenberg 1996), or at single trophic levels, such as zooplankton or piscivorous fish, in natural lakes (Taylor et al. 1991, Larsson et al. 1992). The primary trophic level in lakes, phytoplankton, is an important factor in controlling the fate and transport of OCs in natural waters. Settling algae can serve as vectors for transporting OCs to the sediments, and grazed phytoplankton can transfer OCs into the pelagic food web (Stange and Swackhamer 1994). PCB entry into the food web may be dominated by bioaccumulation at the primary trophic level (Swackhamer and Skoglund 1993). Phytoplankton is also the primary level where eutrophication has direct, measurable effects. Therefore, it is important to elucidate the effects of eutrophication on OC uptake in phytoplankton, and whether these effects are transferred to, and sustained through, the pelagic food webs. Here, we investigate the levels of PCBs in phytoplankton, microzooplankton, macrozooplankton, and planktivorous fish in 19 lakes in a trophic gradient, and in a defined geographic area. Our aim was to investigate if among lake differences in PCB concentrations correlated with trophic status parameters. First, we asked if PCB concentrations in the different compartments of the pelagic food web were negatively related to total phosphorus concentrations in water. Second, we wanted to examine the ''biomass dilution'' theory by investigating the relationships between PCB concentrations in water and organisms and bioaccumulation factors (BAFs), and total plankton biomass.

METHODS

Study sites and sample collection

All of the lakes are located in the southern part of Sweden (56° N, 14° E), in a 19 000-km^2 area, and experience a similar climate. The lakes are dimictic, but the summer stratification of five of the lakes (Vombsjön, Ringsjön, Finjasjön, Sövdesjön, and Krageholmssjön) is irregular. Lake characteristics and limnological variables for the lakes are given in Table 1.

All samples were collected and limnological variables measured in August 1997. We sampled plankton by towing three nets with 150-μm, 45-μm, and 10-μm mesh, connected in series. This yielded three plankton size classes: >150 μm, 45–150 μm, and 10–45 μm. The water volume that passed through the nets was measured with a flow meter placed at the opening of the nets. An additional size fraction, >500 μm, was sampled qualitatively to obtain large zooplankton. Small subsamples were taken from each fraction for species determination and microscopic estimates of detritus content. Hereafter, the different plankton size fractions will be referred to as large macrozooplankton

(>500 μm), macrozooplankton (>150 μm), microzooplankton (45–150 μm), and phytoplankton (10–45 μm). Young-of-the-year roach (*Rutilus rutilus*) were collected with electrofishing. The fish were pooled into composite samples of four to 21 individuals. In two of the lakes, Krageholmsjö and Änghultasjön, no young-of-the-year roach could be obtained. Plankton and fish were frozen after capture, and freeze-dried prior to analysis. Samples for analysis of PCB in water were obtained by collecting unfiltered water underneath the surface microlayer and percolating it through two polyurethane columns via a stainless steel funnel (Agrell et al. 2000). Fifty to 100 liters were sampled in each lake. The times required for the water to percolate through the polyurethane columns were between four and six hours.

Samples for total phosphorus, chlorophyll *a*, and total organic carbon in the water were taken at the same date as biota and water samples, and measured according to Swedish Standard Procedures (SIS 1991). Secchi disc depth and water temperature at ~0.5 m beneath the water surface was also measured.

PCB analyses

PCBs in plankton, fish, and polyurethane columns were Soxhlet extracted by acetone/hexane according to Bremle et al. (1995), using octachloronaphthalene as an surrogate standard. The solvent was reduced in a vacuum centrifuge, and the lipid amounts were determined gravimetrically. The sample was re-dissolved in hexane, followed by an open column step as a clean up. The column contained two layers of silica gel each soaked in concentrated sulfuric acid or 1 M K_2CO_3 (1 mol/L). The solvent contained in the samples was evaporated in a vacuum centrifuge, and was re-dissolved in isooctane prior to the gas chromatographic analysis. For detailed information on preparation of the samples see Bremle et al. (1995). Soxhlet apparatus is available from Wheaton Science Products, Millville, New Jersey, USA. For every 15 samples processed, a chemical blank was run. The average chemical blank for the sum of PCB concentrations (ΣPCB) was 1.1 ng (concentration depended on sample size). PCB adsorption efficiencies on polyurethane columns are given in Agrell et al. (2000). The average polyurethane column field blank for ΣPCB was 3.2 ng (concentration depended on sample size). Polyurethane column field blank concentrations of Domain 7 (consisting of the coeluting IUPAC congeners 24 and 27) and D8 (16, 32) varied considerably (from none detected to 1.9 ng) so sample concentrations of these domains should be interpreted with caution. Sample concentrations were not corrected for blanks.

Gas chromatographic analysis

The samples were analyzed for PCB by capillary gas chromatography/electron capture detection on a Varian Star 3400 cx (Varian, Walnut Creek, California, USA) equipped with an on-column injector. The chromatographic conditions and details are described in Bremle et al. (1995). The PCB components were identified and quantified according to Schulz et al. (1989). Forty-nine PCBs were included in the analyses: Domain number 7 (D7) (IUPAC numbers 24, 27), D8 (16, 32), D10 (29), D13 (31, 28), D14 (20, 33, 53), D16 (45), D20 (49), D21 (47, 48, 75), D23 (44), D24 (37, 59, 42), D25 (41, 64), D27 (40), D29 (63), D32 (66, 95), D34 (91), D36 (92), D38 (90, 101), D39 (99), D41 (83), D42 (97), D44 (85), D45 (136), D47 (82, 151), D50 (123, 149, 118), D51 (134), D53 (146), D54 (132, 153, 105), D56 (130), D58 (160, 138, 158), D59 (129, 126, 178), D60 (175), D61 (187), D62 (183), D63 (128), D65 (185), D66 (174), D67 (177), D68 (202, 171, 156), D69 (173, 157, 201), D70 (172), D72 (180), D74 (191), D75 (200), D77 (170, 190), D78 (198), D79 (199), D81 (189), D82 (208, 195), and D84 (194). PCB domains were identified and quantified on the basis of relative retention times and of response factors obtained for the chromatographic standard pentachlorobenzene. External standards of Clophen and Arochlor mixtures (Analytical Standards AB, Kungsbacka, Sweden) were run regularly to check performance. Extraction efficiencies for octachloronaphthalene were 83% ± 10% for plankton, 71% ± 11% for fish, and 64% ± 7% for polyurethane columns. Sample concentrations were not corrected for recovery.

Data analyses

Water concentrations of freely dissolved PCBs were calculated using the equations from Burkhard (1998):

$$f_{\mathrm{fd}} = 1/(1 + 0.1 \cdot \mathrm{DOC} \cdot K_{\mathrm{oc}} + \mathrm{POC} \cdot K_{\mathrm{oc}}) \quad (1)$$

$$C_{\mathrm{w}}^{\mathrm{fd}} = C_{\mathrm{w}}^{\mathrm{t}} \cdot f_{\mathrm{fd}}, \quad (2)$$

where f_{fd} is the fraction of the chemical that is freely dissolved in the water, DOC is the concentration of dissolved organic carbon, POC is the concentration of particulate organic carbon, K_{oc} is the organic carbon/water (freely dissolved basis) partitioning coefficient for the chemical, $C_{\mathrm{w}}^{\mathrm{t}}$ is the total concentration of the chemical in the water, and $C_{\mathrm{w}}^{\mathrm{fd}}$ is the freely dissolved concentration of the chemical in the water. Values for K_{oc} were estimated from the chemical's K_{ow} (octanol/water) using the relationship from Karickhoff (1981):

$$K_{\mathrm{oc}} = 0.41 K_{\mathrm{ow}}. \quad (3)$$

K_{ow}'s for the different PCB congeners were obtained from Hawker and Connell (1988). Bioaccumulation factors (BAFs) were calculated by dividing concentration of PCB in organisms (ng/kg lipid) with concentration of freely dissolved PCB in water (ng/L).

In the analysis of plankton biomass, one lake (Levrasjön) was excluded because of a massive epilimnic biogenic decalcification. Prior to statistical analysis, total phosphorus and PCB concentration data were $\log_{10}$-transformed owing to their skewed distributions

TABLE 2. ΣPCB concentrations and lipid content (percentage of dry mass) for the compartments water, phytoplankton (10–45 μm), microzooplankton (45–150 μm), macrozooplankton (>150 μm), large macrozooplankton (>500 μm), and young-of-the-year roach, *Rutilus rutilus* (fish) in the pelagic food web in the study lakes in southern Sweden.

		Phytoplankton		Microzooplankton		Macrozooplankton		Lg. macrozooplankton		Fish	
Lake	Water ΣPCB (pg/L)	ΣPCB (ng/g dm)	Lipids	ΣPCB (ng/g dm)	Lipids	ΣPCB (ng/g dm)	Lipids	ΣPCB (ng/g dm)	Lipids	ΣPCB (ng/g dm)	Lipids
Krageholmsjön	123	9	1.3	14	2.7	26	7.8	19	6.6	···	···
Sövdesjön	6	5	1.9	10	3.4	23	6.9	26	7.2	39	6.5
Ringsjön	27	8	0.7	10	1.5	43	9.7	58	7.8	89	10.8
Vombsjön	19	11	1.1	31	7.0	60	12.5	53	8.5	58	6.5
Finjasjön	8	16	2.2	34	3.9	17	1.6	40	6.5	86	10.8
Åsnen	5	48	2.6	47	3.9	25	8.6	36	9.2	34	7.0
Västersjön	5	58	7.6	47	8.6	52	9.7	38	11.3	48	2.9
Vidöstern	7	32	7.4	41	9.3	31	7.1	22	9.3	39	5.5
Levrasjön	6	63	13.6	62	2.4	77	12.5	39	8.3	41	3.0
Kösen	5	42	4.4	29	9.6	23	7.6	28	17.1	43	4.9
Flåren	3	34	7.2	18	3.2	24	8.6	31	14.6	34	6.9
Ivösjön	21	27	6.7	60	13.6	37	5.5	21	7.1	59	4.6
Rottnen	3	58	6.7	40	9.8	44	10.3	33	9.0	37	5.6
Unnen	54	36	10.1	38	12.9	18	9.0	25	9.4	34	5.6
Immeln	13	47	4.4	43	7.0	55	8.7	59	8.5	196	8.6
Madkroken	21	52	6.7	88	13.3	44	14.4	41	7.4	62	7.1
Änghultasjön	31	65	6.0	21	4.9	33	9.3	27	9.3	···	···
Örken	6	57	4.9	34	5.0	68	11.9	49	11.9	286	10.0
Mien	24	47	6.9	50	8.3	27	9.3	30	9.6	58	6.4

Note: dm = dry mass.

(Newton 1988). We performed simple regression analyses to test the dependence of PCB concentrations and lipid content on the trophic status (Tot-P concentrations) of the lakes. We then tested the dependence of PCB concentrations on other environmental variables using a stepwise multiple regression model. All statistics were carried out using StatView (Abacus Concepts, SAS Institute, Cary, North Carolina, USA).

RESULTS

Lake characteristics and water chemistry for the studied lakes are given in Table 1. The different parameters expressing trophic status, total phosphorus, chlorophyll *a*, and Secchi depth were correlated (r = 0.82–0.94, $P < 0.01$). Also, the concentrations of the 49 different PCB domains within the different matrixes included in the study, were correlated (r = 0.29–0.98, $P < 0.05$), except for D13, D14, and D25. Therefore, we chose to use total phosphorus (Tot-P) concentrations in the water as the measure of trophic status, and the sum of the 49 PCB domains (ΣPCB) as the measure of PCB contamination. ΣPCB concentrations and characteristics of the different compartments in all lakes are given in Table 2. Mean fish length in the pooled samples differed among lakes (ANOVA, $P < 0.01$). However, mean fish length did not correlate with lake trophy, lipid content, or ΣPCB concentrations ($P > 0.05$).

Trophic status

Water concentrations of freely dissolved ΣPCB among the lakes ranged from 0.0031 to 0.12 ng/L, with a geometrical mean of 0.012 ng/L. We found no relationship between concentrations of freely dissolved ΣPCB and Tot-P concentrations (μg/L) in the lakes (simple regression, $P > 0.1$).

The dry mass normalized ΣPCB concentrations (ng/g dry mass) in the phytoplankton and microzooplankton were negatively related to the Tot-P concentrations (μg/L) in the lakes (simple regression, $r^2 = 0.78$, $P < 0.01$, and $r^2 = 0.39$, $P < 0.01$, respectively; Fig. 1a). We did not find this relationship for the macrozooplankton or the large macrozooplankton, or for the young-of-the-year roach. Lipid normalized ΣPCB concentrations (ng/g extractable lipid) were not related to the Tot-P concentrations for any of the plankton fractions or the fish.

Lipid content (g extractable lipid/g dry mass) in the phytoplankton, microzooplankton, and the large macrozooplankton were negatively related to the Tot-P concentrations (simple regression, $r^2 = 0.73$, $P < 0.01$, $r^2 = 0.34$, $P < 0.01$, and $r^2 = 0.26$, $P = 0.028$, respectively; Fig. 1b). No significant relationship was found between lipid content and Tot-P concentration for the macrozooplankton or the fish.

The phytoplankton fractions were totally dominated by phytoplankton except in Västersjön where the rotifer *Keratella* was common. Generally, the phytoplankton communities in the most eutrophic lakes (>70 μg/L of Tot-P) were dominated by blue-green algae like *Anabena, Woronochinia,* and *Microcystis.* In the oligotrophic lakes, the communities were more diverse, and no dominating species or taxons were evident. The content

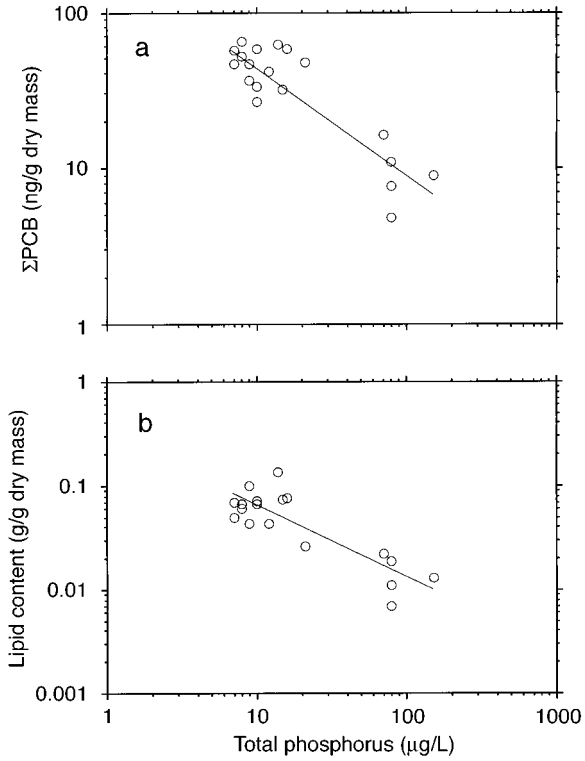

FIG. 1. (a) Linear regression analysis relating the PCB concentration (ng/g dry mass) in the phytoplankton (10–45 μm fractions) with the total phosphorus concentrations (μg/L) in lakes (simple regression: log $y = 2.63 - 0.70$ (log x); $r^2 = 0.78$, $P < 0.01$, df = 18). (b) Linear regression analysis relating the lipid content (g extractable lipid/g dry mass) of the phytoplankton (10–45 μm fractions) with the total phosphorus (μg/L) in lakes (simple regression: log $y = -0.51 - 0.68$ (log x); $r^2 = 0.73$, $P < 0.01$, df = 18).

of detritus was low in all samples (<1%) and not related to the trophic status of the lakes.

The microzooplankton fractions consisted of both phytoplankton and zooplankton with varying relative amounts. In Vombsjön, Finjasjön, and Åsnen, few zooplankton were found, and *Ceratium, Microcystis,* and *Gonyostomum* dominated the samples, respectively. In most lakes the relative amount of phytoplankton were greater than zooplankton, regardless of trophic status. The dominating microzooplankton in all lakes were the rotifers *Keratella* and *Kellicotta.* Other dominating microzooplankton were the rotifers *Tricocerca, Pompholyx, Gastrophus,* and *Ascomorpha,* the cladoceran *Chydoru,* and copepod nauplii.

The macrozooplankton fractions consisted only of zooplankton except in Vombsjön, Finjasjön, and Åsnen where zooplankton dominated but *Ceratium, Microcysti,* and *Gonyostomum* occurred, respectively. The macrozooplankton communities did not differ particularly among lakes. The dominating macrozooplankton in most lakes were the cladocerans *Daphnia galeata, D. cristata, D. cuccullata,* and calanoid and cyclopoid copepods. Other dominating species were the cladocerans *Chydorus, Diaphanosoma, Bosmina, Limnosida,* and *Holopedium.*

In the large macrozooplankton fractions zooplankton were totally dominant, and only in Ringsjön and Finjasjön did we find any phytoplankton, *Aulacosiera* and *Microcystis,* respectively. The composition was similar among lakes, the dominating species being the cladocerans *Daphnia galeata, D. cristata, D. cuccullata, Leptodora kindtii, Limnosida frontosa,* and *Holopedium gibberum.*

To examine which environmental parameters other than trophic status, measured as Tot-P concentration, influenced the ΣPCB concentrations (ng/g dry mass) in the different plankton fractions, the fish, and the water, we performed a stepwise multiple regression with the ΣPCB concentrations (ng/g dry mass) as a dependent variable against four to seven independent variables. Four independent variables were used for the water, six for the phytoplankton (10–45 μm) and microzooplankton (45–150 μm), and seven for the macrozooplankton (>150 μm), the large macrozooplankton (>500 μm), and the fish. The independent variables were: (1) total plankton biomass; (2) water temperature; (3) lake area; (4) lake depth; (5) water concentration of ΣPCB; (6) lipid content of the compartment; and (7) ΣPCB concentration in prey. For water, no variable was entered into the model ($P > 0.05$). For all biotic compartments except large macrozooplankton, the lipid content explained most of the variation in the ΣPCB concentrations ($P < 0.01$, 10–45 μm: $r^2 = 0.66$, 45–150 μm: $r^2 = 0.40$, >150 μm: $r^2 = 0.33$, and fish: $r^2 = 0.33$). For large macrozooplankton no variable was entered ($P > 0.05$). The ΣPCB concentrations were not significantly related to any other independent variable in any of the compartments except for the fish, where the ΣPCB concentration in prey (macrozooplankton) explained an additional 33% of the variation ($P < 0.01$). We found no trends in the lipid content vs. PCB concentration regressions for the different PCB congeners. The log K_{ow}s of the different congeners were not related to the degrees of explanation or the slopes of the regressions.

Biomass dilution

We found a positive correlation between the Tot-P concentration (μg/L) and the total plankton biomass (g dry mass/m^3) in lakes (simple regression: $r^2 = 0.75$, $P < 0.01$; Fig. 2a). Also, the biomasses of the three separate plankton fractions (phyto-, microzoo-, and macrozooplankton) were positively related with the Tot-P concentrations (simple regression: $r^2 = 0.76$, 0.56, and 0.28; $P < 0.01$, $P < 0.01$, and $P = 0.024$, respectively). The regression coefficient for the macrozooplankton was significantly lower than that for the phytoplankton (F test, $F_s = 8.21$, $P < 0.01$) and that for the microzooplankton (F test, $F_s = 4.77$, $P < 0.05$). The regression coefficients for the phytoplankton and the microzooplankton did not differ (F test, $F_s = 0.05$,

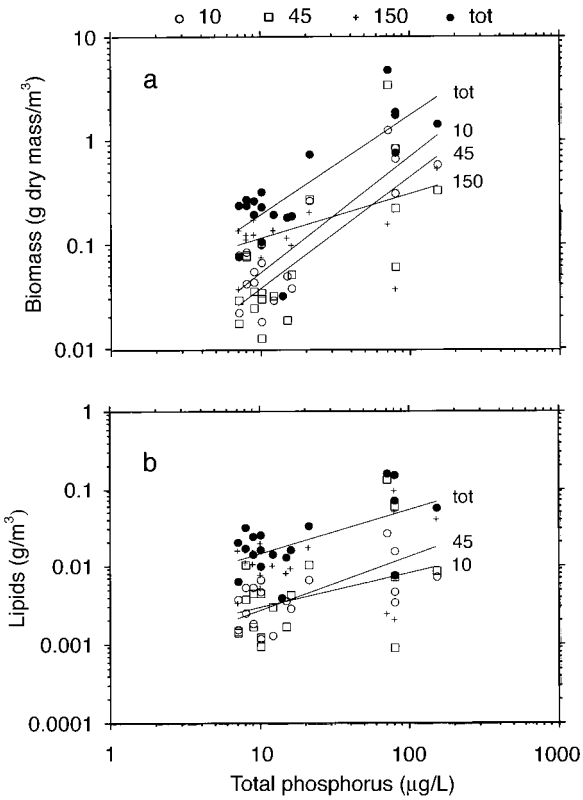

FIG. 2. Linear regression analyses relating the (a) plankton biomass (g dry mass/m^3) and (b) the plankton lipid concentration in water (g/m^3) to the total phosphorus (μg/L) in lakes: ''10'' denotes phytoplankton (10–45 μm fractions), ''45'' denotes microzooplankton (45–150 μm fractions), ''150'' denotes macrozooplankton (>150 μm fractions), and ''tot'' denotes the total plankton biomass and lipid concentration (sum of phyto-, microzoo-, and macrozooplankton). (a) Total, $\log y = -1.60 + 0.93(\log x)$ ($r^2 = 0.75$, $P < 0.01$, df = 17); 10, $\log y = -2.39 + 1.12(\log x)$ ($r^2 = 0.76$, $P < 0.01$, df = 17); 45, $\log y = -2.50 + 1.07(\log x)$ ($r^2 = 0.56$, $P < 0.01$, df = 17); 150, $\log y = -1.38 + 0.43(\log x)$ ($r^2 = 0.28$, $P = 0.024$, df = 17). (b) Total, $\log y = -2.37 + 0.57(\log x)$ ($r^2 = 0.34$, $P < 0.01$, df = 17); 10, $-2.95 + 0.45(\log x)$ ($r^2 = 0.33$, $P = 0.01$, df = 17); 45, $-3.23 + 0.69(\log x)$ ($r^2 = 0.28$, $P = 0.04$, df = 17); 150, not significant.

$P > 0.1$). The mass of plankton lipids in lake water (g lipid/m^3) was positively related to Tot-P concentrations for the phytoplankton and microzooplankton fractions, and for total plankton (simple regression: $r^2 = 0.33$, 0.22, and 0.34; $P = 0.01$, 0.04, and <0.01, respectively; Fig. 2b). The mass of lipids in the macrozooplankton fraction was not related to Tot-P concentrations ($P > 0.1$).

We found no relationship between lipid normalized ΣPCB concentrations (ng/g lipid mass) and total plankton biomass, for any of the compartments (Fig. 3). We did not find any relationships between organism log(BAF) of ΣPCB and total plankton biomass (simple regression: $P > 0.1$; Fig. 3).

DISCUSSION

All the investigated compartments, water, plankton fractions, and fish, contained detectable amounts of PCB. ΣPCB concentrations varied by one order of magnitude in biota, and two orders of magnitude in water among the lakes. The concentrations found are within the range of those previously reported from this area from waters not contaminated by sources other than atmospheric deposition (Larsson et al. 1998). We found no indications of point sources of PCB to the lakes, and as expected from atmospheric source pollution, the concentrations of the individual PCB domains in the different compartments were correlated. The PCB congeners were differentially partitioned in the plankton and the fish. The average lipophilicity increased with increasing trophic level. However, the concentrations did not increase with increasing trophic level except for the very most lipophilic congeners in fish relative to macrozooplankton (see Berglund et al. 2000). Therefore, we believe our assumption that atmospheric deposition is the dominating source of PCB to the lakes is valid, and a comparison of PCB concentrations among lakes is possible.

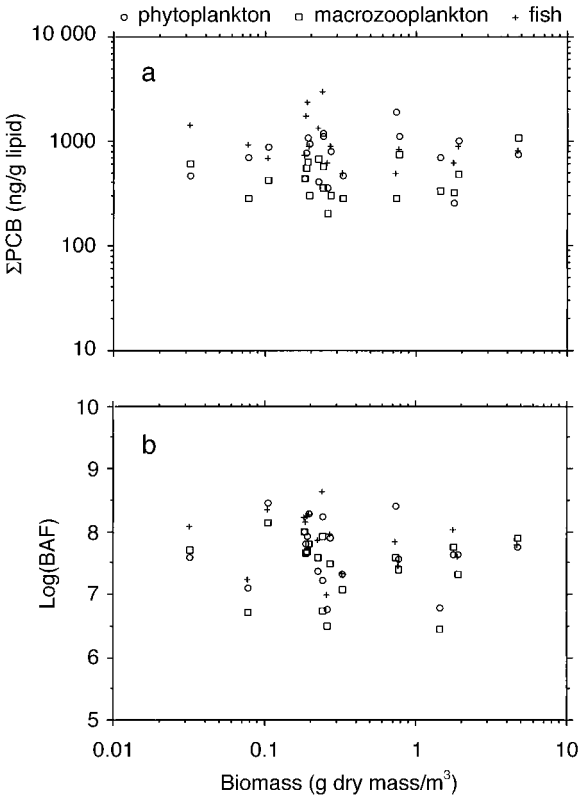

FIG. 3. Scattergrams showing (a) ΣPCB concentrations (ng/g extractable lipid) and (b) log bioaccumulation factors (BAFs) of ΣPCB for phytoplankton (10–45 μm), macrozooplankton (>150 μm), and fish (young-of-the-year roach, *Rutilus rutilus*), against total plankton biomass (g dry mass/m^3) in 19 Swedish lakes. No significant relationships were found in linear regression analyses ($P > 0.1$).

On a dry mass basis, the ΣPCB concentrations in the phytoplankton and microzooplankton were negatively correlated with lake trophy. Taylor et al. (1991) also demonstrated a negative relationship between net plankton (>150 μm) content of persistent pollutants (on a dry mass basis) registered as one principal component, and trophic status in lakes expressed as net plankton biomass. However, in our study, this relationship was only apparent for ΣPCB concentrations in phyto- and microzooplankton expressed on a dry mass basis. On a lipid mass basis, no such relationship existed. When lipid was normalized, there were no differences in PCB concentrations among the lakes for phyto- and microzooplankton. Organochlorines like PCBs have low solubility in water and high lipophilicity. Aquatic organism uptake of OCs can be predicted from the partitioning coefficient between octanol and water (K_{ow}) for the different compounds. Bioaccumulation factors (BAFs), derived from the observed ratio of OC concentration in the organism and the dissolved water concentration expressed in equivalent units, are considered a function of the K_{ow} of the OCs (Mackay 1982, Oliver and Niimi 1988). The BAF is considered directly proportional to the lipid content of the algal cells (Swackhamer and Skoglund 1993), but the algal total organic carbon content may also affect accumulation (Skoglund and Swackhamer 1999). Thus, due to the lipophilicity of OCs, lipid content and, consequently, the accumulation capacity explain a major part of the variability in wet or dry mass normalized PCB concentrations in aquatic organisms (Larsson et al. 1996, Kucklick and Baker 1998). This was also the case in this study. Lipid content explained 33–66% of the variation in ΣPCB concentrations, and was the investigated variable with the highest degree of explanation.

We found a negative relationship between the lipid content of phytoplankton and the trophic status of the lakes. This could be a result of different phytoplankton community compositions with lipid-rich species more prominent in oligotrophic lakes (Larsson et al. 1998), and/or intraspecific changes in lipid content or synthesis in phytoplankton, due to nutrient stress. The analysis of phytoplankton composition in the different lakes indicated that the first might be the case. In the more eutrophic lakes, the phytoplankton community was dominated by blue-green algae, low in lipid content; whereas the communities of the oligotrophic lakes were more diverse, composed of several taxons like Diatomophyceae, Chlorophyceae, Chrysophyceae, and Dinophyceae, all more lipid rich than blue-green algae. However, we can not exclude the second alternative explanation as the phytoplankton sample from the oligotrophic Ivösjön, totally dominated by the blue-green algae *Woronochinia karelica,* had higher lipid content than phytoplankton samples from eutrophic lakes like Krageholmsjön, Ringsjön, Vombsjön, and Finjasjön. The phytoplankton samples from these lakes were also dominated by blue-green algae, such as *Anabena, Woronochinia,* and *Microcystis.* Further, a negative relationship between lipid content of phytoplankton and lake trophy was found in spring samples from the same lakes as in this study (Berglund 1999). In spring, the phytoplankton communities were similar in all lakes, dominated by diatoms, and often of the same species. Algal culture experiments have shown an increased phytoplankton lipid content under nutrient stress (Shifrin and Chisholm 1981, Parrish and Wangersky 1990, Reitan et al. 1994). This lipid accumulation is considered to be partially a result of a steady lipid synthesis combined with reduced cell division rate and protein synthesis caused by the reduced availability of nutrients (Siron et al. 1989, Sukenik and Livne 1991). The seasonal nutrient deficiencies in freshwater systems have been shown to increase lipid concentrations in the particulate fraction (Groeger and Kimmel 1988, Arts et al. 1997). These events were coupled with a collapse of an algal bloom and a succession with another dominant species. Also, in marine ecosystems, an increase in particulate lipid followed the nutrient depletion brought on by diatom blooms (Kattner et al. 1983, Morris et al. 1985, Parrish 1987). However, Wainman and Lean (1992) found contradicting results in lakes, and attributed lipid production to changes in the physical environment, rather than phosphorus limitation. When we normalized ΣPCB concentrations in phytoplankton to lipids, no relationship with lake trophy was found. Thus, the mechanism responsible for the apparent relationship between phytoplankton ΣPCB concentrations and trophic status appears to be the lower lipid content of the phytoplankton in eutrophic lakes.

Unlike for phytoplankton, the lipid contents of macrozooplankton and young-of-the-year roach were not related to the nutrient status of the lakes. Thus, differences in lipid contents at the primary producer level were not transferred to the primary and secondary consumers. The transfer of lipids in aquatic food chains has been demonstrated in several studies (Bourdier and Amblard 1989, Ahlgren et al. 1996). Because zooplankton, and probably most consumer organisms, are capable of little de novo synthesis, lipids are primarily dietary in origin. Although animals can convert one form of lipid to another, certain essential fatty acids are almost exclusively synthesized by plants (Brett and Müller-Navarra 1997). These species-specific fatty acids have been used to elucidate the contribution of the different carbon sources to higher trophic levels in the aquatic food web (Napolitano 1999); and zooplankton lipid composition changes rapidly (within days) in response to the lipid composition of the food (Bourdier and Amblard 1989). Although the qualitative transfer of lipids (e.g., essential fatty acids) in food webs has been established, the results from this study indicate that there is no quantitative food chain transfer of total lipids from primary producers to consumers. The differences in phytoplankton total lipid content between

eutrophic and oligotrophic lakes were not reflected in the zooplankton lipid content.

The food quality of phytoplankton may not be the dominant limiting factor of zooplankton growth and reproduction. If resource (nutrients) competition is responsible for the differences in phytoplankton production and content of lipids, the structural force on the zooplankton may, according to food chain models, be predation rather than resource competition (Persson et al. 1988). Thus, high lipid content in zooplankton may not be a selective advantage in these systems. On the contrary, as planktivorous fish may be structured by resource competition, their preferred prey may be selected towards lipid rich zooplankton (high food quality), decreasing the fitness of these zooplankton. As we found no relationship between zooplankton total lipids (% or g/m^3) and lake trophy, the lipid content in fish should not differ with lake trophy due to differences in prey lipids. This was also the case; we did not find any relationship between roach lipid content and lake trophy.

The higher food quality (i.e., lipid content of phytoplankton) in oligotrophic lakes may result in more efficient energy transfer from producers to herbivores in oligotrophic than in eutrophic lakes. The reduced efficiency with trophic status may affect the slope between total phosphorus and biomass of zooplankton. However, lipid content of phytoplankton alone cannot account for the differences in the relationship with total phosphorus between phytoplankton and zooplankton biomass. When lipid concentration in lakes was expressed on a volumetric basis, it increased with the trophic status of lakes for phytoplankton, but for zooplankton the slope was not different from zero. Thus, although more nutrients increase the volumetric content of lipids in the producer level, this is not transferred to the herbivore level in all lakes. Therefore, some other variable like lipid composition, elemental composition, or algal morphology may influence food quality, and thereby, the efficiency of energy transfers. It has been suggested that the fatty acid composition of food, rather than total lipids, influence the growth and reproduction of zooplankton (Brett and Müller-Navarra 1997); and thereby, affect the efficiency of energy transfer between producers and herbivores.

Thus, the smaller slope of the biomass vs. Tot-P relationship for zooplankton compared to phytoplankton may be accounted for by predation instead of resource competition as a selective force on the zooplankton trophic level, or by lower food quality in eutrophic lakes.

The phytoplankton biomass and lipid content per volume lake water increased with trophic status. Therefore, increased prey availability may permit zooplankton in eutrophic lakes to obtain the same amount of dietary lipids despite lower food quality of the individual phytoplankton. Zooplankton may compensate low food quality by increasing feeding rates (Brett 1993). This could have implications on the PCB accumulation in zooplankton. Uptake of PCBs via food is considered to be the main route of accumulation in consumers, and organochlorines like PCBs have been suggested to biomagnify in the food chain (Russell et al. 1999). We did not find, however, increased zooplankton PCB concentrations with increased trophic status of the lakes in this study. When lipid normalized, the PCB concentrations in phytoplankton were similar among all lakes. Therefore, if zooplankton in all lakes consume and accumulate similar amounts of phytoplankton lipids, they would accumulate similar amounts of PCBs, associated with the phytoplankton lipids. This would result in similar zooplankton PCB concentrations among lakes. Also, it seems that there is no food chain biomagnification of PCBs in these planktonic food chains (Berglund et al. 2000), so possible differences in phytoplankton PCB concentrations due to different trophic status may not be reflected in herbivores or consumers higher up in the food chain (Fig. 4).

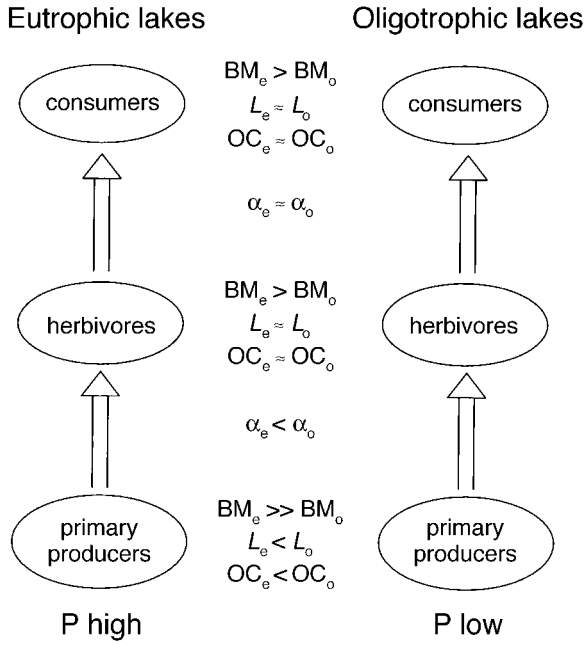

FIG. 4. Conceptual model of energy transfer and effects on organochlorine concentrations in planktonic food chains in nutrient-rich and nutrient-poor systems. BM = biomass (kg/m^3), L = lipid content (%), OC = organochlorine concentration (kg/kg dry mass), and α = food conversion coefficient. Food quality of primary producers in nutrient-rich (P high) systems is poor (L_e), and hence, energy transfer efficiency is low (α_e). However, the food availability is high (BM_e), and differences in lipid content between the systems disappear at the herbivore level. Organochlorine concentrations are mainly governed by the lipid content of the organisms. Subscripts ''e'' and ''o'' denote eutrophic and oligotrophic lakes, respectively.

Zooplankton may also allocate energy to other purposes than growth or energy depots, such as lipids. At

water temperatures above 20°C, cladoceran (e.g., *Daphnia magna*) generation time is approximately 14 d (Pennak 1978). Such a high reproduction rate will have a large impact on the energy balance of the organism, and deplete any possible energy storage such as lipid depots. During colder periods, when reproduction ceases, lipid depots may well be developed in zooplankton (Pennak 1978), and possibly also differ along a trophic gradient of lakes. Hence, seasonal differences in lipid accumulation may explain the negative relationship found by Taylor et al. (1991) between total phosphorus in lakes and persistent pollutants in zooplankton, as the sampling of their study was performed in November.

Larsson et al. (1992) showed that lake trophy influenced persistent pollutant concentration in piscivorous fish (northern pike, *Esox lucius*). They found an inverse relationship between the lake trophy (e.g., total phosphorus and chlorophyll *a*) and the pollutant levels in the fish. In this study, we did not find any such relationship for young-of-the-year, planktivorous roach, neither on a dry mass, nor on a lipid mass basis. Thus, as we found no relationship between lipid normalized PCB concentrations and lake trophy in either pelagic producers, herbivores, or planktivores, it seems unlikely that food chain transfer of pollutants would explain the results found by Larsson et al. (1992) for piscivores. However, the piscivorous fish in the study by Larsson et al. (1992) were three to seven year old pike. These fish represent integrated samples over time, and a predatory strategy foraging on prey from the most littoral to pelagic habitats. The differing feeding habitats of pike means that a variety of prey fish species are included in the diet, and in highly humic lakes even invertebrates such as dragonfly larvae (*Odonata*) are included as prey. In addition, growth of pike differed substantially among lakes, partly explaining the variation in persistent pollutant concentration by growth dilution.

The direct influence of eutrophication, caused by excessive phosphorus loads, on lake ecosystems is mainly an increase in phytoplankton biomass and production. It is also suggested that this increase in phytoplankton biomass supports a greater zooplankton biomass; i.e., eutrophication causes an increase in both phyto-, and zooplankton biomass (Pace 1982, Bays and Crisman 1983). Our results support these effects, as we found a positive correlation between the trophic status of the lakes and the total plankton biomass. However, these results should be interpreted with caution, as our microzooplankton fractions contained large and varying amounts of phytoplankton. The differences in relative amounts of phytoplankton in the microzooplankton fractions among the different lakes may, therefore, influence the slope of the biomass vs. total phosphorus relationship for microzooplankton.

As nutrient stress affects lipid content and quality of phytoplankton, we did not include any trophic status variables (Tot-P, chlorophyll *a*, Secchi depth) in our stepwise multiple regression to discriminate between the two effects of eutrophication, but instead used lipid content and total plankton biomass. The results from the stepwise multiple regression showed that only the fish ΣPCB concentrations were affected by the ΣPCB concentrations in prey. The ΣPCB concentrations in the macrozooplankton were not affected by the concentrations in the phytoplankton, and the ΣPCB concentrations in large macrozooplankton were not affected by concentrations in phytoplankton or microzooplankton. In fish, PCBs are considered to accumulate via food through the gastrointestinal tract, rather than via water through gill exchange (Gobas et al. 1993). Thus, uptake of OCs in fish may be governed mainly by assimilation via food rather than an equilibrium partitioning with water. Therefore, fish concentrations of PCB are unlikely to be influenced by temporal changes in water concentrations, but rather being an integrated effect of concentrations in food during the lifetime of the fish. Zooplankton seem to accumulate PCB via water to a higher extent than fish, although the relative importance of direct partitioning from water and food uptake may vary, both for zooplankton (Harding and Vass 1979, Wyman and O'Connors 1980, Brown et al. 1982), and for fish (Berglund 1999).

The biomass dilution hypothesis predicts that the concentration of contaminants in aquatic organisms should be proportional to the reciprocal of the biomass (Taylor et al. 1991). Using lipid normalized ΣPCB concentrations, we did not find support for this theory. If the plankton community was in the exponential phase of growth at the time of sampling, the dilution effects may not be revealed when comparing the PCB concentrations against biomass. Instead, it may be more appropriate to compare the bioaccumulation factors (BAFs) against biomass, as growth of phytoplankton may be too rapid for equilibrium to be reached between water and phytoplankton (Swackhamer and Skoglund 1993). The BAFs varied over almost two orders of magnitude among lakes, but we did not find any significant relationship between the BAFs for the plankton and the total plankton biomass. Thus, plankton growth rates at sampling time did not seem to differ among the lakes due to trophic status to the extent that it explained the differences in PCB partitioning.

Conclusions

The decreasing lipid content of phytoplankton with lake trophy explained the apparent negative relationship between the dry mass normalized ΣPCB concentrations in phytoplankton and lake trophy. The differences in lipid content at the primary trophic level were not maintained throughout the food webs. No relationship was found between lipid normalized ΣPCB concentrations in biota and total plankton biomass, contrary to what is predicted by the ''biomass dilution''

theory. Nor did we find any relationship between freely dissolved ΣPCB concentrations in water and lake trophy. Instead, lipid content explained most of the variance of ΣPCB concentrations in biota independent of lake trophy.

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