



Sexual difference in PCB concentrations of coho salmon (*Oncorhynchus kisutch*)

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ABSTRACT

We determined polychlorinated biphenyl (PCB) concentrations in 35 female coho salmon (*Oncorhynchus kisutch*) and 60 male coho salmon caught in Lake Michigan (Michigan and Wisconsin, United States) during the fall of 1994 and 1995. In addition, we determined PCB concentrations in the skin-on fillets of 26 female and 19 male Lake Michigan coho salmon caught during the fall of 2004 and 2006. All coho salmon were age-2 fish. These fish were caught prior to spawning, and therefore release of eggs could not account for sexual differences in PCB concentrations because female coho salmon spawn only once during their lifetime. To investigate whether gross growth efficiency (GGE) differed between the sexes, we applied bioenergetics modeling. Results showed that, on average, males were 19% higher in PCB concentration than females, based on the 1994–1995 dataset. Similarly, males averaged a 20% higher PCB concentration in their skin-on fillets compared with females. According to the bioenergetics modeling results, GGE of adult females was less than 1% higher than adult male GGE. Thus, bioenergetics modeling could not explain the 20% higher PCB concentration exhibited by the males. Nonetheless, a sexual difference in GGE remained a plausible explanation for the sexual difference in PCB concentrations.

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1. Introduction

Higher polychlorinated biphenyl (PCB) concentrations in male fish compared with female fish has often been attributed to the shedding of eggs at spawning causing a substantial decline in PCB concentrations of females (Larsson et al., 1993, 1996; Johnston et al., 2002; Rypel et al., 2007). In the case of northern pike (*Esox lucius*) from a Scandinavian lake, Larsson et al. (1993) showed that PCB concentration in the ovaries of the northern pike was about 100 times higher than the whole-body PCB concentration. Consequently, PCB concentration in female northern pike was expected to decrease by nearly 80% immediately after release of eggs. Larsson et al. (1993) documented a decrease in PCB concentration of mature female northern pike with increasing age, whereas PCB concentration of mature males was expected to increase with increasing age. In all other cases, claims that the higher male PCB concentration was due to shedding of eggs were not supported by actual determinations of PCB concentrations in both ovaries and somatic tissue of females. Determinations of PCB concentrations of the ovaries and somatic tissue of female rainbow trout (*Oncorhynchus mykiss*), white sucker (*Catostomus commersoni*), smallmouth bass (*Micropterus dolomieu*), white bass (*Morone chrysops*), yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and lake trout (*Salvelinus namaycush*) have

indicated that release of eggs would not lead to a noticeable drop in PCB concentration of female fish (Niimi 1983; Madenjian et al., 1998b, 2009, 2010). Based on these findings, Madenjian et al. (2009) proposed that release of eggs at spawning could not explain sexual differences in PCB concentrations for most fishes.

Semelparity in fishes offers an approach toward understanding the factors responsible for sexual differences in PCB concentrations that heretofore has been unexplored. Most species of fish are iteroparous; that is, these fish spawn several times during their lifetime (Diana, 2004). Some species of fish, notably Pacific salmon species, spawn only once during their lifetime and then die; these fish are said to be semelparous (Diana, 2004). Quantifying sexual differences in PCB concentrations of adult semelparous fish prior to spawning would be useful in identifying factors causing sexual differences in PCB concentrations, because release of eggs could be ruled out as a plausible hypothesis for the observed sexual difference in PCB concentrations. Therefore, documentation of a sexual difference in PCB concentrations of adult semelparous fish prior to spawning would imply that factors other than release of eggs caused the observed sexual difference.

Coho salmon (*Oncorhynchus kisutch*), a semelparous fish native to the North Pacific, became established in Lake Michigan during the late 1960s via introduction of hatchery reared fish (Wells and McLain, 1972; Sandercock, 1991). Coho salmon populations have supported valuable fisheries both in the North Pacific and in the Laurentian Great Lakes (Sandercock, 1991; Kocik and Jones, 1999). Coho salmon are typically stocked as yearlings into Lake Michigan around the first of April (Stewart et al., 1981). Coho salmon mature during their second year in

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the lake. Typically, age-2 coho salmon congregate near river mouths during late September, and most of the spawning occurs in the rivers during October (Patriarche, 1980). Coho salmon die shortly after spawning.

Knowledge of the underlying causes for sexual differences in contaminant concentrations can be used to arrive at a more efficient sampling design for monitoring contaminant concentrations in fish, and can be used to forecast changes in contaminant concentrations under various environmental scenarios (Sheffy, 1980; Masnado, 1987; Madenjian et al., 1998b; Rypel et al., 2007). Moreover, identification of the important factors determining contaminant concentrations in fish can be used in managing a fishery to reduce contaminant exposure to people consuming fish (Stow et al., 1995).

In addition to release of eggs at spawning, sexual differences in PCB concentrations of fishes have also been attributed to sexual differences in gross growth efficiency (GGE) and sexual differences in habitat use (Madenjian et al., 1998b, 2009). PCB concentration in fish has been shown to be inversely proportional to GGE (Jackson and Schindler, 1996). Therefore, sexual differences in PCB concentrations could possibly be due to sexual differences in GGE. Bioenergetics modeling has been used to investigate sexual differences in GGE.

The objectives of this study were to: (1) determine the degree of difference between the sexes in PCB concentrations of coho salmon, and (2) ascertain whether bioenergetics modeling could explain a sexual difference in PCB concentrations of coho salmon.

2. Methods

2.1. Field methods

Mature but pre-spawning coho salmon were caught in Lake Michigan (by hook and line) and its tributaries (at state-operated weirs) in autumn 1994 and 1995, in conjunction with the Lake Michigan Mass Balance (LMMB) project sponsored by the Great Lakes National Program Office (GLNPO) of the U. S. Environmental Protection Agency. Fish were sacrificed by either a blow to the head or via suffocation while placed in a cooler with ice. All fish were measured (total length, to nearest mm) and weighed (to nearest 0.01, 0.025, or 0.05 kg, depending upon size and scale availability). Stomachs were removed and were either frozen or preserved in 10% formalin, and scales were taken for aging. Fish were then individually wrapped in acetone-rinsed aluminum foil, placed in a polyethylene bag, and frozen until transport to the Great Lakes Science Center (GLSC) for laboratory analysis. Holey and Elliott (1997) and Madenjian et al. (1998a) provide more details on field sampling methods and the LMMB project.

Mature but pre-spawning coho salmon were caught in the fall of 2004 and 2006 from spawning weirs located 6.5 km upstream from Lake Michigan on the Keweenaw and Root Rivers (Besadny Anadromous Fisheries Facility [BAFF], Keweenaw County and Root River Steelhead Facility in Racine County, Wisconsin USA), in conjunction with the salmon propagation program operated by the Wisconsin Department of Natural Resources (DNR). Fish were anesthetized with carbon dioxide until lethargic and then sacrificed with a blow to the head. In 2006, the total length of each fish was measured to the nearest mm, each fish was weighed to the nearest 0.01 kg, and the sex was determined at time of collection. In 2004, total length was measured to the nearest mm at time of collection. In both years, the coho salmon were individually wrapped in solvent-rinsed aluminum foil, then wrapped in kraft paper, and frozen at the fisheries facilities. The fish were later transported to the Wisconsin State Laboratory of Hygiene in Madison for laboratory processing.

2.2. Laboratory processing of coho salmon

At the GLSC, coho salmon were thawed and then composited into groups of five fish of the same sex, similar size, and similar time and

location of sampling. In total, 12 male and 7 female composites were derived from 95 age-2 coho salmon (verified by scale aging). Fish compositing was done to comply with the LMMB protocol (Holey and Elliott, 1997). Mean weight of the coho salmon was calculated for each composite. Each composite was homogenized using a commercial blender. About 50 g of the homogenate was placed in a contaminant-free glass jar, sealed with a lid, and then frozen at -20°C until time of extraction.

At the GLSC, concentrations of 80 different PCB congeners were determined in each composite sample using the procedure described by Schmidt (1997a). Homogenized coho salmon tissue was mixed with anhydrous sodium sulfate. The mixture was extracted in a column using petroleum ether and ethyl acetate. Lipids were removed from extract by a gel permeation column (GPC). Trace lipids remaining after GPC were removed by passing extract through a column packed with silica gel per Schmidt (1997b). Analysis was performed using a gas chromatograph/mass spectrometer and data system. Appropriate quality control measures (blanks, matrix spikes, surrogate standards, and duplicates) were used to ensure accuracy and precision of the analyses (Schmidt, 1997a). Recovery tests for fish tissue sample surrogates ranged from 70 to 120%. Relative percent difference between duplicates averaged 10%. Our determinations of the total PCB concentration in reference material, traditionally used for Great Lakes fish monitoring (Hickey et al., 2006), were within 15% of the original determination. Summing the PCB concentrations of all 80 congeners yielded an accurate estimate of total PCB concentration in the composite sample (Schmidt, 1997a). Lipid concentration for each of the composites was determined gravimetrically (Hesselberg et al., 1990; Schmidt, 1997b). All PCB and lipid concentrations were reported on a wet weight basis.

At the Wisconsin State Laboratory of Hygiene, coho salmon were thawed and filleted. For each coho salmon caught during 2004, weight was determined to the nearest g and sex was determined prior to filleting. For each coho salmon caught during both years, one fillet (skin-on, scale-on) was homogenized in a commercial blender, and approximately 50 g of the homogenate was placed in a contaminant-free glass jars, and frozen at -20°C until extraction and analysis. Because all coho salmon exceeded 500 mm in total length and were mature, all coho salmon were assumed to be age-2 fish. This assumption has been validated by examination of the coded-wire tag (CWT) database for Lake Michigan coho salmon maintained by the Wisconsin DNR, as batches of hatchery reared coho salmon implanted with CWTs have been released into Lake Michigan during the 1980s and 1990s (B. Eggold, Wisconsin DNR, Milwaukee, personal communication). In total, 19 male coho salmon and 26 female coho salmon were processed.

At the Wisconsin State Laboratory of Hygiene, each homogenate was analyzed for lipid content and total PCB concentration, based on Aroclor standards. Analyses were conducted according to methods specified in the Wisconsin State Laboratory of Hygiene manual (1994). A 10-g sample of the homogenate was mixed with 60 g anhydrous sodium sulfate and extracted with 230 mL methylene chloride. Lipid concentration was determined gravimetrically (Schmidt, 1997b). Gel permeation chromatography was used to remove lipid. Trace lipids were removed by further passing the extract through a column of Florisil and silica gel. Analysis for PCBs was performed by gas chromatography with electron capture detection. Quantitation was accomplished by comparison with a standard Aroclor or combination of Aroclors that best matched the sample. The sum of area responses of retention time matched peaks in sample and standard chromatograms was used to calculate concentrations. Appropriate quality control measures (blanks, matrix spikes, surrogate spikes, and duplicates) were undertaken to ensure accuracy and precision of the analyses. Spike recoveries averaged 88%, and relative percent difference of duplicates averaged 11%. All PCB and lipid concentrations were reported on a wet weight basis.

2.3. Data analysis

For both the LMMB dataset and the Wisconsin DNR dataset, mean PCB concentrations of male and female coho salmon were calculated. Then, we calculated the ratio of mean PCB concentration of males with mean PCB concentration of females for both datasets. These ratios were calculated for three reasons. First, one of the objectives of our study was to determine the degree of difference in PCB concentrations between the two sexes, and calculation of these ratios enabled us to accomplish this objective. Second, calculation of these ratios allowed us to compare results from our study with results from previous studies (e.g., Madenjian et al., 1998b, 2009, 2010). Third, to investigate the effect of a sex difference in GGE on a sex difference in PCB concentrations, the ratio of male PCB concentration to female PCB concentration must be estimated (Madenjian et al., 2009). In addition, we compared the ratio from the LMMB dataset with the ratio from the Wisconsin DNR dataset to determine whether these two ratios were in good agreement. Finally, for both the LMMB dataset and the Wisconsin DNR dataset, mean weight and mean lipid concentration were calculated for both male and female coho salmon.

To determine whether PCB concentrations, lipid concentrations, and weights significantly differed between the sexes, we used two-way analysis of variance (ANOVA). The main effects of the ANOVA were fish sample type (either whole fish or skin-on fillet) and sex, and the interaction term was included. An ANOVA was performed for PCB concentration, lipid concentration, and weight. The ANOVA approach enabled us to analyze both datasets simultaneously and thereby substantially increase sample size, and consequently the power of the statistical testing, relative to a separate statistical analysis for each of the two datasets. Power refers to the probability of detecting a significant difference, given that a significant difference exists. We assigned $\alpha = 0.05$ for all statistical testing.

2.4. Bioenergetics modeling

To determine whether the average female coho salmon exhibited a higher GGE than the average male coho salmon, we estimated food consumption by coho salmon in Lake Michigan using the “Wisconsin” bioenergetics model developed by Stewart et al. (1981) and Stewart and Ibarra (1991), and coded into a computer program by Hanson et al. (1997). With this approach, energy losses were calculated as a function of water temperature and coho salmon size, and then an estimate of the amount of food consumption necessary for a coho salmon to achieve the observed size (weight) at a given age was generated. The energy budget of the coho salmon was modeled as:

$$C = G + R + E_g + E_x$$

where C = consumption, G = growth, R = respiration, E_g = egestion, and E_x = excretion. Respiration was modeled as a function of water temperature and coho salmon weight, and egestion and excretion were modeled as being directly proportional to consumption. Please refer to Stewart et al. (1981), Stewart and Ibarra (1991), and Hanson et al. (1997) for more details on the coho salmon bioenergetics model. We assumed that the males and females were equally active, and therefore the swimming speed submodel was identical for both sexes (Stewart et al., 1981; Stewart and Ibarra, 1991). The model time step was one day.

Model inputs included coho salmon growth, water temperature, coho salmon diet composition, and energy density of prey and predator (coho salmon). Coho salmon are typically stocked as yearlings into Lake Michigan in early April, and average weight at stocking is 33 g (Stewart and Ibarra, 1991; Madenjian et al., 1998a). Thus, we assigned 1 April as the start day for our bioenergetics model simulations. Based on previous studies (Madenjian et al., 1998a), coho salmon growth rate in Lake Michigan varied little between the sexes.

Therefore, we assumed that coho salmon mean weight at time of stocking was equal to 33 g for both males and females, and we assumed that coho salmon mean weight on 1 April during the second year in the lake was equal to 872 g for both males and females (Madenjian et al., 1998a). The average date of capture of coho salmon used in our study was 15 October. We calculated the grand mean weight for both males and females used in our study to estimate the mean weight of males and females on 15 October during the second year in Lake Michigan; these mean weights were then used in our bioenergetics model simulations. The water temperature regime experienced by coho salmon in Lake Michigan was taken from Stewart and Ibarra (1991). The diet schedule for coho salmon in Lake Michigan was taken from Madenjian et al. (1998a). Energy density data for both coho salmon and its prey in Lake Michigan were taken from Stewart et al. (1981) and Stewart and Ibarra (1991).

Using the coho salmon bioenergetics model, we calculated food consumption by an average male and average female coho salmon in Lake Michigan from time of stocking through 15 October of the second year in the lake. This was accomplished by first running a simulation for yearling coho salmon from the time of stocking (1 April) through 1 April of the second year in the lake. Then, a simulation was run from 1 April through 15 October of the second year in the lake.

Once food consumption was estimated via the bioenergetics modeling, then cumulative GGE was calculated by dividing increase in growth from the time of stocking (when an average coho salmon weighed 33 g Madenjian et al., 1998a) by the cumulative amount of food consumption required to achieve the increase in growth. In addition, we calculated the ratio of female cumulative GGE to male cumulative GGE on both 1 April and 15 October of the coho salmon's second year in the lake.

3. Results

3.1. Data analysis

Based on the LMMB dataset, mean PCB concentrations of male and female coho salmon at age 2 in the fall were 1.30 mg/kg and 1.10 mg/kg, respectively (Fig. 1). Thus, the ratio of mean male PCB concentration with mean female PCB concentration was equal to 1.187. Based on the Wisconsin DNR dataset, mean PCB concentrations in skin-on fillets of male and female coho salmon at age 2 in the fall were 0.71 mg/kg and 0.59 mg/kg, respectively (Fig. 1). Thus, on average, male PCB concentration in the skin-on fillets was 20.4% higher than female PCB concentration in the skin-on fillets. In sum, results from the whole-fish PCB determinations of the LMMB dataset were in good agreement with results from the skin-on fillet PCB determinations with regard to the ratio of mean male PCB concentration with mean female PCB concentration.

Based on both the whole-fish determinations and the skin-on fillet determinations, lipid concentration in males was slightly higher than lipid concentration in females. For the LMMB dataset, mean lipid concentrations in males and females were 5.23% and 3.99%, respectively. For the Wisconsin DNR dataset, mean lipid concentrations in skin-on fillets of males and females were 2.34% and 1.82%, respectively.

Mean sizes of the coho salmon were similar between the two datasets. For the LMMB dataset, mean weights of males and females were 2896 g and 3181 g, respectively. For the Wisconsin DNR dataset, mean weights of males and females were 3008 g and 2625 g, respectively. Pooling both datasets, mean weights of males and females were 2923 g and 2944 g, respectively. Thus, averaging over several years of data, sizes of coho salmon as age-2 fish in the fall differed very little between the sexes.

Based on ANOVA results, PCB concentration was significantly higher in males compared with females ($F = 5.56$; $df = 1,60$; $P = 0.0216$). In addition, PCB concentration was significantly higher

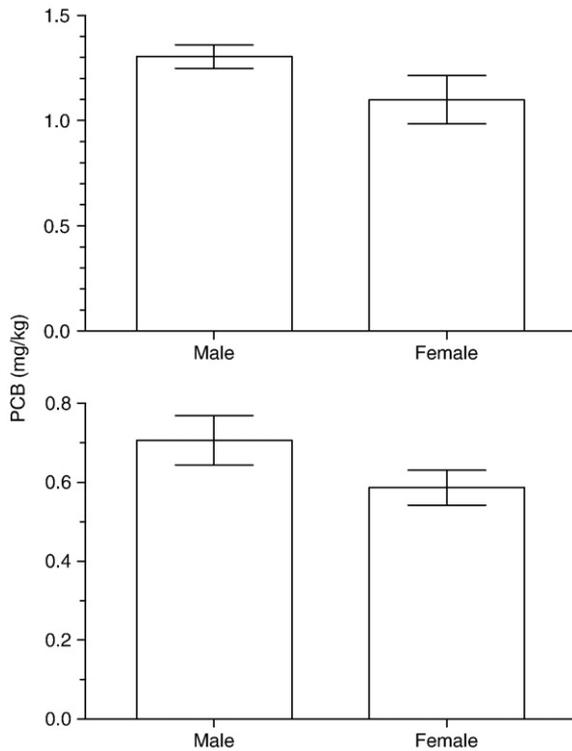


Fig. 1. Mean PCB concentrations in whole fish without the stomach for male and female age-2 coho salmon from Lake Michigan during the fall, 1994–1995 (upper panel). Mean skin-on fillet PCB concentrations for male and female age-2 coho salmon from Lake Michigan during the fall, 2004 and 2006 (lower panel). Bar represents one standard error.

in whole fish (from the LMMB dataset) than in skin-on fillets (from the Wisconsin DNR dataset) ($F=64.94$; $df=1,60$; $P<0.0001$). Similarly, lipid concentration in males was significantly higher than lipid concentration in females ($F=5.09$; $df=1,60$; $P=0.0277$). Lipid concentration was significantly higher in whole fish than in skin-on fillets ($F=41.82$; $df=1,60$; $P<0.0001$). Coho salmon weight did not differ significantly between the sexes or between the LMMB and the Wisconsin DNR datasets ($P>0.37$). The interaction term in all three ANOVAs was insignificant ($P>0.18$).

3.2. Bioenergetics modeling

Cumulative GGE of coho salmon in Lake Michigan showed little variation with age or sex (Table 1). For both sexes, cumulative GGE slightly decreased from 0.250 on 1 April during the second year in the lake to 0.245 on 15 October during the second year in the lake. Ratio of female cumulative GGE to male cumulative GGE was either equal to

Table 1
Cumulative consumption^{a, b} and cumulative gross growth efficiency (GGE), by age and sex, for coho salmon from Lake Michigan (United States).

Date during second year in lake	Males			Females		
	Weight at age (g)	Cumulative consumption (g)	Cumulative GGE	Weight at age (g)	Cumulative consumption (g)	Cumulative GGE
1 Apr	872	3361	0.250	872	3361	0.250
15 Oct	2923	11,787	0.245	2944	11,872	0.245

^a Estimates of consumption based on application of the Wisconsin bioenergetics model.

^b Coho salmon were stocked as 33-g yearlings into Lake Michigan during April.

one or between 1.000 and 1.001 (Fig. 2). Thus, female cumulative GGE exceeded male cumulative GGE on 15 October by less than 0.1%.

4. Discussion

Our results indicated that, on average, PCB concentration of mature male coho salmon from Lake Michigan in the fall was about 20% greater than PCB concentration of mature female coho salmon from Lake Michigan in the fall. Because all of these fish were caught prior to spawning and coho salmon are semelparous, release of gametes could not explain the observed sexual difference in PCB concentrations. PCB concentration is inversely proportional to GGE (Madenjian et al., 1994; Jackson and Schindler, 1996). Therefore, if the 20% greater PCB concentration in males was solely due to a sexual difference in GGE, then the ratio of female GGE to male GGE should be equal to 1.20. However, our bioenergetics modeling indicated that the ratio of female GGE to male GGE was less than 1.001. Thus, our bioenergetics modeling could not explain the 20% higher PCB concentrations in male coho salmon.

However, it is plausible that our bioenergetics modeling underestimated the ratio of female GGE to male GGE. Any type of extra energy expenditure by mature males during the spawning period was not specifically taken into account within the bioenergetics modeling framework (Hanson et al., 1997), and therefore male GGE may have been slightly overestimated. For example, Lucas et al. (1993) and Altimiras et al. (1996) have shown that the heartbeat rate of mature male Atlantic salmon (*Salmo salar*) exceeded that of mature females in a Scottish river during the spawning season by about 45%, and these researchers contended that this higher heartbeat rate would have translated into higher energy expenditure, due to higher swimming activity, by the mature males. Based on the bioenergetics model by Stewart et al. (1981), if male swimming speed was about 20% greater than female swimming speed, then food consumption by males would be 10% greater than that by females. In addition, one of the implicit assumptions of the bioenergetics model was that the energy efficiency of producing ovarian tissue is equal to the energy efficiency of producing somatic tissue. However, Diana and Mackay (1979) have presented data indicating that, at least in some fishes, production of ovarian tissue is more energy efficient than production of somatic tissue. Consequently, we may have slightly underestimated female GGE. Relatively high energy efficiency for producing ovarian tissue would suggest that resting metabolic rate of mature females was less than resting metabolic rate of mature males. According to the Stewart et al. (1981) bioenergetics model, a decrease in resting metabolic rate of roughly 20% would lead to a 10% reduction in food consumption. Given these results of our preliminary exploratory analysis of sex differences in both swimming activity and resting metabolic rate, a sexual difference in GGE

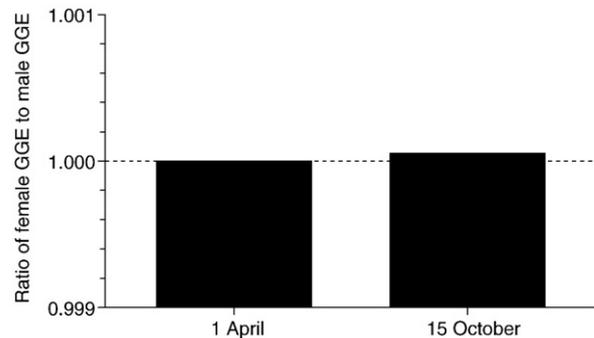


Fig. 2. Estimates of the ratio of female cumulative gross growth efficiency (GGE) to male cumulative GGE for coho salmon from Lake Michigan (United States). Estimates based on application of the Wisconsin bioenergetics model (Stewart et al., 1981; Stewart and Ibarra 1991; Hanson et al., 1997). Dashed line represents a 1:1 ratio between female cumulative GGE and male cumulative GGE.

may still possibly account for most or all of the sexual difference in PCB concentrations of coho salmon from Lake Michigan.

Some evidence suggested that habitat use did not substantially differ between the sexes of coho salmon in Lake Michigan. First, the lack of growth differences between sexes provided support for the contention that the sexes shared the same habitat in Lake Michigan. Holtby and Healey (1990) hypothesized that similar growth rates between the sexes for coho salmon from the Pacific coast of North America implied that males and females were feeding in the same general area of the Pacific Ocean, whereas substantially higher female growth rate compared with male growth rate implied that females were feeding in different areas of the Pacific Ocean than males. Growth data for Lake Michigan coho salmon indicated that males and females grew at very similar rates (R. Elliott, unpublished data, B. Eggold, personal communication, P. Peeters, Wisconsin DNR, Sturgeon Bay, personal communication), and therefore the sexes would not be spatially separated for the bulk of their feeding in Lake Michigan, based on the Holtby and Healey (1990) hypothesis. Second, examination of the diet data from the LMMB project indicated that coho salmon diet composition did not differ between the sexes (R. Elliott, unpublished data).

Although, in general, lipid concentration is positively correlated with PCB concentration in fish, the magnitude to which fish accumulate PCBs is regulated by food chain biomagnification and food consumption (Weininger, 1978; Borgmann and Whittle, 1991). For coho salmon, both lipid content and PCB concentration were higher in males than in females. In contrast, although lipid concentration was higher in females than in males, PCB concentration in male walleyes was higher than PCB concentration in female walleyes (Madenjian et al., 1998b, 2009). In sum, PCB concentration has been shown to be higher in males than in females in fishes such as walleye, lake trout, and coho salmon (Madenjian et al., 1998b, 2009, 2010), whereas males have the higher lipid concentration in some of these fishes, while females have the higher lipid concentration in the other fishes. Thus, the observed sexual differences in PCB concentrations were not consistently in accord with the observed sexual differences in lipid concentrations.

Based on rainbow trout and lake trout data, we would not expect the PCB concentration in female coho salmon to decrease after spawning. In Lake Ontario, rainbow trout, which shares the genus *Oncorhynchus* with coho salmon, had an average PCB concentration of 5.25 mg/kg in the somatic tissue, whereas egg concentrations averaged only 2.05 mg/kg (Niimi, 1983). Consequently, PCB concentration in rainbow trout females was expected to actually increase by about 10% immediately after spawning. For lake trout, which shares the family Salmonidae with coho salmon, PCB concentration in females was expected to increase by 13.5% immediately after spawning (Madenjian et al., 2010). We would expect PCB concentration in coho salmon females to also show a slight increase immediately after spawning. Therefore, although maternal transfer of PCBs to eggs has been documented in salmonids (Miller 1993; Ewald et al., 1998; Svendsen et al., 2007), we would expect that this maternal transfer cannot explain sex differences in PCB concentrations of any of the salmonid species, regardless of whether the species is iteroparous or not.

Total PCB concentrations estimated by comparison with standard Aroclors (the methodology used by the Wisconsin DNR) have been shown to be very similar to total PCB concentrations estimated by summing the concentrations of the detectable PCB congeners (the methodology used in the LMMB study) (Maack and Sonzogni, 1988; Schmidt, 1997a; L. Schmidt, U. S. Geological Survey, La Crosse, Wisconsin, personal communication). Therefore, the Aroclor method used by the Wisconsin DNR should yield similar results to the LMMB method with regard to determining total PCB concentration in fish tissues. In a previous study, the Aroclor method was used to determine total PCB concentration in both whole coho salmon and coho salmon skin-on fillets; results revealed that the mean ratio of whole-fish PCB concentration to skin-on fillet PCB concentration was 1.70 (Amrhein

et al., 1999). Forming the ratio of mean PCB concentration in whole fish to mean PCB concentration in skin-on fillets from the data used in our study yielded 1.85, which is reasonably close to the ratio of 1.70 obtained by Amrhein et al. (1999). The similarity in these two ratios provided further support for the contention that estimates of total PCB concentration were comparable between the two methodologies.

The sexual difference in PCB concentrations of Lake Michigan coho salmon was similar to the sexual difference in PCB concentrations of Lake Ontario lake trout. The lake trout, an iteroparous fish, is the top native predator in Laurentian Great Lakes ecosystems. Madenjian et al. (2010) showed that male lake trout from Lake Ontario were 22% higher in PCB concentration than female lake trout from Lake Ontario, and similarly we found 20% greater PCB concentrations in males from our study. Also, Lake Michigan coho salmon and Lake Ontario lake trout had similarly small sexual differences in growth rates. In contrast, female walleyes grew substantially faster than male walleyes from a suite of pristine lakes, as female weight at age exceeded male weight at age in these walleye populations by as much as 52% (Madenjian et al., 2009). Moreover, male walleye PCB concentration exceeded female walleye PCB concentration by 32% in these pristine lakes (Madenjian et al., 2009). The sexual difference in GGE would be expected to increase with an increasing sexual difference in growth rate, given that a faster growth rate is usually associated with higher GGE (Larsson et al., 1992; Madenjian et al., 1994). Thus, the observed sexual differences in PCB concentrations in coho salmon, lake trout, and walleye were in accord with the gradient in sexual differences in growth rate across these three fish species. Madenjian et al. (2009) were able to explain a portion of the sexual difference in PCB concentrations of walleyes from South Manistique Lake, a pristine lake, via bioenergetics modeling, whereas the portion of the sexual difference in PCB concentrations of Lake Michigan coho salmon or Lake Ontario lake trout explained via bioenergetics modeling was either practically negligible or zero. Perhaps if more details on the sexual differences in energy expenditure were included in the bioenergetics model, then the bioenergetics modeling would explain all of the sexual difference in PCB concentrations for Lake Michigan coho salmon, Lake Ontario lake trout, and the walleyes from pristine lakes.

5. Conclusion

We documented that, on average, PCB concentrations in males were about 20% greater than PCB concentrations in females for Lake Michigan coho salmon at age 2 in the fall. Because coho salmon are semelparous and the fish were caught prior to spawning, this sexual difference in PCB concentrations could not be explained by the release of gametes. Further, this sexual difference in PCB concentrations could not be explained by our bioenergetics modeling. However, the current fish bioenergetics models may not be sufficiently detailed to fully explore food consumption differences between adult male and female fish. Therefore, a sexual difference in GGE remained a plausible explanation for the observed sexual difference in PCB concentrations of Lake Michigan coho salmon, as well as for Lake Ontario lake trout and walleyes from pristine lakes. Additional research on the energetic demands of mature coho salmon, as well as on the energetic costs of producing ovarian tissue versus producing somatic tissue for adult female coho salmon, would be needed to determine whether a sexual difference in GGE could explain a portion or all of the sexual difference in PCB concentrations of coho salmon.

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References

- Altimiras J, Johnstone ADF, Lucas MC, Priede IG. Sex differences in the heart rate variability spectrum of free-swimming Atlantic salmon (*Salmo salar* L.) during the spawning season. *Physiol Zool* 1996;69:770–84.
- Amrhein JF, Stow CA, Wible C. Whole-fish versus filet polychlorinated-biphenyl concentrations: an analysis using classification and regression tree models. *Environ Toxicol Chem* 1999;18:1817–23.
- Borgmann U, Whittle DM. Contaminant concentration trends in Lake Ontario lake trout (*Salvelinus namaycush*): 1977 to 1988. *J Gt Lakes Res* 1991;17:368–81.
- Diana JS. Biology and ecology of fishes. second edition. Traverse City, Michigan: Cooper Publishing Group, LLC; 2004. 498 pp.
- Diana JS, Mackay WS. Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*). *J Fish Res Board Can* 1979;36:481–7.
- Ewald G, Larsson P, Linge H, Okla L, Szarzi N. Biotransport of organic pollutants to an inland Alaska lake by migrating sockeye salmon (*Oncorhynchus nerka*). *Arctic* 1998;51:40–7.
- Hanson PC, Johnson TB, Schindler DE, Kitchell JF. Fish bioenergetics 3.0. Madison, Wisconsin: University of Wisconsin, Sea Grant Institute; 1997. WISCU-T-97-001.
- Hesselberg RJ, Hickey JP, Nortrup DA, Willford WA. Contaminant residues in the bloater (*Coregonus hoyi*) of Lake Michigan, 1969–1986. *J Gt Lakes Res* 1990;16:121–9.
- Hickey JP, Batterman SA, Chernyak SM. Trends of chlorinated organic contaminants in Great Lakes trout and walleye from 1970 to 1998. *Arch Environ Contam Toxicol* 2006;50:97–110.
- Holey ME, Elliott RF. Quality assurance project plan for coho sampling for contaminants and diet analysis. Volume 1 of Lake Michigan Mass Balance (LMMB) study methods compendium: sample collection techniques. EPA-905-R-97-012a Chicago, Illinois: U. S. Environmental Protection Agency, Great Lakes National Program Office; 1997.
- Holtby LB, Healey MC. Sex-specific life history tactics and risk-taking in coho salmon. *Ecology* 1990;71:678–90.
- Jackson LJ, Schindler DE. Field estimates of net trophic transfer of PCBs from prey fishes to Lake Michigan salmonids. *Environ Sci Technol* 1996;30:1861–5.
- Johnston TA, Fisk AT, Whittle DM, Muir DCG. Variation in organochlorine bioaccumulation by a predatory fish: gender, geography, and data analysis methods. *Environ Sci Technol* 2002;36:4238–44.
- Kocik JF, Jones ML. Pacific salmonines in the Great Lakes basin. In: Taylor WW, Ferreri CP, editors. Great Lakes fisheries policy and management: a binational perspective. East Lansing: Michigan State University Press; 1999. p. 455–88.
- Larsson P, Collvin L, Okla L, Meyer G. Lake productivity and water chemistry as governors of the uptake of persistent pollutants in fish. *Environ Sci Technol* 1992;26:346–52.
- Larsson P, Okla L, Collvin L. Reproductive status and lipid content as factors in PCB, DDT, and HCH contamination of a population of pike (*Esox lucius* L.). *Environ Toxicol Chem* 1993;12:855–61.
- Larsson P, Backe C, Bremle G, Eklöv A, Okla L. Persistent pollutants in a salmon population (*Salmo salar*) of the southern Baltic Sea. *Can J Fish Aquat Sci* 1996;53:62–9.
- Lucas MC, Johnstone ADF, Priede IG. Use of physiological telemetry as a method of estimating metabolism of fish in the natural environment. *Trans Am Fish Soc* 1993;122:822–33.
- Maack L, Sonzogni WC. Analysis of polychlorobiphenyl congeners in Wisconsin fish. *Arch Environ Contam Toxicol* 1988;17:711–9.
- Madenjian CP, Carpenter SR, Rand PS. Why are the PCB concentrations of salmonine individuals from the same lake so highly variable? *Can J Fish Aquat Sci* 1994;51:800–7.
- Madenjian CP, Elliott RF, Schmidt LJ, DeSorcie TJ, Hesselberg RJ, Quintal RT, et al. Net trophic transfer efficiency of PCBs to Lake Michigan coho salmon from their prey. *Environ Sci Technol* 1998a;32:3063–7.
- Madenjian CP, Noguchi GE, Haas RC, Schrouder KS. Sexual difference in polychlorinated biphenyl accumulation rates of walleye (*Stizostedion vitreum*). *Can J Fish Aquat Sci* 1998b;55:1085–92.
- Madenjian CP, Hanchin PA, Chernyak SM, Begnoche LJ. Sexual difference in PCB concentrations of walleyes (*Sander vitreus*) from a pristine lake. *Sci Total Environ* 2009;407:4526–32.
- Madenjian CP, Keir MJ, Whittle DM, Noguchi GE. Sexual difference in PCB concentrations of lake trout (*Salvelinus namaycush*) from Lake Ontario. *Sci Total Environ* 2010;408:1725–30.
- Masnado RG. Polychlorinated biphenyl concentrations of eight salmonid species from the Wisconsin waters of Lake Michigan. Wisconsin Department of Natural Resources Fish Management Report Number 132; 1987. Madison, Wisconsin.
- Miller MA. Maternal transfer of organochlorine compounds in salmonines to their eggs. *Can J Fish Aquat Sci* 1993;50:1405–13.
- Niimi AJ. Biological and toxicological effects of environmental contaminants in fish and their eggs. *Can J Fish Aquat Sci* 1983;40:306–12.
- Patriarche MH. Movement and harvest of coho salmon in Lake Michigan, 1978–1979. Fisheries Research Report 1889. Ann Arbor, Michigan: Michigan Department of Natural Resources; 1980.
- Rypel AL, Findlay RH, Mitchell JB, Bayne DR. Variations in PCB concentrations between genders of six warmwater fish species in Lake Logan Martin, Alabama, USA. *Chemosphere* 2007;68:1707–15.
- Sandercock FK. Life history of coho salmon (*Oncorhynchus kisutch*). In: Groot C, Margolis L, editors. Pacific salmon life histories. Vancouver: University of British Columbia Press; 1991. p. 395–445.
- Schmidt LJ. Analysis of total PCBs and PCB congeners and trans-nonachlor in fish by gas chromatography / negative chemical ionization single ion mass spectrometry. Volume II of Lake Michigan Mass Balance (LMMB) study methods compendium: organic and mercury sample analysis techniques. EPA-905-R-97-012b. Chicago, Illinois: U. S. Environmental Protection Agency, Great Lakes National Program Office; 1997a. p. 389–99.
- Schmidt LJ. Extraction and lipid separation of fish samples for contaminant analysis and lipid determination. Volume II of Lake Michigan Mass Balance (LMMB) study methods compendium: organic and mercury sample analysis techniques. EPA-905-R-97-012b. Chicago, Illinois: U. S. Environmental Protection Agency, Great Lakes National Program Office; 1997b. p. 381–8.
- Sheffy TB. The PCB monitoring program in Wisconsin – surveillance strategy and use of data. In: Eaton JG, Parrish PR, Hendricks AC, editors. Aquatic toxicology, ASTM STP 707. Philadelphia: American Society for Testing and Materials; 1980. p. 155–63.
- Stewart DJ, Ibarra M. Predation and production by salmonine fishes in Lake Michigan, 1978–1988. *Can J Fish Aquat Sci* 1991;48:909–22.
- Stewart DJ, Kitchell JF, Crowder LB. Forage fishes and their salmonid predators in Lake Michigan. *Trans Am Fish Soc* 1981;110:751–63.
- Stow CA, Carpenter SR, Madenjian CP, Eby LA, Jackson LJ. Fisheries management to reduce contaminant consumption. *BioScience* 1995;45:752–8.
- Svendsen TC, Vorkamp K, Frederiksen M, Rønsholdt B, Frier J. Body burdens of persistent halogenated compounds during different development stages of anadromous brown trout (*Salmo trutta*). *Environ Sci Technol* 2007;41:5980–5.
- Weininger D. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. dissertation, 1978, University of Wisconsin, Madison, 232 pp.
- Wells L, McLain AL. Lake Michigan: effects of exploitation, introductions, and eutrophication on the salmonid community. *J Fish Res Board Can* 1972;29:889–98.
- Wisconsin State Laboratory of Hygiene. Methods for organic analysis. Madison: University of Wisconsin; 1994.