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Bioaccumulation of PCBs in Arctic seabirds: influence of dietary exposure and congener biotransformation

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Contaminant patterns is linked to phylogeny and species-specific differences in enzyme systems and activity.

Abstract

Four seabird species and their prey (zooplankton or fish) were collected in the Barents Sea to determine how dietary exposure, cytochrome P450 (CYP) enzyme activities and sex influenced their hepatic PCB concentrations and accumulation patterns. Five males and five females from each seabird species (little auk (*Alle alle*), Brünnich's guillemot (*Uria lomvia*), black guillemot (*Cepphus grylle*) and black-legged kittiwake (*Rissa tridactyla*)) were analysed. PCB concentrations could not be explained directly by carbon source (δ^{13}C) or trophic position (δ^{15}N), but by a combination of dietary parameters (δ^{13}C, δ^{15}N, migratory pattern, age) and contaminant metabolism. Contrary to previous studies, the PCB pattern differed among seabirds, with a higher proportion of persistent congeners (% of PCB-153, $R_{PCB\text{-}153}$) in black-legged kittiwake than in auks. The PCB pattern also differed among auks, with little auk as the most efficient biotransformer (highest $R_{PCB\text{-}153}$ values of persistent congeners). Based on high $R_{PCB\text{-}153}$ values, Brünnich's guillemot poorly metabolised *ortho–meta*-unsubstituted congeners, whereas black guillemot poorly metabolised *meta–para* unsubstituted congeners. Species-specific differences in PCB biotransformation were confirmed by metabolic indices, where PCB patterns in seabirds were adjusted for PCB pattern in prey. The relative contribution of *ortho–meta*-unsubstituted congeners to $\sum$PCBs decreased with increasing EROD activity. There were no differences in PCB concentrations, PCB patterns or cytochrome P450 enzyme activities between males and females. CYP P450 activities (CYP1A- and CYP2B/3A-like: EROD and testosterone 6β-hydroxylation, respectively) were low and did not correlate with concentrations of non- or mono-*ortho* Cl-substituted PCBs (NO- and MO-PCBs), or with total toxic equivalent concentrations (TEQs) for dioxin-like effects of NO- and MO-PCBs.

Keywords: Stable isotopes; Larids; Alcids; Biotransformation; Feeding rate; Toxic equivalent concentrations; Metabolic index

1. Introduction

The Barents Sea region sustains a highly productive marine ecosystem in the Arctic, supporting a variety of wildlife species of which seabirds are numerous. Compared to other Arctic regions, high levels of organic contaminants have been found in Barents Sea mammals and some seabirds, with particularly high abundance of polychlorinated biphenyls (PCBs) (de March et al., 1998; Muir et al., 2000; de Wit et al., 2004). PCBs, which have been used for industrial purposes due to their chemical inertness, reach this Arctic region mainly through atmospheric transport and ocean currents, and there are few or no local sources in the Barents

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Sea (de March et al., 1998). The hydrophobicity and biological recalcitrance of PCBs results in bioaccumulation in lipid-rich tissues of biota, often with increasing concentrations with tropic position in food webs (e.g. Borgå et al., 2001a; Fisk et al., 2001a). PCB accumulation in food web components, including in the Barents Sea, is highly dependent on exposure (generally related to diet and thus trophic position) and physiology of the target species (e.g. biotransformation capacity) (e.g. Fisk et al., 2001a; Hop et al., 2002).

Although total PCB and its contribution to sum organochlorines in birds have been related to diet and phylogeny (e.g. Buckman et al., 2004), detailed avian PCB patterns have been reported to be independent of trophic position and food sources (Braune and Norstrom, 1989; Borlakoglu et al., 1990). In addition, when comparing different seabird species, the PCB pattern was found to be relatively similar across species (Borlakoglu et al., 1990). However, in the Barents Sea, similar PCB patterns were found among gulls that differ in trophic positions and PCB concentrations, whereas gulls and auks with comparable PCB concentrations differed in PCB pattern (Borgå et al., 2001a). Gulls had a higher proportion of persistent PCBs than auks, a difference which might result from differences in biotransformation, with gulls being better biotransformers than auks.

The cytochrome P450 enzyme system (CYP) plays an important role in regulating a variety of endogenous substances such as hormones. CYP isoforms are also involved in the first oxidative step of contaminant biotransformation (Walker, 1998). The presence and activity of CYP isoforms determine an organism's ability and capacity to biotransform contaminants and, thus, its contaminant levels and patterns (Murk et al., 1994; Walker, 1998). Based on PCB patterns in tissues, birds are suggested to eliminate congeners with chlorine (Cl) unsubstituted *meta–para* positions (through CYP2B/3A-like enzymes) to a higher extent than congeners with Cl-unsubstituted *ortho–meta* positions (through CYP1A-like enzymes) (Braune and Norstrom, 1989; Borlakoglu et al., 1990). Non- and mono-*ortho* Cl-substituted PCBs (NO-PCB and MO-PCBs) have high potency for coplanar configuration, and thus induction of CYP1A enzymes. Both NO- and MO-PCBs have been found in Arctic air (Harner et al., 1998), ice-associated amphipods (Borgå et al., 2001b), Canadian Arctic seabirds (Braune and Simon, 2003) and European Arctic glaucous gulls (*Larus hyperboreus*) (Daelemans et al., 1992). Although positive correlations have been found between PCB concentrations and various biochemical parameters (including CYP1A enzymes) in Barents Sea glaucous gull (Henriksen et al., 2000), no studies are available on PCB toxicity in seabirds occupying lower trophic levels in the Barents Sea. To evaluate aryl hydrocarbon (Ah) receptor mediated toxicity of NO- and MO-PCBs, toxic equivalency factors (TEF) were established for these congeners by the World Health Organization (Van den Berg et al., 1998). TEF is the order of magnitude toxicity of a compound relative to that of 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD), which has a coplanar configuration and is assumed to be the most toxic compound acting through the Ah-receptor complex. The TEFs combined with the organism's concentrations are used to calculate toxic equivalent concentrations (TEQs). Whereas several studies have been carried out on CYP activity and its relationship to PCB concentrations or pattern in the high trophic level glaucous gull and marine mammals from the Barents Sea (Wolkers et al., 1999; Henriksen et al., 2000), seabirds at the intermediate trophic levels have so far not been studied.

The disparity between results on avian PCB pattern motivates closer investigation of which factors influence avian PCB accumulation. The present study investigates the PCB bioaccumulation in one gull species (black-legged kittiwake (*Rissa tridactyla*)) and three auks (little auk (*Alle alle*), Brünnich's guillemot (*Uria lomvia*), black guillemot (*Cepphus grylle*)) from the Barents Sea. These long-lived seabirds are particularly numerous in the Barents Sea region, especially during the breeding season, and represent the 3rd to 4th trophic levels in the food web. Their main diet is calanoid copepods, larger zooplankton and fish, and fish, respectively, for little auk, Brünnich's guillemot, and black guillemot and black-legged kittiwake (Lønne and Gabrielsen, 1992; Mehlum and Gabrielsen, 1993; Weslawski et al., 1999). Whereas kittiwake migrates, the auks reside in the Nordic waters throughout the year (Anker-Nilssen et al., 2000). These species were selected as they are very abundant and important in the flux of energy in the Svalbard and the Barents Sea, and there are no data available from the European Arctic on CYP activities and TEQs in lower trophic level avian species.

The objective of the present study was to investigate the relationship between avian hepatic

(i) PCB concentrations and dietary parameters such as trophic position (δ^{15}N), carbon source (δ^{13}C), feeding rate, migration pattern, and sex.
(ii) PCB pattern and biotransformation ability due to phylogeny and selected CYP enzyme activities (ethoxyresorufin *O*-deethylation (EROD) and testosterone hydroxylation).
(iii) PCB TEQ values and CYP induction.

2. Materials and methods

2.1. Species and sampling

The seabirds were collected in the marginal ice zone of the north-central (76°08′–76°96′N, 32°52′–33°31′E)

and north-western (76°46′–77°45′N, 27°00′–28°13′E) Barents Sea from 9 to 20 May 1999, using a shotgun with steel pellets. Five females and five males from each species were randomly selected from a pool of hunted birds (total sample size = 40). Within 15 min after death, the seabirds were dissected and liver samples for analyses of CYP enzyme activities were stored frozen in liquid nitrogen. Liver and muscle samples were frozen at −20 °C in containers of polypropylene and aluminium foil, respectively, and analysed for PCBs and stable carbon and nitrogen isotopes, respectively. Body mass (g), sex, age (juvenile/adult based on plumage) were registered. The seabirds' main prey were collected simultaneously and analysed for PCBs as described in detail elsewhere (Borgå et al., 2001a; Borgå et al., 2002).

A seabird's daily feeding rate is determined by its daily energy requirement (Gabrielsen et al., 1991; Ellis and Gabrielsen, 2002). Based on the measured body mass and its species-specific relationship with basal and field metabolic rates (Gabrielsen et al., 1991; Ellis and Gabrielsen, 2002), daily energy requirements were calculated for each seabird species. Given the energy density of the species' prey items in the Barents Sea (Gabrielsen et al., 1991; Gabrielsen and Ryg, 1992) and the assimilation efficiencies of seabirds (Brekke and Gabrielsen, 1994), the respective weight-specific feeding rates were calculated assuming a diet of 100% copepods in little auk, 20% euphausiids, 20% amphipods and 60% polar cod in Brünnich's guillemot, and 100% polar cod in black guillemot and kittiwake, based on previous dietary analysis of these species in the Barents Sea (Lønne and Gabrielsen, 1992; Mehlum and Gabrielsen, 1993; Weslawski et al., 1999).

2.2. Chemical analyses

The hepatic concentrations of *ortho* Cl-substituted PCBs were determined by high-resolution gas chromatography (HRGC) at the Environmental Toxicology Laboratory (ETL) at the Norwegian School of Veterinary Science. Methods with modifications for extraction, clean up, separation and identification are described in previous publications (Brevik, 1978; Borgå et al., 2001a). In short, internal standards (PCB-29, -112 and -207: Promochem, GmbH, Germany) were added to the individual livers before homogenisation (Cole Parmer ultrasonic homogeniser, 4710 Series, Cole Parmer Instrument Co., Chicago, IL, USA), and extraction of lipids and PCBs was carried out with cyclohexane and acetone (Rathburn Chemicals, Walkerburn, Scotland). A portion of the lipid extract was used to gravimetrically determine the content of extractable organic matter (Sartorius analytic A200S, Satorius AG, Göttingen, Germany), mainly neutral lipids. To remove lipids, extracts were washed with a surplus of concentrated sulphuric acid (Scanpure, Chemscan A/S; Elverum, Norway) before separation of PCBs by HRGC. The GC (Agilent 6890 Plus GC system, Agilent Technologies) was equipped with two fused silica capillary columns of different polarity (SPB-5 and SPB-1701; 60 m, 0.25 mm ID, 0.25 μm film; Supelco inc.) and ^{63}Ni-micro electron capture detector (Agilent Technologies).

The samples were analysed for PCB congeners -28, -31, -47, -52, -66, -74, -99, -101, -105, -110, -118, -128, -137, -138, -141, -149, -151, -153, -156, -157, -170, -180, -183, -187, -189, -194, -196, -199, -206, -209 (Ballschmiter and Zell, 1980). Most congeners were quantified on the SPB-5 column, except PCB-52, -101, -105 and -149 which had a better resolution on the SPB-1701 column. Recoveries of the analysed PCBs ranged from 78 to 122% (mean 93%). The congener dependent quantification limit (= 3 × detection limit) ranged from 0.04 to 0.19 ng g^{-1} wet weight (mean 0.09). The reproducibility, precision, linearity and sensitivity of the analyses were within the accredited requirements of NS-EN ISO/IEC 17025.

Hepatic lipid extracts (4–6 samples depending on species, see Table 1 footnote) from the ETL were shipped to Axys Analytical Services (Sidney, Canada), where non-*ortho* Cl-substituted PCBs (NO-PCBs: PCB-77, -81, -126, -169) were isolated and quantified using the United States Environmental Protection Agency method 1668A. This technique is an isotope-dilution, congener-specific method using ^{13}C-labelled PCB-77, -81, -126, -169 standards added to the extract. Lipids were removed by gel permeation chromatography, and NO-PCBs were isolated using a carbon column. GC-HR mass spectrometry was performed on a Micromass Autospec Ultima magnetic sector mass spectrometer.

The liver microsome EROD rates were determined fluorimetrically as described by Wolkers et al. (1998), whereas testosterone hydroxylation activities were determined using high pressure liquid chromatography according to Wortelboer et al. (1992).

Stable isotope ratios were analysed in seabirds' muscles at the Institute for Energy Technology, Kjeller, Norway as described in details by Hop et al. (2002). Stable isotope values of δ^{15}N and δ^{13}C (SI) were expressed as SI = (($R_{sample}/R_{standard}$)−1)1000, where R is the corresponding ratio of ^{15}N/^{14}N or ^{13}C/^{12}C related to standard values in atmospheric air (IAEA-N-1 and 2) or Pee Dee Belemnite (PDB: USGS 24), respectively. To convert δ^{15}N into trophic levels, the formula for seabirds by Fisk et al. (2001a) was used (trophic level = 3 + (δ^{15}N − 10.1)/3.8).

2.3. Data treatment and statistical analyses

The PCBs were divided into metabolic groups depending on Cl-substitution in the *ortho–meta* and *meta–para* position (Table 1), which influences the persistency of congeners in homeotherms (Boon et al.,

Table 1
Hepatic polychlorinated biphenyl (PCB) concentrations (ng g^{-1} lipid weight), carbon and nitrogen isotope ratios ($\delta^{13}C$, $\delta^{15}N$), cytochrome P450 enzyme activities (CYP), body mass and hepatic lipid content (arithmetic mean ± SE, (min–max)) in four seabird species[a] from the Barents Sea, May 1999

	Vicinal H-atoms in		# Cl in	Little auk,	Brünnich's guillemot,	Black guillemot,	Kittiwake,
	only *om*[b]	*mp*[c]	*ortho*	*Alle alle*	*Uria lomvia*	*Cepphus grylle*	*Rissa tridactyla*
PCBs							
∑NO-PCBs[d]			0	1.4 ± 0.1 (0.9–2.5)	1.0 ± 0.1 (0.5–1.3)	1.1 ± 0.2 (0.4–2.4)	1.3 ± 0.4 (0.4–4.0)
∑MO-PCBs[e]			1	869.3 ± 161.7 (425.8–2023.8)	572.4 ± 68.0 (315.9–1032.2)	684.9 ± 52.8 (398.1–1027.2)	1402.9 ± 185.4 (696.7–2351.2)
∑DI-PCBs[f]			2	2339.8 ± 412.5 (1068.6–4724.8)	891.6 ± 132.2 (365.5–1615.8)	1562.1 ± 114.8 (923.4–2357.5)	5990.2 ± 900.0 (2178.3–9960.9)
∑PCB group I[g]	–	–	0–4	1340.5 ± 234.2 (590–2745.7)	500.9 ± 67.8 (141.9–813.3)	690.6 ± 40.5 (469.9–933.5)	3994.6 ± 639.7 (1373.0–7024.4)
∑PCB group II[h]	+	–	=2	1083.2 ± 201.7 (482.2–2254.9)	447.2 ± 71.0 (208.6–875.1)	706.6 ± 52.5 (426.3–1066.5)	2483.218 ± 350.2 (965.8–3905.4)
∑PCB group III[i]	+	–	<2	868.5 ± 161.7 (424.9–2023.2)	561.8 ± 67.3 (296.5–1016.0)	667.28660 ± 52.4 (386.8–1010.6)	1380.603 ± 181.4 (689.1–2298.3)
∑PCB group IV[j]		+	=2	159.0 ± 25.7 (73.5–300.6)	40.0 ± 4.3 (23.4–59.9)	274.9 ± 31.8 (98.9–491.3)	108.2 ± 17.9 (51.2–230.0)
∑PCB group V[k]	–	+	>2	33.4 ± 3.5 (18.5–52.9)	4.4 ± 1.1 (2.2–12.8)	61.6 ± 6.6 (25.0–110.4)	31.5 ± 4.3 (19.3–65.4)
∑PCBs[l]				3483.0 ± 605.9 (1631.7–6787.6)	1545.2 ± 204.4 (712.7–2749.8)	2383.3 ± 176.7 (1395.7–3595.2)	7981.0 ± 1161.2 (3110.6–12794.9)
∑TEQ[m]				0.16 ± 0.04 (0.10–0.27)	0.08 ± 0.01 (0.05–0.10)	0.08 ± 0.01 (0.06–0.11)	0.17 ± 0.02 (0.06–0.32)
∑TEQ wet weight				0.01 ± 0.00 (0.003–0.01)	0.00 ± 0.00 (0.001–0.004)	0.00 ± 0.00 (0.001–0.005)	0.01 ± 0.00 (0.005–0.01)
Diet descriptors							
$\delta^{13}C$ (‰)				−21.4 ± 0.1 −22.0 to −20.8	−21.0 ± 0.1 −21.3 to −20.6	−21.9 ± 0.1 −22.1 to −21.6	−21.3 ± 0.1 −21.9 to −20.8
$\delta^{13}N$ (‰)				10.5 ± 0.1 9.5–11.0	13.1 ± 0.1 12.8–13.6	14.2 ± 0.1 13.7–15.0	13.5 ± 0.1 12.9–14.2
Trophic position[n]				3.0 ± 0.04 2.7–3.1	3.7 ± 0.02 3.6–3.80	4.0 ± 0.03 3.8–4.2	3.8 ± 0.04 3.6–4.0
CYP activities (pmol min^{-1} mg $protein^{-1}$)							
EROD[o]				36.9 ± 3.2 21.3–51.3	8.2 ± 1.5 3.0–16.2	10.1 ± 0.7 7.0–13.4	12.0 ± 1.4 4.7–20.3
Testosterone 6β-hydroxylation				118.5 ± 7.8 87.2–175.9	139.7 ± 14.8 78.3–211.4	89.8 ± 9.7 59.9–160.5	129.1 ± 8.3 94.2–167.2
Body mass (g)				181.0 ± 3.6 165.0–195.0	1053.2 ± 17.7 965.0–1130.0	465.0 ± 21.9 370.0–560.0	421.2 ± 13.0 370.0–500.0
Hepatic lipid content (%)				4.1 ± 0.2 3.2–4.9	3.6 ± 0.4 2.5–6.0	5.3 ± 1.0 2.5–13.8	7.7 ± 1.3 3.0–14.5

[a] Five males (M) and 5 females (F) were analysed from each species, except for the analysis of non-*ortho* Cl-substituted PCBs where $n = 4, 5, 5, 6$ for in little auk (1F/3M), Brünnich's guillemot (2F/3M), black guillemot (4F/1M) and kittiwake (3F/3M), respectively.
[b] *Ortho–meta* position.
[c] *Meta–para* position.
[d] ∑NO-PCBs = PCB-77, -81, -126, -169. Non-*ortho* Cl-substituted PCBs.
[e] ∑MO-PCBs = PCB-28, -31, -66, -74, -105, -118, -156, -157, -189. Mono-*ortho* Cl-substituted PCBs.
[f] ∑DI-PCBs = PCB-47, -52, -99, -101, -110, -128, -137, -138, -141, -153, -170, -180, -194. Di-*ortho* Cl-substituted PCBs.
[g] ∑PCB group I = PCB-153, -169, -180, -183, -187, -189, -194, -196, -206, -209 (no vicinal H-atoms).
[h] ∑PCB group II = PCB-47, -99, -128, -137, -138, -170 (vicinal H-atoms only in *ortho–meta* positions, ≥2 Cl in *ortho*-position).
[i] ∑PCB group III = PCB-28, -66, -74, -77, -81, -105, -126, -118, -156, -157 (vicinal H-atoms only in *ortho–meta* positions, <2 Cl in *ortho*-position).
[j] ∑PCB group IV = PCB-31, -52, -101, -110, -141 (vicinal H-atoms in *meta–para* positions, ≤2 Cl in *ortho*-position). PCB-31 and -110 have vicinal H-atoms also in *ortho–meta* positions.
[k] ∑PCB group V = PCB-149, -151, -199 (vicinal H-atoms in *meta–para* positions, >2 Cl in *ortho*-position).
[l] ∑PCBs = sum of all analysed congeners.
[m] ∑TEQ based on all NO-PCB and the MO-PCB congeners -105, -118, -156, -157, -189.
[n] Trophic position = $3 + ((\delta^{15}N - 10.1)/3.8)$, based on Fisk et al. (Fisk et al., 2001a).
[o] EROD = ethoxyresorufin *O*-deethylation.

1997). Group I is persistent due to lack of vicinal hydrogen atoms (H), and groups II and III have vicinal H-atoms only in *ortho–meta* positions. Metabolism of group II is inhibited due to the steric hindrance by di-*ortho* Cl-substitution, whereas group III may be metabolised by CYP1A mediated enzymes due to non- or mono-*ortho* Cl-substitution (*om*-congeners). Groups IV and V may be metabolised due to vicinal H-atoms in *meta–para* positions (*mp*-congeners), group IV with two or less *ortho* Cl-substitutions and group V with more than di-*ortho* Cl-substitutions. Furthermore, the congeners were categorised as non-, mono-, or di-*ortho* Cl-substituted (NO-, MO-, or DI-PCBs, respectively), with respectively decreasing coplanar configuration and ability to induce CYP1A-like isoenzymes through binding to the aryl hydrocarbon receptor. Based on avian toxic equivalency factors (TEFs) for dioxin-like PCBs (Van den Berg et al., 1998), $\sum$toxic equivalent concentrations (TEQs) were calculated for NO- and MO-PCBs based on wet weight concentrations. The TEF approach assumes that the toxic response through the Ah-receptor is dose or concentration additive, and the TEFs were recommended based on various in vivo and in vitro dose–response curves for different avian species (Van den Berg et al., 1998).

The PCB pattern in seabirds and their prey was calculated as a proportion of each congener to the recalcitrant PCB-153 ($R_{\text{PCB-153}}$). The metabolic index (MI) was calculated to determine the accumulation of a congener in seabirds relative to the accumulation of PCB-153 ($\text{MI} = R_{\text{PCB-153\_seabird}}/R_{\text{PCB-153\_prey}}$) (Tanabe et al., 1988). The seabirds' diet composition was assumed to be the same as described above for calculation of feeding rate.

SAS 8.0 for Windows (SAS Institute Inc., 1989) was used for univariate statistics (ANOVA Type III Sum of Squares, Tukey–Kramer's test, Spearman rank correlations (r_s)), such as interspecific comparison of lipid content, stable isotope ratios and CYP activities. For correlations such as between different PCB groups and CYP enzyme activities, ANOVA Type III Sum of Squares was used with species as covariant to account for the effect of species. The comparison of PCB concentrations among species was done on lipid adjusted concentrations, as the hepatic lipid content differed among species (ANOVA, $F_{3,36} = 4.71$, $p = 0.0071$).

Direct (constrained) multivariate ordination analysis (redundancy analysis RDA) was carried out in CANOCO 4.5 for Windows (Ter Braak and Šmilauer, 1998) to analyse the structure in the seabirds' PCB concentrations and patterns ($R_{\text{PCB-153}}$ values), and to relate this structure to the explanatory variables δ^{15}N, δ^{13}C, EROD, testosterone hydroxylation, sex, feeding rate and species identity. To reduce variance heterogeneity and skewness, data were log-transformed prior to ordination, which was performed on the variance–covariance matrix, adjusting for lipids in the ordination of concentrations. Since NO-PCBs were analysed in 4–6 samples per species (see Table 1 footnote), they were excluded from the ordination analyses. Initially, the analyses only included congeners found in all species, thus excluding PCB-31, -52, -110, -141, -149, -151, -189, -199 and -206. Values below quantification limit (1% of the data) were replaced by randomly generated normally distributed data, assuming ½ the detection limit as the mean, with 40% variation (StatPlus V2.5 in Excel 2002 for Windows). However, as this excluded most *mp*-congeners, also congeners missing from only one species were included. This resulted in a final inclusion of 24 congeners and exclusion of PCB-141, -151, -189, -199 and -206, and missing values were replaced as described above (6.7% of the data). Congeners with low $R_{\text{PCB-153}}$ ($<5\%$) and high cumulative fits ($>50\%$) (PCB-31 and -196), were excluded from the final RDA to avoid that congeners associated with higher uncertainty dominated the ordination. Significant explanatory variables were forward selected manually using Monte Carlo test with unrestricted permutations ($\alpha = 0.05$) (Ter Braak and Šmilauer, 1998). After selecting significant explanatory variables, the significance of each extracted canonical axis was analysed by Monte Carlo test with unrestricted permutations under the reduced model ($\alpha = 0.05$). To investigate the relationship between seabird species and the highly species-specific explanatory variables, an initial RDA was performed with seabird species as explanatory variable, and diet (δ^{15}N and δ^{13}C), feeding rate and CYP activity (EROD and testosterone 6β-hydroxylation) as response variables.

The multivariate ordination assigns scores to the samples (e.g. individual birds) and response variables (e.g. PCB congeners). The scores are linear combinations of the explanatory variables and are presented relative to their ordination axes (Figs. 1, 2 and 5). PCBs are presented as arrows pointing to the direction of increasing value. Categorical and continuous explanatory variables are presented by centroids (e.g. seabird species) and arrows (e.g. feeding rate), respectively. Rules of interpretation of the diagram are described elsewhere (Ter Braak, 1995; Van Wijngaarden et al., 1995; Van den Brink and Ter Braak, 1999).

3. Results

3.1. Seabird characteristics

All seabirds were adults, except for black guillemot of which 7 were yearlings. Little auk was by far the smallest and lightest species (Table 1), whereas black guillemot and kittiwake had intermediate weights followed by Brünnich's guillemot as the heaviest species (Tukey–Kramer, $p < 0.05$ for all comparisons except between

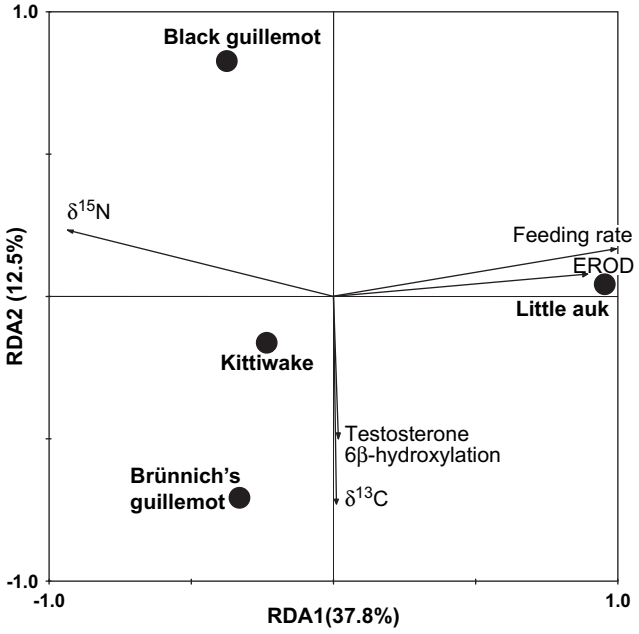

Fig. 1. Direct multivariate ordination analysis (redundancy analysis RDA) of relationship between the four seabird species and chemically-derived trophic position (δ^{15}N) and carbon source (δ^{13}C), feeding rate and CYP activities (EROD and testosterone 6β-hydroxylation). Black circles are centroid scores of the seabird species (mean of samples per species), whereas arrows are continuous response variables (diet, enzyme activity and feeding rate) pointing in the direction of increasing values. Seabird species explained 50.5% of the total variance, and the fraction of the unconstrained explained variance displayed by each ordination axis is given in brackets.

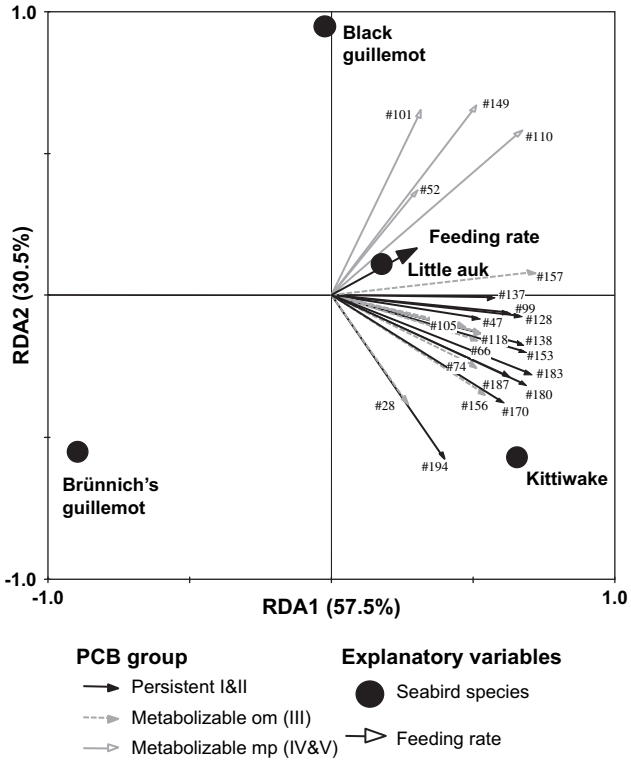

Fig. 2. Biplot (from redundancy analysis RDA) of PCB concentrations in four different seabird species from the Barents Sea in May 1999 with significant explanatory variables ($p = 0.002$). Nominal explanatory variables are given as centroids (mean of samples per species), and arrows of PCBs and feeding rate point in the direction of increasing values. The total variation (53.4%) was accounted for by the constrained ordination, and each axis' contribution is given in brackets. The fraction of unconstrained variance accounted for by each axis is given in brackets. The PCB grouping is according to Table 1.

kittiwake and black guillemot). As body mass was used to calculate weight- and species-specific feeding rates, body mass was replaced by feeding rate in the RDA. The feeding rates were 0.80, 0.35, 0.42, 0.43 g day^{-1} g^{-1} for little auk, Brünnich's guillemot, black guillemot and kittiwake, respectively.

Of the total variance in feeding rates, carbon source, trophic position and CYP activities, 50.5% was explained by the seabird's phylogeny (Fig. 1). Higher EROD activity and feeding rate, and lower trophic position was found in little auk than in the other species, and lower testosterone 6β-hydroxylation and δ^{13}C levels were found in black guillemot than in the other seabirds (Fig. 1). The ordination axes significantly related the variance of the explanatory variables to seabird species (Monte Carlo $F = 12.2$, $p = 0.002$, for all axes). More specifically, the interspecific variance in δ^{13}C values was minor, ranging from -22.1 to -20.6‰ (Table 1), with lowest δ^{13}C values for black guillemot, intermediate for little auk and kittiwake, and highest for Brünnich's guillemot (Tukey–Kramer, $p < 0.05$ for all comparisons except between kittiwake and little auk or Brünnich's guillemot) (Fig. 1). Little auk had the lowest trophic position (range: 2.7–3.1) assigned by δ^{15}N, Brünnich's guillemot and kittiwake had intermediate trophic positions (range: 3.6–4.0), and black guillemot the highest (range: 3.8–4.2) (Tukey–Kramer, $p < 0.05$ for all comparisons except between kittiwake and Brünnich's guillemot) (Fig. 1). When species variation was accounted for, δ^{13}C and trophic position were not related (ANOVA $F_{1,34} = 0.61$, $p = 0.4402$).

The EROD activity ranged from 3 to 51 pmol min^{-1} mg protein^{-1} and was higher in little auk than the other species (Table 1, Fig. 1, Tukey–Kramer, $p < 0.05$). Testosterone hydroxylation activity was only observed at the 6β-position, and ranged from 50 to 250 pmol min^{-1} mg protein^{-1} (Table 1). The testosterone 6β-hydroxylation was lower in black guillemot than in Brünnich's guillemot and kittiwake, whereas no difference was found between the other species (Fig. 1, Tukey–Kramer, $p < 0.05$). When species variation was accounted for, the CYP activities were not correlated (ANOVA, $F_{1,37} = 0.03$, $p = 0.8528$).

Neither carbon source, trophic position nor CYP activities differed between males and females within each species (ANOVA, $F_{1,8} < 2$, $p > 0.200$). When species variation was accounted for, the CYP activities were not related to body mass (ANOVA $F_{1,34} < 2.8$ $p > 0.1035$),

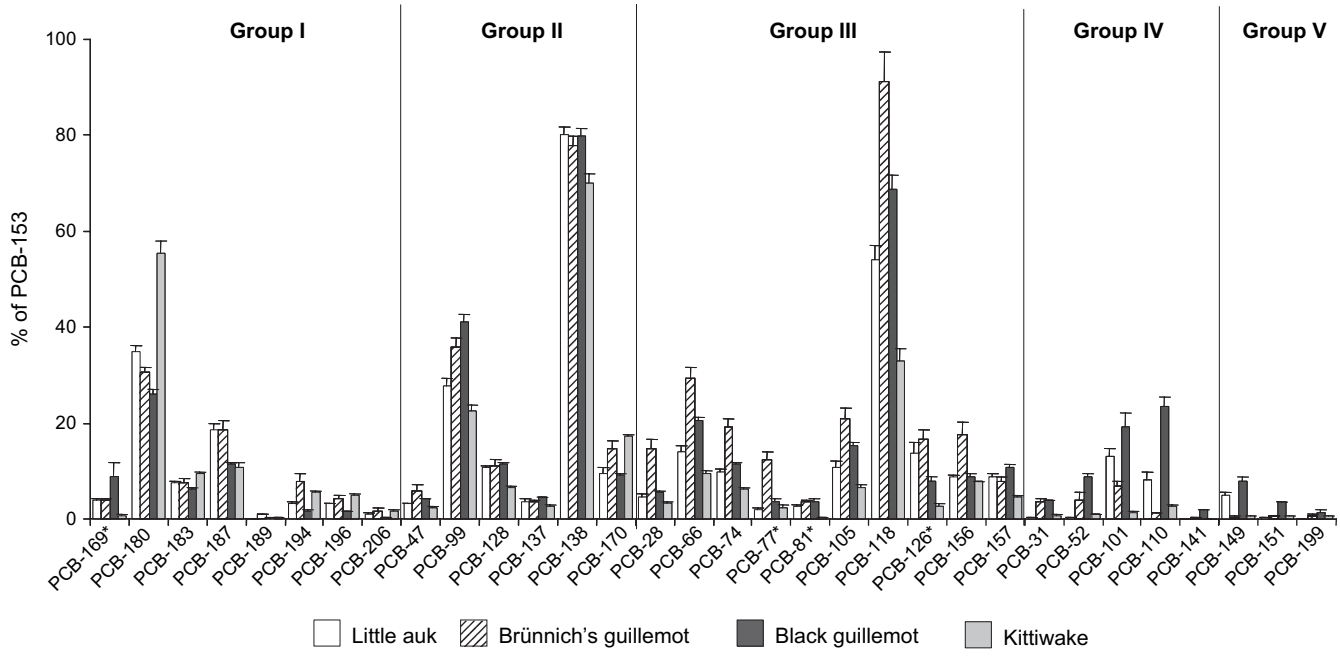

Fig. 3. Polychlorinated biphenyl (PCB) pattern in four different seabird species from the Barents Sea in May 1999 is presented as values relative to PCB-153 ($R_{PCB\text{-}153}$ values) (mean + SE). Sample size $n = 10$ for each species, except for Brünnich's guillemot where one extreme was excluded, and except for PCB-77, -81, -126, and -169, where four to six birds were analysed per species (see Table 1 footnote). *PCB-77, -81, -126, and -169 were multiplied with 100 to make visible on the same scale as the other congeners. The PCB grouping is according to Table 1.

however, the smallest species (little auk) had the highest EROD activities (Table 1).

3.2. PCB concentrations and patterns, TEQ values and metabolic indices

∑PCBs ranged from 700 to 13 000 ng g^{-1} lipid weight, depending on species (Table 1). The individual sums of persistent PCBs (groups I and II) were highest in kittiwake followed by little auk and black guillemot, and then by Brünnich's guillemot (Table 1, Tukey, $p < 0.05$). The *om*-metabolizable PCB group III was higher in kittiwake than all other species (Table 1, Tukey, $p < 0.05$). The *mp*-metabolizable PCB groups IV and V were highest in black guillemot, followed by little auk and kittiwake, and then by Brünnich's guillemot (Tukey, $p < 0.05$).

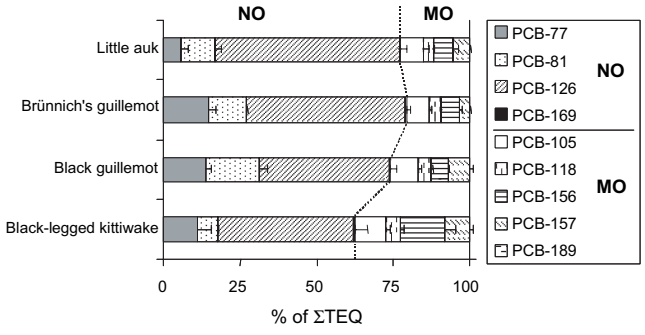

Fig. 4. Relative contribution (arithmetic mean + 1SE) of non- (NO) and mono-*ortho* (MO) polychlorinated biphenyls (PCBs) to ∑toxic equivalent concentrations (TEQ). Only PCBs with toxic equivalent factors in Van den Berg et al. (1998) are included.

Direct ordination (RDA) of PCB concentrations resulted in the four seabird species and feeding rate as significant explanatory variables (Monte Carlo $F = 15.9–23.8$, $p = 0.002$ for all variables) (Fig. 2). Feeding rate correlated highly with species identity and was automatically selected along with species, pointing in direction of little auk, although it did not contribute in explaining additional variance in PCB concentrations. Even though three ordination axes significantly explained the variation in PCB concentrations (Monte Carlo $F = 12.5–21.7$, $p = 0.002$ for all axes), only axes 1 and 2 are presented due to the higher degree of variance explained (42.0, 22.3, 9% of total variance explained by axes 1, 2 and 3, respectively). The seabirds species differed significantly in PCB concentrations (ANOVA of samples' scores on ordination axes, $p < 0.0001$), however, little auk was not different from kittiwake and black guillemot along axis 1, Brünnich's guillemot was not different from kittiwake along axis 2 and from kittiwake and black guillemot along axis 3 (Tukey test of samples' scores on ordination axes, $p < 0.05$). When the effect of species was accounted for, neither chemically-derived trophic position nor carbon source, CYP activities or sex explained the differences in PCB

concentrations among species, due to their high degree of species-dependency as illustrated in Fig. 1.

The NO-PCB concentrations were low relative to other PCB congeners, with mean sum ranging from 1.0 to 1.4 ng g^{-1} lipid weight depending on species (Table 1). The concentrations of NO-PCBs were lower than 0.2% of PCB-153 for each congener, whereas the concentrations of MO-PCBs were higher, more than 10% of the PCB-153 concentration for all congeners (Fig. 3). Mean ∑TEQ ranged from 1 to 13 pg g^{-1} wet weight, depending on species (Table 1). Highest TEQ values were found in little auk and Brünnich's guillemot. Although the MO-PCB concentrations were higher than the NO-PCB concentrations, NO-PCBs contributed 70–80% to ∑TEQ, depending on species (Fig. 4). When species variation was accounted for, neither concentrations of ∑PCB, ∑NO-, ∑MO-, ∑DI-PCBs nor ∑TEQ were related to chemically-derived trophic position or carbon source or CYP activities (ANOVA $F_{4,35} < 2.89$, $p > 0.0986$ for all analyses).

The PCB pattern in all species was dominated by the persistent PCB-153, -138, -118, -180 and -99 (Fig. 3). The persistent PCBs (groups I and II) contributed 74–90% to ∑PCBs in kittiwake, whereas the contribution of groups IV and V to ∑PCBs was <3% (Table 1). PCB groups VI and V contributed 2–17% to ∑PCBs in auks. Compared to the other species, Brünnich's guillemot had high $R_{PCB\text{-}153}$-values of most PCBs in groups II and III, whereas black guillemot had high $R_{PCB\text{-}153}$-values of groups IV and V. Kittiwake had low $R_{PCB\text{-}153}$-values of group IV. RDA of the seabirds' $R_{PCB\text{-}153}$-values showed the same differences between species as inferred from the individual $R_{PCB\text{-}153}$-values (Fig. 5), and all seabird species differed significantly in PCB pattern (ANOVA of samples' scores on ordination axes, $p < 0.0001$). More specifically, both little auk and black guillemot differed from Brünnich's guillemot by having high relative proportion of metabolizable *mp*-congeners (groups IV and V), whereas Brünnich's guillemot had more metabolizable *om*-congeners (group III) (Tukey test of samples' scores on ordination axes, $p < 0.05$). Common for the auks was a higher relative contribution of metabolizable PCBs compared to kittiwake (Fig. 5). The only significant explanatory variable was seabird species and feeding rate (Monte Carlo $F = 3.75$–6.25, $p = 0.002$–0.006), whereas the other explanatory variables did not contribute to explain additional variance. Sex did not explain any variation in the seabirds' PCB pattern (results not shown). Of the total variance, 16.0, 10.7 and 6.9% were explained by axes 1, 2 and 3, respectively, which significantly explained the extracted variation in $R_{PCB\text{-}153}$-values (Monte Carlo $F = 5.88$, $p = 0.002$).

When species variation was accounted for, the relative contribution of congener group III to ∑PCBs slightly decreased with increasing EROD activity

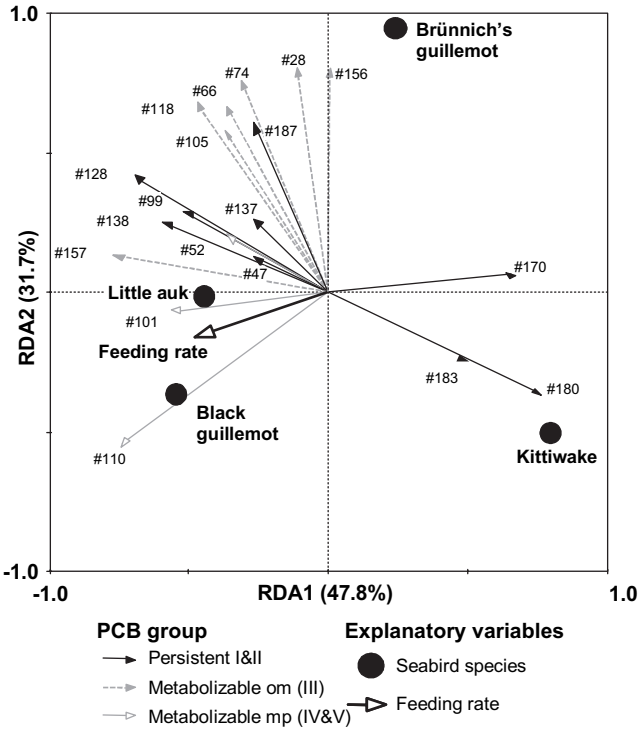

Fig. 5. Ordination diagram of PCB pattern ($R_{PCB\text{-}153}$ values) in four different seabird species from the Barents Sea in May 1999 with significant explanatory variables ($p = 0.002$). Nominal explanatory variables are given as centroids (mean of samples per species), and arrows of PCBs and feeding rate point in the direction of increasing values. The total variation (33.5%) was accounted for by the constrained ordination, and each axis' contribution is given in brackets. The PCB grouping is according to Table 1.

(ANOVA, $F_{4,35} = 3.91$, $p = 0.0558$). The other metabolic groups did not show any relationship between their relative contribution to ∑PCBs and CYP enzymes.

The seabirds' metabolic indices (MI), which reflects the seabirds' congener pattern adjusted for the prey's PCB content (prey PCB concentration in Table 2), differed among PCBs in species-specific manner (Fig. 6). All seabirds had low bioaccumulation of *mp*-congeners

Table 2
Lipid content (%) and polychlorinated biphenyl (PCB) concentrations (ng g^{-1} lipid weight) in the seabirds' main zooplankton and fish prey from the Barents Sea in May 1999 (arithmetic mean ± SE)

Species	Group	*n*	Lipid	∑PCB9[e]
Calanus glacialis and *C. hyperboreus*[a]	Copepod	15	2.6 ± 0.2	43.3 ± 4.6
Thysanoessa inermis[b]	Euphausiid	9	1.8 ± 0.2	74.5 ± 8.8
Themisto libellula[c]	Amphipod	3	1.9 ± 0.4	120.2 ± 27.1
Boreogadus saida[d]	Fish	12	3.8 ± 0.4	120.6 ± 22.6

[a] Samples of 580–1135 pooled individuals.
[b] Samples of 100–115 pooled individuals.
[c] Samples of 7–16 pooled individuals.
[d] Samples of individually homogenized fish.
[e] ∑PCB9 = PCB-28, -31, -52, -99, -105, -118, -138, -153, -180.

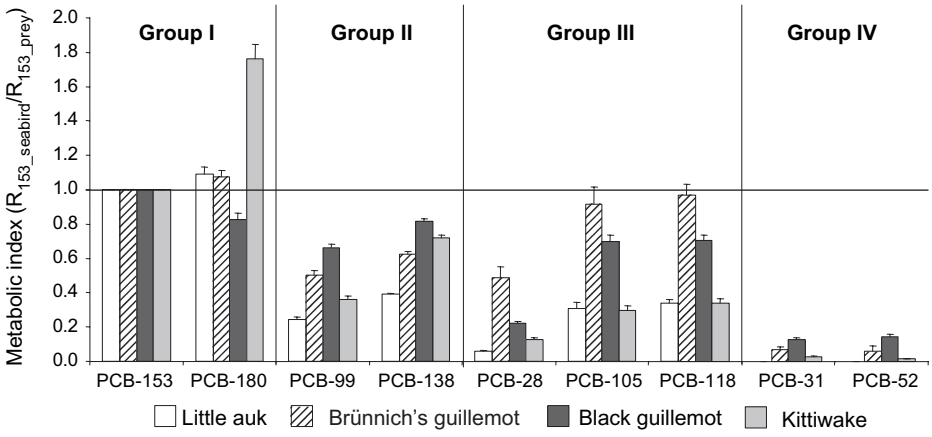

Fig. 6. PCB pattern in four different seabird species from the Barents Sea in May 1999 adjusted for the pattern in the mean prey (metabolic index = $R_{PCB\text{-}153\_seabird}/R_{PCB\text{-}153\_prey}$) (mean + SE). The metabolic index describes whether a congener accumulates more (>1) or less (<1) than the persistent PCB-153. The PCB groups refer to the structure described in Table 1.

relative to PCB-153 (groups VI and V, MIs < 0.2), and intermediate bioaccumulation of *om*-congeners relative to PCB-153 (group II and III, MI ≈ 0.2–1). They had highest bioaccumulation relative to PCB-153 of persistent congeners without vicinal H-atoms (group I, MIs ≈ 1–2) (Fig. 6).

4. Discussion

The present study shows that PCB concentrations and congener patterns in seabirds result from a combined effect of dietary factors and biotransformation. The independent effect of each of these factors is difficult to assess due to their high species-specificity and, thus, collinearity. Another factor confounding the relationships may be the different time-scales regarding changes in an organism's PCB concentrations, CYP activities and stable isotope ratios. Contaminant half-lives in birds are months to years (Clark et al., 1987; Drouillard and Norstrom, 2003), CYP activities may reflect physiological changes over days (Schuetz et al., 1984), and stable isotope ratios may reflect dietary and conditional changes on the basis of weeks to months (Hobson and Clark, 1992). Given the lack of year-specific age-determination, age-related PCB accumulation and CYP activity could not be accounted for in this study.

4.1. PCB concentrations and TEQs in Arctic seabirds

Although comparison of PCB residues between studies is difficult due to variation caused by confounding factors such as the organism's age, sex, reproductive cycle and condition (e.g. Henriksen et al., 1996), the hepatic PCB concentrations were compared with corresponding levels in similar species from earlier studies on a lipid weight basis. No studies are available on NO-PCBs and TEQ values in these seabird species from the European Arctic, or on hepatic PCB concentrations in little auk from the European Arctic.

When compared to other Arctic seabirds, the present ∑PCB concentrations in black and Brünnich's guillemot were comparable to, or in the higher range of, those recently reported from east and west Greenland and northern Baffin Bay in the Canadian Arctic, whereas the present kittiwake and little auk levels were higher than those reported from Greenland and Canada (de Wit et al., 2004; Buckman et al., 2004). Higher PCB concentrations in the Barents Sea biota have also been reported in seabird eggs and marine mammals (ringed seals *Phoca hispida* and polar bears *Ursus maritimus*) (de March et al., 1998; Muir et al., 2000; de Wit et al., 2004).

For the European Arctic, ∑PCB concentrations in black and Brünnich's guillemots were generally within the same range, or in the lower range, as those reported from the Barents Sea marginal ice zone in June 1995 (Borgå et al., 2001a). The present mean levels in kittiwake were generally lower than those reported from the Svalbard area in 1991 (Savinova et al., 1995), the north Norwegian coast in 1992 (Henriksen et al., 1996), and Bjørnøya in the southern Barents Sea in June 1995 (Borgå et al., 2001a).

The present study's PCB–TEQs were lower than in similar species from the Canadian Arctic in 1993 (Braune and Simon, 2003). The present lower PCB concentrations and TEQ values are in accordance with a general temporal decrease in Arctic PCB levels, as reported for seabirds' eggs (Barrett et al., 1996; Braune et al., 2001) and polar bears (Henriksen et al., 2001).

4.2. Influence of dietary exposure and sex on PCB levels and patterns

The $\delta^{13}C$ varied between species, with lowest and highest values in black and Brünnich's guillemot,

respectively. Because the $\delta^{13}C$ values reflect the source of carbon to a system, species with enriched $\delta^{13}C$ values are usually influenced by terrestrial carbon from benthic or inshore feeding, whereas offshore pelagic feeders often have lower $\delta^{13}C$ values (Hobson, 1993). However, the present range of $\delta^{13}C$ values was much smaller than in studies where true benthic (e.g. common eider *Somateria mollisima*) and pelagic feeders (e.g. northern fulmar *Fulmarus glacialis*) are compared (Dahl et al., 2003). The seabirds' trophic positions determined by stable nitrogen isotopes generally confirmed those inferred from dietary data. Trophic position was lowest for little auk, intermediate for Brünnich's guillemot and kittiwake and highest for black guillemot. Being predominantly fish-feeders, black guillemot and kittiwake were expected to occupy the same trophic position (Lønne and Gabrielsen, 1992; Mehlum and Gabrielsen, 1993), but black guillemot had higher $\delta^{15}N$ values than kittiwake. Relatively high $\delta^{15}N$ in black guillemot was also shown in previous studies (Fisk et al., 2001a; Hop et al., 2002). This indicates that black guillemot feeds higher in the food web, presumably on demersal or larger fish during pursuit diving, whereas kittiwake is a surface feeder on smaller pelagic fish, and occasionally on amphipods and euphausiids (Lønne and Gabrielsen, 1992; Mehlum and Gabrielsen, 1993).

Increasing PCB levels with trophic position have been shown previously for seabirds and seals in Arctic marine food webs (Fisk et al., 2001a; Hop et al., 2002), and among Arctic seabirds from the Canadian Arctic (Buckman et al., 2004). In the present study, however, PCB levels were high in little auk occupying the lowest trophic position, and generally lower in black guillemot occupying the highest trophic position. Likewise, kittiwakes had lower $\delta^{15}N$ and higher PCB concentrations than black guillemot. In the Canadian Arctic studies, seabird species spanning over a larger range of trophic positions were included, from little auk (trophic level 3) to glaucous gull (trophic level 5) (Buckman et al., 2004). However, in glaucous gulls from Bjørnøya, Barents Sea, only a weak relationship was reported between organochlorine levels and trophic position (Sagerup et al., 2002). The present study's discrepancy between $\delta^{15}N$ and PCB concentrations may be due to different turnover rates of proteins versus contaminants, suggesting a previous diet of more contaminated prey for kittiwake in the over-wintering area or by occasionally feeding on seal blubber from carcasses after polar bear kills (Lønne and Gabrielsen, 1992). As the stable isotopes have half-lives of less than 30 days in muscle (Hobson and Clark, 1992), the $\delta^{15}N$ in kittiwake reflects the diet in the marginal ice zone rather than in the over-wintering area. Black guillemot, on the other hand, is an Arctic resident throughout the year (Anker-Nilssen et al., 2000) and is not observed feeding on seal carcasses. In addition, a higher metabolic rate, and thus feeding rate, in gulls compared to auks of similar size (Ellis and Gabrielsen, 2002), may contribute to higher PCB concentrations in kittiwake compared to black guillemot. Finally, the low PCB levels in black guillemots may be due to their young age (yearlings). Generally juveniles have accumulated less contaminant than adults (Donaldson et al., 1997; Bustnes et al., 2003), and their PCB levels might not yet have reached equilibrium with the dietary contaminant exposure.

Alternative prey and migration does not help explain the high PCB levels in little auk, which is a northern species and a strict feeder on herbivorous calanoid copepods with low trophic position and contaminant concentrations (Hop et al., 2002). However, like in kittiwakes, the higher feeding rate in little auk (due to its lower body mass) may contribute to the relatively high PCB concentrations, despite its low trophic position. Increased feeding rate was found to increase the PCB uptake rate constant from food in experimental studies of ringed doves (*Streptopelia rissoria*) (Drouillard and Norstrom, 2003). In addition, the high lipid contents in calanoid copepods (40% of dry weight, (Scott et al., 1999)) might contribute to elevated PCB concentrations in little auk if the higher assimilation efficiency of lipids than proteins (Brekke and Gabrielsen, 1994) influences the PCB uptake (Gobas et al., 1999). However, the ringed dove study showed that PCB assimilation efficiencies were similar between doves fed a high or a low lipid content diet (Drouillard and Norstrom, 2003).

Like in Canadian Arctic seabirds (Buckman et al., 2004), there were no sex differences in PCB concentrations. However, sample sizes in both studies were small (<7 per sex and species), hence the results must be treated with some caution.

4.3. CYP enzymes in relation to PCB concentrations and TEQ values

The seabirds' EROD and testosterone hydroxylation activities differed among species, although auks were not distinctly different from kittiwakes. Little auk had the highest EROD activity compared to the other species, and higher than that measured in glaucous gull from the same area (Henriksen et al., 2000). The EROD activity in the other seabirds was lower than in glaucous gulls. Overall, the EROD activities were low compared to seabirds from more industrialised areas (Bosveld and Van den Berg, 1994). However, comparisons between studies should be done with caution as species differ widely in CYP response and as inter-laboratory differences in CYP-assays may cause additional variation between studies (Bosveld and Van den Berg, 1994).

NO- and MO-PCBs are known inducers of CYP1A enzymes (Safe, 1994), however, EROD activity was neither related to $\sum$NO-, $\sum$MO-PCB concentrations,

or ∑TEQs. The present study's seabird TEQ values were 100–200 times lower than the lowest observable effect level (LOEL) for CYP1A induction (EROD) in common terns (*Sterna hirundo*) (25 ng g^{-1} TEQ lipid weight liver) (Bosveld et al., 2000). Even though the effect threshold varies depending on species and sample matrix, the presently investigated Arctic seabirds therefore seem well below the threshold levels for effects mediated through the Ah-receptor. In the present study, the TEQ values were calculated from NO- and MO-PCBs. In Canadian Arctic kittiwake and Brünnich's guillemot, NO-PCB contributed 40–60% to ∑TEQ when TEQs were calculated also for furans and dioxins (Braune and Simon, 2003).

The high EROD activity in little auk compared to the other auks and kittiwake may be caused by a higher feeding rate (Braune and Norstrom, 1989; Ronis and Walker, 1989), but also by a diet with different inducers, including natural inducers such as carotenoids from the calanoid copepods. Calanoid copepods are rich in carotenoid pigments that may induce EROD activity (Gradelet et al., 1996), which in combination with a higher feeding rate results in higher exposure to inducers of CYP1A. Similar to glaucous gulls from the Barents Sea (Henriksen et al., 2000), testosterone hydroxylation was only observed at the 6β-position at comparably low levels in all seabirds. EROD and testosterone 6β-hydroxylation activities were not correlated, suggesting involvement of different CYP enzymes.

4.4. PCB pattern and biotransformation abilities

Contrary to previous avian studies (e.g. Borlakoglu et al., 1990), the PCB patterns differed significantly among the seabirds in the present study, especially between kittiwake and auks, but also among the auks. The higher relative contribution of persistent PCBs, such as in kittiwake than in auks, suggests a higher ability in the former to biotransform PCBs. Although the present CYP activities in all seabirds were low, the contribution of PCB group III (*om*-congeners) to ∑PCBs decreased with increasing EROD activity, suggesting that CYP1A-like activity influenced the PCB pattern. Despite higher PCB biotransformation in kittiwake, both EROD and testosterone 6β-hydroxylation activities were low and comparable to the guillemots. The finding of high contribution of persistent congeners and low CYP activities in kittiwake might be due to its migration and overwintering in more southern and industrialised areas. Feeding on more contaminated prey might result in a temporary induction of CYP-mediated enzymes, leading to increased PCB biotransformation and elevated relative proportion of persistent congeners in the PCB pattern. By the time of collection the CYP activities may have decreased to low levels due to the relatively low contamination levels in Barents Sea prey. Another explanation for the high concentrations of persistent PCBs in kittiwake may be an occasional seal blubber diet (Lønne and Gabrielsen, 1992), which will increase the exposure to persistent PCBs, as seals efficiently biotransform other PCBs (Wolkers et al., 1998).

The little auk seems to be the most efficient PCB biotransformer of the auks, due to its high relative contribution of persistent PCBs, low relative contribution of *om*-congeners compared to Brünnich's guillemot, and low relative contribution of *mp*-congeners compared to black guillemot. Higher metabolic capacity was found in Brünnich's guillemot than black guillemot for *mp*-congeners, whereas Brünnich's guillemot had higher relative contribution of *om*-congeners than black guillemot. The high relative contribution of *om*-congeners in Brünnich's guillemot concurs with its low EROD activity, and suggests a lower ability to metabolise these congeners compared to the other investigated species. As previous Canadian studies suggested elevated biotransformation of chlorinated pesticides in Brünnich's guillemot compared to other auks (Fisk et al., 2001b), biotransformation of PCBs and chlorinated pesticides in seabirds seems mediated through different enzyme systems. The higher contribution of *mp*-congeners in black guillemot than in Brünnich's guillemot coincided with the lowest testosterone 6β-hydroxylation, suggesting low CYP2B/3A activity and a consequently low biotransformation ability in black guillemot.

Some pattern-differences between species may also be due to dietary differences. However, the metabolic index (MI) confirmed the biotransformation difference among seabird species. Although the seabirds may have fed upon prey not adjusted for, there is only small difference in PCB patterns among prey (relative to that in seabirds) due to their low biotransformation ability (Borgå et al., 2001a). MIs for all congeners, except for PCB-180, were higher in black and Brünnich's guillemot than in kittiwake, supporting lower biotransformation in auks than in kittiwake. The relative high MIs for *om*-congeners, although there are interspecific differences, are in accordance with previous findings showing that these *om*-PCBs are slowly cleared from birds (Braune and Norstrom, 1989; Borlakoglu et al., 1990). Similarly, the low metabolic indices of *mp*-congeners indicate that these PCBs are readily cleared from birds, as shown previously (Braune and Norstrom, 1989; Borlakoglu et al., 1990).

In summary, the interspecific PCB pattern in seabirds suggests that the contaminant pattern is strongly linked to their phylogeny and species-specific differences in their enzyme system and activity, resulting both from long-term specialisation (potential) and on short-term exposure (induction). However, potential influence of age and sex on CYP induction and PCB concentrations in these species remains to be investigated.

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