



Fat content and condition factor explain levels of dioxins and PCBs in whitefish (*Coregonus* sp.) from Sweden's major lakes

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ABSTRACT

Whitefish (*Coregonus* sp.) are an ecologically and economically important species in large, temperate lake ecosystems, including North America's Laurentian Great Lakes. While levels of persistent organic pollutants have generally declined in many large-lake systems, unexpectedly high concentrations of polychlorinated dibenzo-p-dioxins (PCDDs), dibenzofurans (PCDDFs), and biphenyls (PCBs) have been detected in whitefish from Sweden's two largest lakes, Vänern and Vättern, prompting an extensive investigation. This study analyzed 282 whitefish samples collected between 2015 and 2022 from these lakes and from the Gulf of Bothnia—a large, brackish basin of the Baltic Sea known for long-standing contamination issues. Whitefish dorsal muscle tissue was collected from commercial catches and analyzed to quantify the contaminant levels. We used generalized linear models to assess which spatial, temporal, and morphometric variables explained variation in toxic equivalent (TEQ) levels. While whitefish from Lake Vänern had higher contaminant levels than those from oligotrophic Lake Vättern, this difference was largely explained by their higher fat content. The total length was positively associated with TEQ, while the condition factor showed a negative association in Lake Vättern whitefish, suggesting a greater mobilization of contaminants from lipids to muscle due to starvation-related effects. Similar to recent observations in some Laurentian Great Lakes, we found no significant temporal decline in TEQ during the study period. Our findings provide a European large-lake perspective on the complex factors governing contaminant bioaccumulation in a key fish species, offering valuable comparative insights for Great Lakes science and management.

1. Introduction

Polychlorinated dibenzo-p-dioxins and dibenzofurans (PCDD/Fs, often simply “dioxins/furans”) and polychlorinated biphenyls (PCBs) have for decades been known to pose environmental and human health risks because of their toxicity, persistence, and bioaccumulating properties (EFSA Panel on Contaminants in the Food Chain (CONTAM) et al., 2018). They continue to pose a persistent, though somewhat mitigated, threat to lake and coastal ecosystems and human health worldwide via legacy contamination (Glynn et al., 2020; González and Domingo, 2021; Grasman et al., 2025; Karlsson et al., 2023).

In the Laurentian Great Lakes (LGL), continuous trend monitoring of

PCDD/F and PCB content in fatty fish species has shown that the levels, in general, have declined substantially (Gandhi et al., 2019; GLFMSP, 2024). Similar time trends have been observed in European waters, for example, the Baltic Sea (Polak-Juszczak et al., 2022), the Northeast Atlantic (OSPAR, 2023), and the Mediterranean Sea (Miniero et al., 2014).

It was therefore surprising when the Swedish Food Agency reported in 2010 that significantly elevated levels of PCDD/Fs and PCBs had been detected in whitefish (*Coregonus* sp.) from Lake Vänern—Sweden's and western Europe's largest lake, covering almost 6000 km² and qualifying as one of the large lakes of the world (Herdendorf, 1982). The observation was followed by investigations in the second-largest lake in

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Sweden, Lake Vättern (approximately 1900 km²), which also showed elevated, although not as high, levels of organochlorine compounds (County Administrative Boards, 2015). This led to the implementation of a regulation stating that fishermen are not allowed to sell whitefish unless it can be proven that levels of dioxins and PCBs are below the marketing thresholds of the European Union (European Commission, 2011). These thresholds apply to muscle tissue and are 3.5 pg TEQ/g w. w. (wet weight) for PCDD/F and 6.5 pg TEQ/g w.w. when dioxin-like PCBs also are included, where TEQ is the total toxic equivalent (DeVito et al., 2024; Van den Berg et al., 2006). This regulation entails that whitefish from Lake Vänern and Lake Vättern cannot be sold fresh, which is a major drawback for the local fishery. The initial findings also led to a comprehensive sampling campaign between 2015 and 2019 (Hällén et al., 2020), which served as the empirical basis for this paper.

Whitefish and their cisco relatives (*Coregonus* spp.) are often the most abundant and valuable species for commercial, tribal, and recreational fisheries in many large, temperate lake ecosystems, most notably the Laurentian Great Lakes (Ebener et al., 2010) and Fennoscandia (Degerman et al., 2001; Verliin et al., 2013). They are also vital for inland fisheries in many European countries (Anneville et al., 2025). Whereas knowledge of historical and current levels of PCDD/Fs and PCBs in whitefish from the LGL is relatively robust (Gandhi et al., 2019; Rawn et al., 2017), empirical data from European waters are sparse and scattered. Given that large lakes like the LGL and Europe's largest lakes function as comparable "inland seas" with complex food webs, understanding the drivers of contaminant bioaccumulation in one system can provide critical insights for the other.

This paper aims to investigate the association between the total TEQ-levels of PCDD/Fs and dl-PCBs, fat content, length, and weight of whitefish, as well as possible time trends, and seasonal variations. Studied areas include Lake Vänern, Lake Vättern, and the Gulf of Bothnia in the northern Baltic Sea. Variability between and within these areas was also investigated. The Gulf of Bothnia was included to widen the scope from just the largest lakes and include another area that is also challenged by organochlorine pollution (Polak-Juszczak et al., 2022; Strandberg et al., 2000), and in which commercial and household fishing is common.

In our statistical analysis, we use the total TEQ of PCDD/Fs and dl-PCBs based on the 2005 evaluation of the Toxic Equivalence Factors (TEF) (Van den Berg et al., 2006), in order to allow for straightforward comparison with other studies. However, in 2022, a re-evaluation of the TEFs was published (DeVito et al., 2024), and to accommodate these changes, we also include a section comparing the TEQ (pg/g) based on the 2005 and 2022 evaluations, respectively.

2. Methods

2.1. Sampling and data collection

Whitefish were caught between 2015 and 2019 by local fishermen in Lake Vänern, Lake Vättern, and the Gulf of Bothnia (Electronic Supplementary Material (ESM) Appendix S1). Immediately after the catch, the fish were frozen and sent to IVL Swedish Environmental Research Institute in Stockholm, Sweden, for morphometric measurements and preparation of muscle samples for chemical analysis. The fish were caught with selective fishing equipment, namely gill nets and fish traps.

Our sampling was primarily designed to assess whether commercially caught whitefish from these areas comply with current EU thresholds for PCDD/Fs and dl-PCBs in fish aimed for human consumption. The regulation states that a subsample of the catch must have a mean TEQ below a certain threshold (European Union, 2017), meaning that a "sample" normally consists of a pool of individuals. We did, however, also analyze individual fish to obtain a sense of the inter-individual variation within a pool. Here we define "sample" as the muscle tissue analyzed for PCDD/Fs and dl-PCBs, which may consist of a mix of muscle tissue from several specimens or tissue from a single

specimen. A skinless middle section of the dorsal muscle was used. A total of 282 samples were analyzed (Table 1). Fifty-one samples were prepared as pooled samples with equal amounts of muscle tissue from 2 to 10 fishes, while the remaining samples (231) were analyzed individually. Each fish in a pooled sample was taken from the same catch, meaning that the catch date and catch site were identical within the pooled samples. Thus, as for the individual samples, a pooled sample represents one catch site at one time point. To estimate the variability within the pooled samples, individual samples caught at the same place and time were used to mimic a pool. To obtain stability in the results, we only included catches of at least five individual whitefish. The average standard deviation of the total TEQ of PCDD/Fs and dl-PCBs was 2.5 TEQ, and the average coefficient of variation (CV) was 47 % (ESM Table S1).

Fulton's condition factor, CF (Nash et al., 2006), was calculated as $CF = 100 * weight(g) / length(cm)^3$ based on length and weight data from either individual fish or from pooled samples. For pooled samples, we used the average length and weight of the pooled fish to calculate a representative CF for that sampling unit. The somatic weight was used in the calculation of CF.

The collated dataset was somewhat unbalanced with most samples originating from Lakes Vänern and Vättern and with a general lack of samples from the summer period from these lakes. To adjust for this unbalance, complementary samples were analyzed in 2022, which were not part of the original sampling campaign (2015–2019). Thus, there are no samples from 2020 and 2021. All complementary samples from 2022 were from Lake Vättern. The number of samples per year, across all areas, were the following: 2015 = 31, 2016 = 23, 2017 = 93, 2018 = 96, 2019 = 34, 2020 = 0, 2021 = 0, 2022 = 5. The complete data set is provided in ESM Appendix S1.

3. Chemical analysis

Analysis was performed according to US EPA Methods 1613 and 1668, including all associated quality assurance and quality control procedures. The instrumentation was a Thermo DFS Magnetic Sector High-Resolution Gas Chromatography–High-Resolution Mass Spectrometry (HRGC–HRMS) operating at a resolution of $R = 10,000$ with EI ionization, coupled to a GC Trace Ultra equipped with an Rxi-5Sil MS column (60 m × 0.25 mm ID × 0.25 μm film thickness) with He as the carrier gas. Recoveries of spiked mass-labelled standards were in the 60–120 % range. Fat content was determined gravimetrically after Soxhlet extraction (according to EPA 1613 12.4.1). The estimated measurement uncertainty (95 % confidence interval) for fat content was 10 %. The limit of quantification (LOQ) was < 0.7 pg TEQ/g for WHO-PCDD/F-TEQ and < 0.6 pg TEQ/g for WHO-dl-PCB-TEQ. When above LOQ, the measurement of uncertainty for each individual congener of PCDD/F and dl-PCB was 25 %.

Table 1

Number of samples per area and season. Numbers in parentheses denote how many of the samples are pooled samples of muscle tissue from more than one whitefish specimen. Samples were collected 2015–2022.

Area	Season	n
Lake Vänern	Spring	67 (17)
	Summer	0 (0)
	Fall	8 (3)
Lake Vättern	Winter	34 (6)
	Spring	64 (9)
	Summer	4 (1)
Gulf of Bothnia	Fall	39 (9)
	Winter	31 (6)
	Spring	6 (0)
Total	Summer	27 (0)
	Fall	2 (0)
	Winter	0 (0)
Total		282 (51)

3.1. Statistical analysis

3.1.1. Modelling contaminant levels

To assess the relationship between contaminant levels (sum of PCDD/Fs + dl-PCBs, pg TEQ/g w.w.) and morphometric and spatio-temporal variables, we used a mixed-model approach to account for the hierarchical structure and unbalanced nature of our data (Bosker and Snijders, 2011; Cnaan et al., 1997). Moreover, we used a generalized approach to account for the heteroscedasticity in the data, as the variance increases with higher TEQ values. The model class is thus a generalized linear mixed model (GLMM) (Stroup, 2012). This class of models is flexible since non-normal distributions are allowed if their distribution belongs to an exponential family (Dobson and Barnett, 2018), and it accommodates both random and fixed effects.

In GLMMs, as for general linear models, the set of fixed and random effects is related to the response variable via a link function. Fixed effects represent what are commonly called explanatory variables or independent variables. Random effects, on the other hand, are random variables assumed to be normally distributed with mean zero and a variance of σ^2 . Thus, in the model estimation, a variance estimate is obtained. The rationale for including random effects is that the observed levels are randomly picked from a large population of possible levels. We want to obtain information on the population level, rather than only the observed levels included in the data. Including a random effect can also be motivated because it reduces the degrees of freedom occupied by the fixed effects. Both these arguments apply to the catch sites in our data. They can be seen as coming from a large population of possible catch sites. We are interested in the contribution from the whole population of catch sites, and there are many catch sites included, which would consume many degrees of freedom if included as a fixed effect (i.e., it would decrease the statistical power).

TEQ was assumed to follow a gamma-distribution, and the natural logarithm was used as the link function. The gamma distribution was chosen because the data exhibit increasing variance with increasing values of the response variable. This was verified by plotting standardized residuals versus fitted values (ESM Fig. S5). If the standard deviation increases linearly with the response and a gamma distribution is assumed, the coefficient of variation (CV) is constant (Faraway, 2016), and the model does not suffer from overdispersion. The gamma distribution is also appropriate because it is defined only for positive values, which is consistent with TEQ.

Statistical significance of fixed effects was evaluated using Likelihood-ratio tests. For the post-hoc analysis, Tukey's test was applied (Montgomery, 2019). The software used was R (R Core Team, 2021) and R-studio (RStudio Team, 2021), and models were fitted using the lme4-package (Bates et al., 2015). Model diagnostics were evaluated through visual inspection of plots of deviance residuals vs fitted values and normal QQ-plots of deviance residuals (Figure S 6). All R-code is provided in ESM Appendix S3. Additional tables and figures not included in the manuscript are found in ESM Appendix S2.

3.1.2. Variable selection

Spatial information was represented by two variables: *Area* (Lake Vänern, Lake Vättern, or the Gulf of Bothnia) and *Site*, representing specific catch-sites within any of the three larger areas (ESM Appendix S1). *Site* was included in the model as a random effect, allowing model intercepts to vary randomly across catch-sites. *Area* was included as a fixed effect. The full set of variables is described in Table 2.

The inclusion of fish weight in the model was considered, but the high correlation between weight and length ($r = 0.80$) justified including only one of these variables to avoid multicollinearity. Additionally, weight had more missing values (26 observations) than length (one observation). Hence, we used the z-score-standardized *Length* as a continuous fixed effect in the model. Fulton's condition factor, CF, was also included as a fixed effect.

Seven observations lacked either a reported length or somatic

Table 2

Variables included in the statistical model, variable type, variable class (continuous/categorical), levels for the categorical variables, and units for the continuous variables. ^a Σ PCDD/F + dl-PCB pg TEQ/g w.w. TEQ was calculated by using the WHO toxic equivalency factors (TEFs) (Van den Berg et al., 2006). “-” not applicable for categorical variables and condition factor which is unitless. ^bSee ESM Appendix S1.

Variable name	Type	Levels	Class	Unit
TEQ ^a	Response	–	Continuous	pg TEQ/g w.w.
Area	Fixed effect	Lake Vänern, Lake Vättern and Gulf of Bothnia	Categorical	–
Fat	Fixed effect	–	Continuous	percent
Length	Fixed effect	–	Continuous	cm
Year	Fixed effect	–	Continuous	years
Condition factor	Fixed effect	–	Continuous	–
Season	Fixed effect	Spring, summer, fall and winter	Categorical	–
Site	Random effect	35 levels ^b	Categorical	–

weight. These values were imputed to avoid excluding the observations from the model. Notably, all five observations from 2022 lacked somatic weight, making deletion undesirable. The imputation could be performed with high accuracy; for observations missing somatic weight, total weight was available, and the two variables are strongly correlated. Likewise, the only observation missing length had weight recorded. Linear regression models were therefore fitted with the available variable as the response, and the predicted values were used for imputation. Scatterplots of all combinations of continuous fixed effects are presented in ESM Fig. S3.

Temporal variation was accounted for by including *Year* as a continuous fixed effect. *Season* (spring, summer, fall, winter) was initially included as a candidate predictor, but due to unbalanced sampling across seasons, the *Season* variable was removed. All subsequent interpretations of other predictors (*Fat content*, *Area*, *Length*, etc.) are therefore based on the model refitted without *Season*. *Condition factor* was mean-centered to improve the interpretability of the regression coefficients and reduce multicollinearity of interaction terms (Schielzeth, 2010).

First-order interactions between *Fat content* and the other fixed effects were initially included in the model, but they were not statistically significant and therefore removed from the model (ESM Table S2). However, the interaction between *Area* and *Condition factor* was statistically significant and improved overall model fit according to the Akaike Information Criterion (AIC) (ESM Table S8).

Because Lake Vättern had samples from all seasons, a separate model was fitted using only the Lake Vättern subset to investigate a possible seasonal effect. However, the season variable was not significant in that estimation (ESM Table S3).

4. Results

4.1. Fat content and length show a positive association with TEQ

In the model estimation, *Fat content* and *Length* were statistically significant, with positive coefficients (Table 3). Since the model used a logarithmic link function, the model estimates are interpreted as changes in percent. Thus, holding all other variables constant, a 1 % increase in the fat content of a whitefish is estimated to increase the expected TEQ by 21 % (calculated as $100 \cdot (\exp(0.19) - 1)$ since the model is log-linear). A 1 cm increase in the length of a whitefish is

Table 3

Model estimates, degrees of freedom (df), test statistic, and p-values based on likelihood ratio test^a, Wald t-test^b, Tukey's multiple comparison test^c. Estimates of categorical variables are in relation to the reference level which is included in the intercept. The reference level is Area = Lake Vänern. Tukey's test results between Lake Vättern and the Gulf of Bothnia can be found in [ESM Table S7](#). Tukey's test comparing the slope of the condition factor to zero for each area is found in [ESM Table S9](#). Note that estimates and significances for each level of Area correspond to the condition factor at its mean value, since the interaction between Area and Condition factor is included in the model and Condition factor is mean-centered. Likelihood ratio test results of the interaction between Area and Condition factor are found in [ESM Table S8](#).

Variable	Estimate	df	Test statistic	p-value
Intercept	0.91	1	5.7 ^b	<0.001
Fat content	0.19	1	91 ^a	<0.001
Area = Lake Vättern	-0.46	1	2.2 ^c	0.077
Area = Gulf of Bothnia	-1.5	1	6.0 ^c	<0.001
Length	0.033	1	6.8 ^a	0.0090
Year	-0.013	1	0.24 ^a	0.62
Condition factor	-0.29	1	-0.7 ^b	0.48
Lake Vättern*Condition factor	-2.3	1	3.0 ^b	0.0073
Gulf of Bothnia*Condition factor	-1.1	1	-1.1 ^b	0.47
Site (random effect)	Std.dev = 0.29	-	-	-

estimated to increase the expected TEQ by 3.4 %, holding all other variables constant.

4.2. Condition factor shows a negative association with TEQ in Lake Vättern

The interaction between Area and Condition factor had a negative parameter estimate and was significant, but only for Lake Vättern. This indicates that after accounting for fat content, length, year of capture, and area, fish with higher condition factors tend to have lower TEQ in Lake Vättern but not in the other areas ([Table 3](#); [ESM Table S8](#), [Table S9](#), and [Fig. S1](#)). The interpretation of the estimates indicates that a 0.1 unit

increase in condition factor, a biologically relevant difference ([ESM Fig. S2](#)), for a whitefish in Lake Vättern is estimated to reduce the expected TEQ with 23 %, holding all other variables constant.

4.3. Differences between Lake Vänern and Lake Vättern explained by fat content

Whitefish from the Gulf of Bothnia had the significantly lowest TEQ of the three areas, while there were no significant differences between Lake Vänern and Lake Vättern ([Fig. 1](#), [Fig. 2](#)). It should, however, be emphasized that these results are marginal effects and therefore represent estimates of the differences in TEQ between areas while keeping all other variables in the model constant. In addition, since an interaction between Area and the mean-centered Condition factor is present in the model, the results apply when the condition factor takes its mean value.

The raw data show a substantial difference in fat content between whitefish from Lake Vänern and Lake Vättern ([Fig. 1](#), [Fig. 2](#)). If the model is refitted without Fat content ([Fig. 2](#)), whitefish from Lake Vänern have the significantly highest TEQ. This indicates that the differences in TEQ between whitefish from Lake Vänern and Lake Vättern are primarily driven by differences in fat content.

4.4. Minor differences between the seasons and years

The Season variable was, as mentioned, removed due to the unbalanced sampling across seasons, for example, only summer samples from Lake Vättern (n = 4) and the Gulf of Bothnia (n = 27), and only winter samples from Lake Vänern (n = 34) and Lake Vättern (n = 31). Re-fitting the model without Season yielded similar results for the Area variable ([ESM Tables S4–S7](#)). In addition, the model restricted to Lake Vättern, the only lake with observations from all seasons, showed no significant seasonal effect ([ESM Table S3](#)). This suggests that the seasonal imbalance does not affect inferences regarding area differences. The Year variable was also not significant (p > 0.05), indicating no detectable time trends in TEQ between 2015 and 2022.

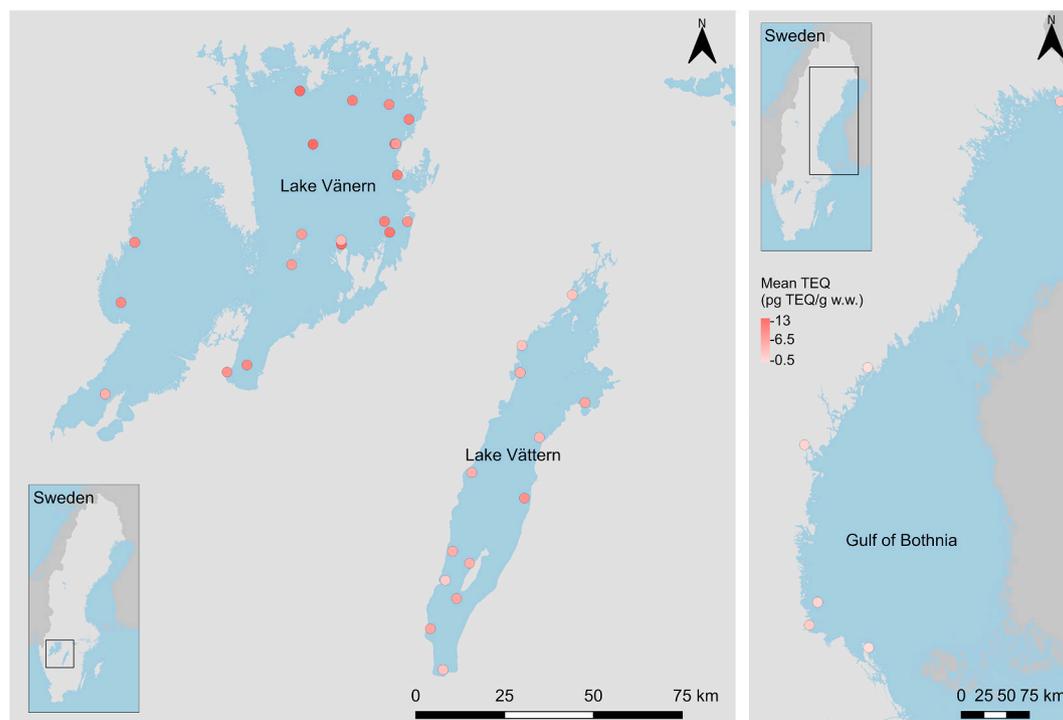


Fig. 1. Map showing the mean TEQ (pg TEQ/g w.w.) in whitefish muscle tissue based on 2005 TEF-values at each catch site in lakes Vänern and Vättern and the Gulf of Bothnia. Samples were collected 2015–2022.

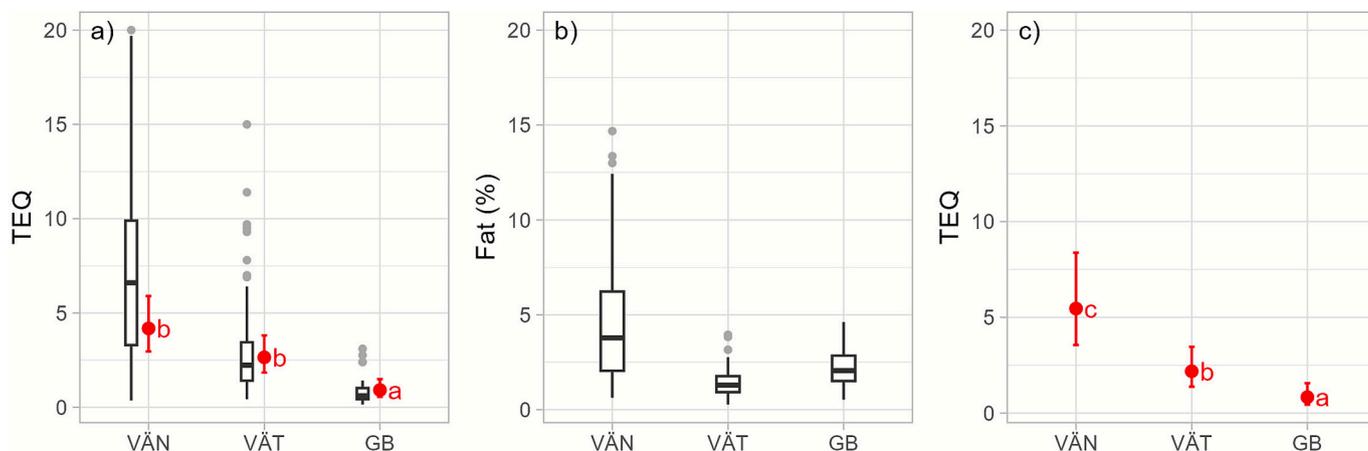


Fig. 2. Differences in TEQ (pg/g w.w.) in whitefish between Lake Vänern (VÄN), Lake Vättern (VÄT), and the Gulf of Bothnia (GB) (a). Red dots and error bars represent estimated marginal means and 95% confidence intervals per group. Mean values not significantly different from each other share at least one common letter. Boxplot of fat content (%) of whitefish from the three areas (b). Differences in TEQ (pg/g w.w.) between the areas where fat is excluded from the model (c). All boxplots represent raw data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

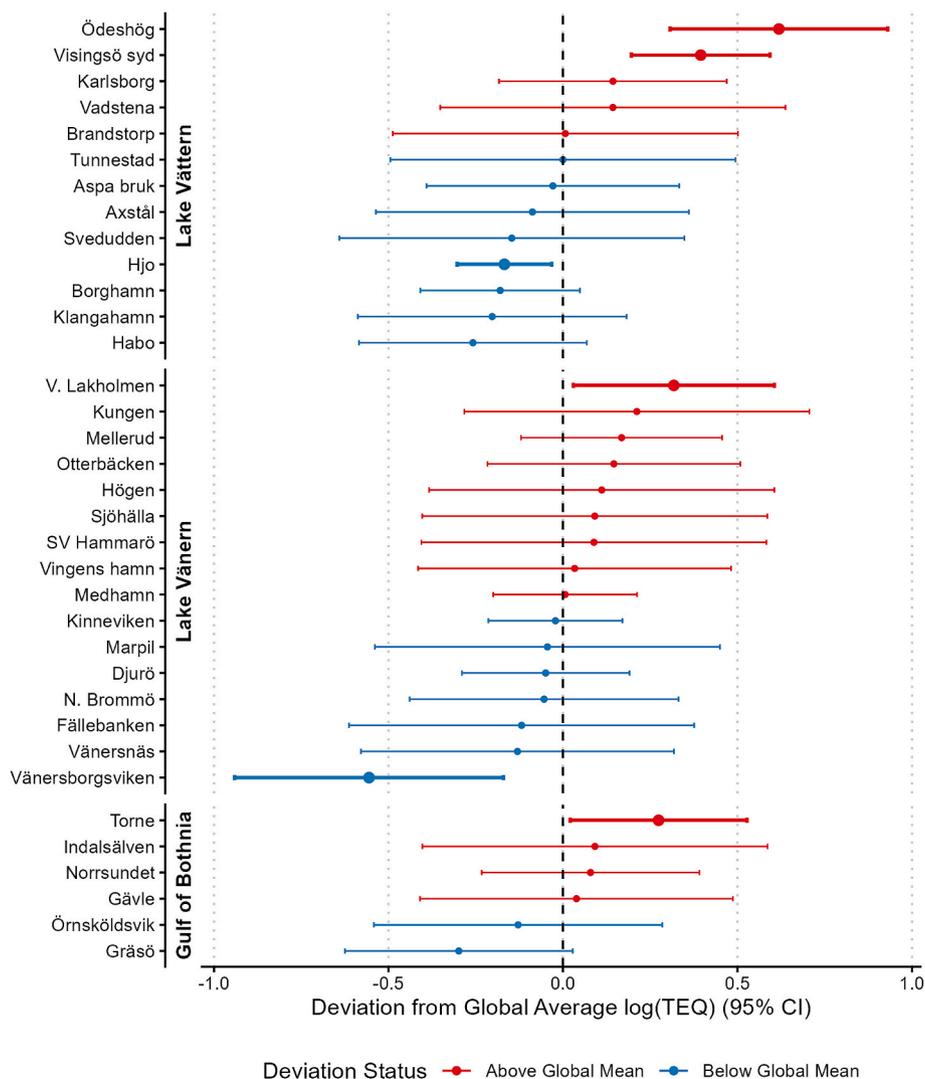


Fig. 3. Random effects distribution for the catch sites grouped by Area. The random effects are displayed as deviations from the global mean (zero) with their corresponding 95% confidence intervals. Effects that do not overlap zero are considered statistically significant and are denoted by bold points and lines.

4.5. Deviating catch sites

In each area, whitefish from some individual catch sites had TEQ either significantly above or below the global catch site average (Fig. 3). In Lake Vänern, whitefish from the site V. Lakholmen had TEQ above the average, while TEQ in Vänersborgsviken were below the average. In Lake Vättern, elevated TEQ were noted in whitefish from the catch sites Visingsö syd and Ödeshög, while whitefish from Hjo had TEQ below the average. In the Gulf of Bothnia, one catch site stood out: Torne, with above-average TEQ. Coordinates for each catch site are provided in the data file (ESM Appendix S1).

4.6. Comparison of TEQs based on 2005 and 2022 equivalency factors

For all the whitefish samples included in the statistical modelling, the total TEQ (pg TEQ/g w.w.) is substantially lower (on average 47 % lower) under the 2022 TEF re-evaluation compared to the 2005 evaluation (Fig. 4). A closer examination showed that the observed difference was largely driven by the revised TEF for PCB 126, which was lowered from 0.1 to 0.05. Across all samples of whitefish in our dataset, PCB 126 contributed on average 64 % of the total TEQ under the 2005 evaluation. Consequently, reducing its TEF by 50 % has a substantial impact on the overall TEQ.

5. Discussion

5.1. High fat content and contaminant levels in Lake Vänern whitefish

Differences in fat content were shown to be the main driver of higher TEQ in whitefish from Lake Vänern compared to Lake Vättern. However, whitefish from the Gulf of Bothnia had significantly lower contaminant content than the other two areas, even when controlling for fat content. Why the whitefish from Lake Vänern have higher fat content compared to the other areas is unknown. Possible explanations include, but are not limited to, food availability, food quality, genetic differences, or a combination of these factors.

The capacity of organisms to store lipids is dependent on the amount and quality of available food. A study from Lake Michigan on lake whitefish (*Coregonus clupeaformis*) found a negative relationship between whitefish densities, overall growth, and fat content during a period of declining primary production (Dove and Chapra, 2015). This suggests that food availability has a strong effect on the fat deposition

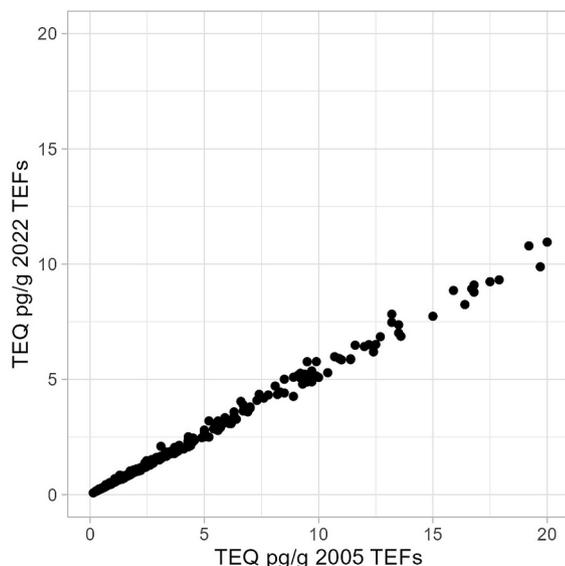


Fig. 4. Comparison of TEQ values (Σ PCDD/F + dl-PCB, pg TEQ/g w.w.) calculated using the 2005 and 2022 re-evaluations of the TEFs.

capacity of lake whitefish, and thus also likely other closely related coregonids in similar systems. Our study areas are comparable to the Laurentian Great Lakes in this respect, and similar relationships may apply.

In our study, Lake Vättern stands out in terms of its ultra-oligotrophic state, with average summer chlorophyll-A concentrations around 1 $\mu\text{g/L}$ (ESM Table S10), while Lake Vänern and the Gulf of Bothnia show higher levels of around 3 $\mu\text{g/L}$. If fat content in whitefish were the sole result of bottom-up processes, we would expect the fat content of whitefish from Lake Vänern and the Gulf of Bothnia to be similar—which they evidently are not. Hence, other drivers are likely more important.

Food quality is known to affect the growth, fatty acid composition, and lipid stores of fish (Parrish, 2009). Using different formulations of fish feed, Koskela et al. (1998) managed to increase growth rate and fat deposition in European whitefish using a high-fat diet. The availability of energy-rich prey may therefore be a better predictor of whitefish fat content compared to overall food availability or ecosystem trophic status. Both Lake Vättern and Lake Vänern harbor the energy-rich glacial relict crustaceans *Mysis relicta*/*Mysis salemaai* and *Pontoporeia quadrispinosa*, which adult whitefish feed heavily on (Nilsson, 1974; Svårdsson et al., 1988). While mysids are also present in the Gulf of Bothnia, the food preferences and the feeding strategies of the whitefish there seem to be very different, relying mainly on littoral gastropods and, to a lesser extent, benthic amphipods (Hägerstrand et al., 2018; Verliin et al., 2011), compared to the more benthopelagic feeding mode prevalent in the lakes. Although the relative energy content of littoral snails compared to mysids and *Pontoporeia* spp. are unknown, it is reasonable to assume that the energetic gains of a diet heavy in shelled gastropods are lower compared to a diet based on energy-rich crustaceans. Moreover, since pelagic mysids are nektobenthic omnivores that prey extensively on both zooplankton and benthic food sources (Hryciuk et al., 2015; Sierszen et al., 2011; Viherluoto et al., 2000), they have the capacity to accumulate significant amounts of organochlorine compounds and serve as a vector further up in the food chain (Lester et al., 2009; Parmanne et al., 2006). Given that mysid density in Lake Vänern is approximately twice as high compared to Lake Vättern (Kinsten, 2025), while pelagic fish biomass in a mysid-consuming size range is at comparable levels (Rogell and Axenrot, 2025a, 2025b), the per-biomass availability of mysids is higher in Lake Vänern. This correlates to a higher growth rate of whitefish in Lake Vänern compared to Lake Vättern (ESM Fig. S4) and could potentially explain the exceptionally high fat and contaminant levels in Lake Vänern.

Lastly, a genetic component to the variation in fat levels could also be a contributing factor, as fat deposition in whitefish appears to have a strong genetic component (Kause et al., 2011; Quinton et al., 2007), and it cannot be excluded that the Lake Vänern stock is genetically predisposed to store greater amounts of lipids. Moreover, it should be noted that our results may have been confounded by the presence of different whitefish subspecies. In Lake Vättern, for example, there are three identified ecotypes of whitefish (Sandström et al., 2020), and similar ecotypes are also present in Lake Vänern (Svardsson and Freidenfelt, 1974). Some of these forms differ both genetically and morphologically. They also have different feeding and habitat preferences and spawning patterns, which may give rise to seasonal differences, or differences between catch-sites, as well as affect the relationship between TEQ and fat content. In Lake Vänern, fishermen have reported that for a given place and time, it is possible to catch either very lean or very fatty whitefish, suggesting that genetic differences between populations may be important. We did not attempt to distinguish between the ecotypes in this study.

5.2. Condition factor explains contaminant levels in Lake Vättern

While holding fat content fixed in the model, we found a significant negative effect of condition factor, CF (Nash et al., 2006), on the TEQ in

whitefish from Lake Vättern, but not from the other two areas. The pattern observed in Lake Vättern can often be explained by growth dilution, where a higher CF implies a higher growth rate and a larger body mass to distribute a certain amount of contaminants (Herendeen and Hill, 2004). Wu et al. (2023) reported observations in fish from a tropical reservoir, where levels of certain metals (Fe, Ni, Cu, and Cd) decreased with increasing CF, consistent with growth dilution. Using bioenergetic modelling, Madenjian et al. (2016) suggested growth dilution as one of the drivers behind observed differences in PCB levels between male and female flounders from New Jersey, US (coastal waters), whereas Karimi et al. (2007), using an experimental setup, found evidence that consumption of high-quality food supporting growth can reduce methylmercury concentrations in fish.

However, an alternative explanation for the same pattern is a starvation effect, where nutritionally challenged individuals, or individuals with poor health status, have recently depleted their lipid stores and thereby mobilized contaminants into other tissues (Jørgensen et al., 1999). While growth dilution would be a fair assumption in a system where growth rate is high, starvation as a mechanism is more likely in the case of Lake Vättern whitefish, as food availability, and possibly also food quality, is poorer in this lake compared to other areas.

5.3. Spatio-temporal variation in PCDD/Fs and dl-PCBs

Although our dataset was unbalanced across seasons, re-fitting the models without the *Season* variable showed that this did not change the conclusions for the other predictors. In Lake Vättern, the only area with observations from all four seasons, *Season* was not significant. We therefore conclude that seasonal variation does not bias our main findings regarding fat content and spatial differences in TEQ.

No significant decrease in TEQ was noted over the years during which the samples were collected. However, these data are not optimal for detecting time trends. First, the measurements span a relatively short period, covering only five consecutive years (2015–2019) with a few complementary samples from 2022. This means that the statistical power regarding the time trend is low. Second, fluctuations in weather conditions or modifications in the fishing procedure could also have resulted in yearly variations in which ecotype of whitefish were caught, further complicating the detection of any underlying time trend.

5.4. Spatial variation among catch sites

A plausible explanation for the observed deviation between catch-sites within each area could be differences in external loading from local point sources. Pulp and paper manufacturing is a primary industrial sector along the shores of Lake Vänern, Lake Vättern, and the Gulf of Bothnia. Historically, the bleaching of pulp using elemental chlorine has been a source of PCDD/Fs to the environment (Jonsson et al., 1993). However, the deviations in TEQ between catch sites do not show any association with distance to pulp mill effluent discharges, nor with the degree of contamination in sediments (Hällén and Karlsson, 2018; Malmäus et al., 2012), nor with the PCDD/F levels recorded in other fish studies previously addressing the effects of Swedish pulp mill effluents (Karlsson et al., 2023; Sandström et al., 2016). To the best of our knowledge, no other industrial or societal loading can explain the differences observed within the study areas. Variations in biological conditions, as discussed above (e.g., food availability and choice), seem more likely to explain the significant deviations in TEQ levels between catch sites.

Another remark in this discussion is that, since all fish in this study were caught with selective fishing equipment (gill nets and fish traps), the analyzed fish are highly representative of the length and weight of whitefish being sold commercially, but not necessarily the complete stock. Since length showed a positive association with TEQ, there are likely larger individuals with higher TEQ in the investigated areas. It is interesting to note that in Lake Erie, one of the Laurentian Great Lakes,

the average TEQ in whitefish was 5–15 pg/g w.w. during 1999–2009, and no reduction in TEQ was observed over that period (Gandhi et al., 2019). Instead, recent measurements suggest stable or even increasing TEQ levels in Lake Erie whitefish. In comparison, measurements in lake trout (*Salvelinus namaycush*) from the other Great Lakes (Lake Superior, Lake Huron, and Lake Ontario) show declining temporal trends and have all reached levels < 3 pg TEQ/g w.w (Gandhi et al., 2019). In the Baltic Sea, there is also evidence for declining PCDD/F and PCB levels in Atlantic salmon (*Salmo salar*) (Polak-Juszczak et al., 2022) and herring (*Clupea harengus*) (Airaksinen et al., 2014), ranging from 2.6 to 5.5 % per year (Glynn et al., 2020).

Possibly, the slower response in whitefish from lakes Vänern, Vättern, and Erie reflects its preference as adults to feed on macrozoobenthos (Herbst et al., 2013; Malbrouck et al., 2006). PCDD/Fs have a strong affinity for particles and accumulate in sediments; as a result, benthic animals are more exposed to legacy contamination than planktonic pelagic species. The relative importance of benthic versus pelagic pathways is therefore a critical factor determining contaminant fate in large lake food webs globally. Different diet choices have been recognized as a vital driver to explain differences in TEQ in herring from different subbasins and ecotypes in the Baltic Sea (Goodall et al., 2024; Parmanne et al., 2006).

Several TEF-schemes have been developed over the last decades (Bhavsar et al., 2008). Therefore, it is not straightforward to compare past and current TEQs reported using different TEFs without explicitly specifying the underlying congener concentrations. Bhavsar et al. (2008) found that the total TEQ based on the 2005 re-evaluation was, on average, 22 % lower than total TEQ from the 1998 evaluation in a dataset of almost 1500 fish samples from the Laurentian Great Lakes. Applying the 2022 TEFs, many fewer of the muscle samples exceed the threshold value for marketing within the European Union (6.5 pg TEQ/g w.w) (Fig. 4). The 2022 panel aimed to align TEF assignments more closely with the underlying data rather than relying heavily on conservative (or rounded) consensus assumptions. In many cases, this led to TEFs being reduced compared to prior values—particularly for congeners like PCB 126, 1,2,3,7,8-PeCDD, and 2,3,4,7,8-PeCDF (DeVito et al., 2024).

Regarding whitefish from the Swedish Great Lakes, it was the reduced TEF for PCB 126 that substantially impacted total TEQ. The new TEF for PCB 126 stems from a re-evaluation of its relative potency based on new human (Wimmerová et al., 2016) and cross-species (Black et al., 2012) data, as well as improved statistical and meta-analytic approaches (Ring et al., 2023). Clearly, how scientific understanding of the toxicity of various PCDD/F and PCB congeners evolves may have major implications for fisheries management and for dietary guidance related to human consumption of fish contaminated with dioxin-like chemicals.

6. Conclusions

The analysis in this study of whitefish from three areas in Sweden shows that the TEQ levels are generally higher in lakes Vänern and Vättern compared to the coastal areas of the Gulf of Bothnia. The variation in TEQ within the areas can be explained by fat content, fish length, and the condition factor (the latter only in the oligotrophic Lake Vättern). We found that the comparably high TEQ in whitefish from Lake Vänern is mainly related to an exceptionally high fat content for the species. Whitefish from the Gulf of Bothnia had lower TEQ than those from the other areas, even when controlling for fat content.

Ultimately, this investigation of a European large-lake system provides a valuable comparative framework for understanding and managing the persistent challenge of legacy contaminants in whitefish populations of the Laurentian Great Lakes and other temperate large-lake systems.

CRedit authorship contribution statement

Hannes Waldetoft: Writing – original draft, Software, Methodology, Formal analysis, Data curation. **M. Gunnar Andersson:** Writing – review & editing, Methodology. **Joakim Hällén:** Writing – review & editing. **Hans Nyquist:** Writing – review & editing, Methodology. **Martin Ogonowski:** Writing – review & editing, Formal analysis. **O. Magnus Karlsson:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used Google Gemini 2.5 Pro and GitHub Copilot for R Studio (version 1.300.0) in order to assist in writing code for Fig. 3. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jglr.2026.102745>.

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