Elemental Inventory in Fish Otoliths Reflects Natal Origin of Atlantic Herring (*Clupea harengus*) From Baltic Sea Juvenile Areas

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Despite centuries of human exploitation and research on Atlantic herring (*Clupea harengus*) in Europe, there is still much uncertainty on where major nursery areas are located. However, understanding the quantitative contribution of particular coastal systems to adult fish populations is of utmost importance to secure sustainable fish resources. Routinely, marker elements indicating certain hydrological conditions, which are incorporated into calcified structures, the so-called otoliths, are used to trace the origin of fish. However, as in the Baltic Sea, small and large scale salinity gradients potentially masking specific salinity signals. Based on the entire elemental inventory of the otolith core region, indicating the chemical signature of the spawning area, we developed a unique elemental fingerprinting index (*EFI*), allowing comparisons of multi-elemental chemical signatures from within and between herring juvenile areas. Our results show significantly distinct chemical "fingerprints" on the scale of particular bays and estuaries, which were not detectable with the usual marker elements. We further demonstrate that heavy metals levels drive the potential to distinguish natal origin of herring. These findings provide an essential baseline for further studies on the impact of small scale productivity for exploited fish resources and central components of marine food webs.

Keywords: *Clupea harengus*, Western Baltic Sea, inshore spawning areas, age-0 herring, otolith chemistry, elemental fingerprinting, LA-ICP-MS

INTRODUCTION

Coastal ecosystems are highly productive, serving as crucial spawning and juvenile habitats for many fish species worldwide (Blaber and Blaber, 1980; Orth et al., 1984; Shulman, 1985). At the same time, coastal systems are under increasing anthropogenic pressure, resulting in global losses of species biodiversity and habitat degradation (Lotze et al., 2006; Worm et al., 2006; Waycott et al., 2009). However, management of natural fish resources is widely limited to fishery regulations for adult stocks. Regional coastal zone management rarely includes a certain focus on important fish nursery areas although impacts can have drastic consequences on resilience and recruitment strength of a fish population. The definition after Beck et al. (2001) emphasizes the concept of a nursery

area, revealing the importance to identify the quantitative contribution of particular areas to the adult population of fish or invertebrates. Accordingly, a nursery area is not just one of multiple areas inhabited by juveniles of a population, but is defined as an area, which contributes a greater than average number of individuals to the adult population (Beck et al., 2001; Dahlgren et al., 2006). According to these quantitative aspects, research is nowadays increasingly focused on studies on juvenile-adult habitat connectivity and dependency of fish species on certain habitats (Thorrold et al., 2001; Forrester and Swearer, 2002; Gillanders, 2002a). This connectivity and dependency aspect is highly relevant to evaluate the relation between habitat availability and fish population dynamics and at the same time exposed a great lack of knowledge on general life history and migratory patterns of economic important fish species with a great uncertainty of obligate or facultative habitat use (Able, 2005).

Otoliths are the calcified ear stones in teleost fish and were formerly used for annual age and growth estimations (Beamish, 1979; Hoyer et al., 1985). During the last decades the scope of otolith research further expanded and resulted in new scientific applications, such as otolith microstructure analyses for age estimates of early life stages on a daily scale (Nishimura and Yamada, 1984; Campana and Moksness, 1991), otolith shape analyses for stock identification (Campana and Casselman, 1993; Tracey et al., 2006) and chemical analyses of the otolith core region to investigate elemental signals and spatial differences in juvenile fish otoliths (De Pontual et al., 1999; Gillanders and Kingsford, 2003; Hamer et al., 2003). This otolith chemistry approach takes advantage of specific fish otolith characteristics, being metabolically inert, growing continuously without resorption and incorporating elements into their growing surface. Hence, these calcified structures reflect the physical and chemical characteristics of the ambient water, where the fish is residing during the early ontogeny (Campana, 1999). With the implementation of otolith microchemistry, a new age of fishery research was established, resulting in studies concerning stock discrimination analyses (Geffen et al., 2011; Heidemann et al., 2012) and fish migration patterns (Limburg, 1995; Barnett-Johnson et al., 2008), mainly based on elements indicating hydrologic conditions like strontium and barium, which are known as markers for salinity gradients (Kennedy et al., 2002; Elsdon and Gillanders, 2005). Further approaches to investigate habitat connectivity were predominately based on a few selected elements in tropic and sub-tropic fishes (Milton et al., 1997; Thorrold et al., 2001). Studies concerning the elemental inventory of fish otoliths and habitat connectivity of economically important fish species in the North Atlantic region, such as flatfishes, cod and herring, are rather scarce (but see Brophy et al., 2003; Vasconcelos et al., 2008; Thorisson et al., 2011).

The Atlantic herring (*Clupea harengus*, L. 1958) is one of the most economically important marine fishery target species in the world (FAO, 2016). Moreover, this small pelagic fish is of high ecological relevance, linking different trophic levels in the marine food web (Casini et al., 2004; Möllmann et al., 2004). In the Baltic Sea, *C. harengus* is a highly migratory fish, accomplishing annual migrations between their feeding
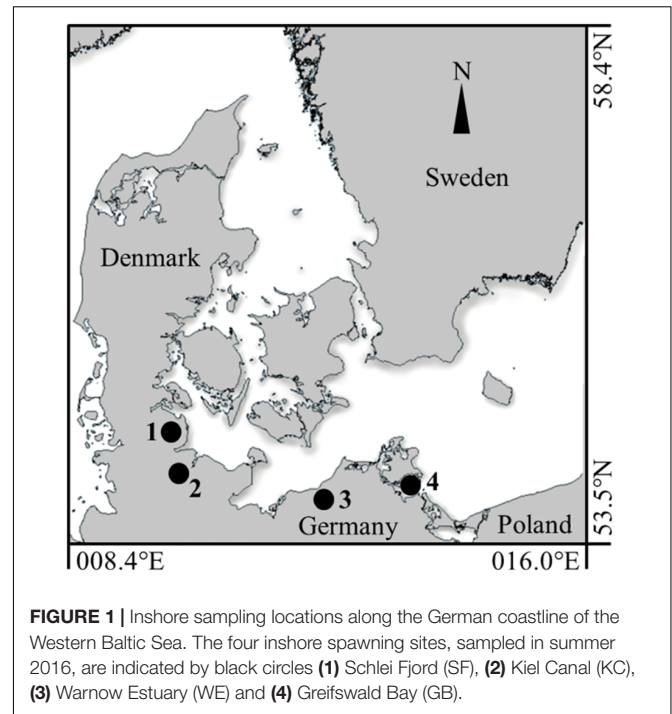

FIGURE 1 | Inshore sampling locations along the German coastline of the Western Baltic Sea. The four inshore spawning sites, sampled in summer 2016, are indicated by black circles **(1)** Schlei Fjord (SF), **(2)** Kiel Canal (KC), **(3)** Warnow Estuary (WE) and **(4)** Greifswald Bay (GB).

grounds in the Kattegat-Skagerrak and their coastal spawning grounds located in bays, estuaries and lagoons along the coastal Western Baltic Sea during spring, showing a distinct homing behavior (Wheeler and Winters, 1984; McQuinn, 1997). This herring population is of high economic value for the Western Baltic Sea region. Herring reproduction success is affected by multiple abiotic and biotic parameters (Holliday and Blaxter, 1960; Laine and Rajasilta, 1999; Peck et al., 2012; Kotterba et al., 2017), as well as by human-induced stressors, such as pollution (Dethlefsen et al., 1996; Incardona et al., 2012) or eutrophication (Aneer, 1987; Rahikainen et al., 2017; von Nordheim et al., 2018). Eutrophication processes in the past decades led to severe habitat degradation of important spawning areas in Baltic coastal waters (Kääriä et al., 1988; Kanstinger et al., 2016). Western Baltic herring recruitment decreased during the past two decades and remained on a low level ever since, reaching the lowest value of the time-series in 2017 (ICES, 2018). The reasons for this decline are still unclear, but evidence mounts for a synergy of eutrophication, climate change and resulting ecological cascades negatively affecting the survival of early life stages (Moll et al., 2018). However, quantitative studies on the contribution of single coastal juvenile habitats to the adult herring population are lacking, but are of vital importance to understand the impact of local hazards to fish population dynamics and to establish adequate coastal zone management strategies.

The objectives of this study are to identify differences in the elemental composition of age-0 herring otoliths from different inshore spawning areas along the Western Baltic coastline. Hypothesizing that herring otoliths from different juvenile areas differ in their elemental composition, we created an elemental fingerprinting index (*EFI*) based on a multi-element approach.

MATERIALS AND METHODS

Age-0 Herring Sampling

All four inner coastal sampling sites are anthropogenic-influenced spawning areas for the Western Baltic spring spawning herring population, located along the German coastline of the Western Baltic Sea. In June 2016, sampling was conducted in the eutrophic Schlei Fjord (SF: ~54.62°N, 09.09°E) and in Kiel Canal (KC; ~54.33°N, 09.72°E), an artificial waterway with heavy ship traffic, connecting the Baltic Sea and the North Sea. Furthermore, young-of-the-year (YOY) herring was sampled in the Warnow Estuary (WE; ~54.12°N, 12.10°E), with its dockyard and landing pier for cruise liners and ferries, and the eutrophic Greifswald Bay (GB; ~54.25°N, 13.50°E) (see **Figure 1**). YOY herring was caught by beach seine (7 m opening, 5 mm mesh size, wing height 1.5 m) in the SF sampling area and by purse seine (40 m length, 4 mm mesh size, 3 m height) in KC, both nets were pulled by two people. Sampling areas WE and GB were sampled with a ring trawl of 1 m diameter (1550 μm mesh size) onboard a research vessel. Hydrological parameters [sea surface temperatures (SST) and salinity] were either recorded with a hand held field probe (YSI Professional Plus) or a remotely operated CTD. The characteristics of each sampling site, including abiotic parameters during sampling, mean total length (TL mm) of YOY herring, as well as numbers of individuals per sampling site are summarized in **Table 1**. Herring were frozen immediately after the catch and were transported to the laboratory for otolith dissection.

Young-of-the-year herring sampling was conducted under current licenses for wild fish sampling according to Mecklenburg-Western Pomeranian (Germany) fishery law (§11 LFischG, Landesamt für Landwirtschaft, Lebensmittelsicherheit und Fischerei, Mecklenburg-Vorpommern).

Sample Processing

Prior to otolith dissection, microscope slides were washed in 2% nitric acid (Rotipuran Supra 69%, Carl Roth), were rinsed with ultrapure water and were dried under a flow cabin to keep them free from dust particles. Double-sided adhesive transparent pads, placed on the cleaned glass slides, were used as otolith fixing material (for further information, see **Supplementary Figure 1**). Herring otoliths were dissected under a microscope (Olympus SD 30) and sagittal otoliths were removed with non-metallic equipment to minimize potential contamination. After dissection, each otolith (either left or right sagittal otolith) was rinsed in ultrapure water several times to remove any adhesive tissue and 30 otoliths per sampling area were used for chemical analysis of habitat-specific signatures, except for GB (n = 15). The chosen sample size was above the commonly accepted standard for this kind of analysis (Gillanders, 2002a; Hamer et al., 2003) and was assumed to be adequate to test our hypotheses. Otoliths were transferred and placed on the fixing material. Microscope slides with attached otoliths were stored in a plastic vials for further processing in the laboratory.

Analytical Methods

Elemental composition of herring otolith core regions were analyzed with the laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS) technique, using a ThermoFinnigan ELEMENT2 ICP-MS with a Nd:YAG UP213 laser ablation system at the Max Planck Institute of Chemistry in Mainz, Germany. The certified reference material NIST612 (National Institute of Standards and Technology) and the micro analytical reference material MACS3 (United States Geological Survey) were used for calibration (Jochum et al., 2007; Jochum et al., 2011) and were analyzed prior to sample measurement and reference material measurements were constantly repeated to ensure quality. Otolith core regions were ablated with 80 μm laser spot size at 60% power with a pulse repetition rate of 10 Hz and energy densities of ~10.2 J cm^{-2}. Dwell durations of otoliths were operated manually, due to individual otolith size and thickness. Further technical information of the New Wave laser ablation system and the operating parameters for the ELEMENT2 ICP-MS (further information is given in **Supplementary Table 1**).

Data Analysis

Values near detection limits were excluded and only elements with no more than two missing values were considered for the analysis. In total, the following 17 elements were used: lithium (Li), boron (B), sodium (Na), magnesium (Mg), silicon

TABLE 1 | Description of each inshore sampling area [Schlei Fjord (SF), Kiel Canal (KC), Warnow Estuary (WE), Greifswald Bay (GB)] with respective water body type, prevailing salinity ranges in PSU (Messner and von Oertzen, 1990; Feibicke, 1997; Kafemann et al., 2000), abiotic parameters at sampling location (SST and salinity), number of analyzed individuals and mean total length TL [mm] of caught age-0 herring with standard deviation.

Location	Water body type	Salinity range PSU	SST °C	Salinity PSU	No. of individuals	Mean TL mm
SF	Fjord	Mesohalin	20.8	4.03	30	37.2 (±2.9)
	42 km	3–18				
KC	Artificial water way	Mesohalin	20.0	7.05	30	38.0 (±1.8)
	97 km	2.5–15				
WE	Estuary	Mesohalin	20.1	10.7	30	23.2 (±3.5)
	12.6 km^2	5–18				
GB	Lagoon	Mesohalin	Ø18.3	Ø7.8	15	22.7 (±2.2)
	514 km^2	5–10				

The SST and salinity for GB are averaged due to different pooled stations.

(Si), manganese (Mn), iron (Fe), cobalt (Co), copper (Cu), zinc (Zn), rubidium (Rb), strontium (Sr), tin (Sn), barium (Ba), lead (Pb), thallium (Tl) and uranium (U). Potential chemical differences between different sampling locations were visualized by multidimensional scaling (MDS-plot), using the PRIMER Software (Version 6.1.13) and the dissimilarity matrix of calculating the Euclidean distances. Elemental concentrations were $\log(x+1)$-transformed for standardization. Statistical tests were performed with the software SPSS, statistical significance (significance level of $p < 0.05$) was tested by using one-way analysis of variance (ANOVA). Data sets were tested for variance homoscedasticity by Levene's test. Due to variance heteroscedasticity and unequal sample sizes, statistical significances were tested with ANOVA including Welch correction (Welch, 1938) which also compensates for non-normal distributions and *post-hoc* test for inhomogeneous variances and sample sizes (Games Howell test). *EFI* values were tested for significant differences within and between sampling areas using Welch Test and Games Howell *post-hoc* test to investigate significant differences between the four sampling sites.

Elemental Fingerprinting Index (*EFI*)

We visualized chemical otolith signatures for each spawning area by radar plots, based on the relative mean proportion of each element to the highest concentration found among the total of 105 individuals included in this study. We modified a well-established ecological overlap index (Schoener index, Schoener, 1974) to create the *EFI*, a novel measure of similarity between 2 fish individuals considering numerous chemical signatures in their otoliths. The $EFI_{i,j}$ describes the comparison of two fish individuals that includes 17 elements and was calculated according to the following equation:

$$EFI_{i,j} = \frac{2 \times \sum_{x=1}^{17} \min\left(conc\_x_i;\ conc\_x_j\right)}{\sum_{x=1}^{17} \left(conc\_x_i +\ conc\_x_j\right)}.$$

Where $conc\_x_i$ and $conc\_x_j$ represent the concentrations of element x in fish i and fish j, respectively, while $\min\left(conc\_x_i;\ conc\_x_j\right)$ represents the lower value of these two concentrations (for detailed information, see **Supplementary Figures 2**, **3**). The *EFI* ranges from 0 to 1, where a value of 0 indicates that two compared individuals are most different in otolith elemental composition, whereas a value of 1 indicating the highest similarity in elemental composition of two comparing individuals. We conducted elemental concentration comparisons for all individuals within one sampling area resulting in $\binom{30}{2} = 435$ pairs for each sampling area (except for GB: $\binom{15}{2} = 105$ pairs).

And comparisons of all individuals between the different sampling areas:

$$\binom{60}{2} - 2 \times \binom{30}{2} = 900 \text{ pairs for each comparison}$$

(GB: $\binom{45}{2} - \left(\binom{30}{2} + \binom{15}{2}\right) = 450$).

Subsequently, we tested whether the variance among the *EFI*s derived from comparisons within the areas differed significantly from the *EFI*s obtained from comparisons of individuals from differing areas.

RESULTS
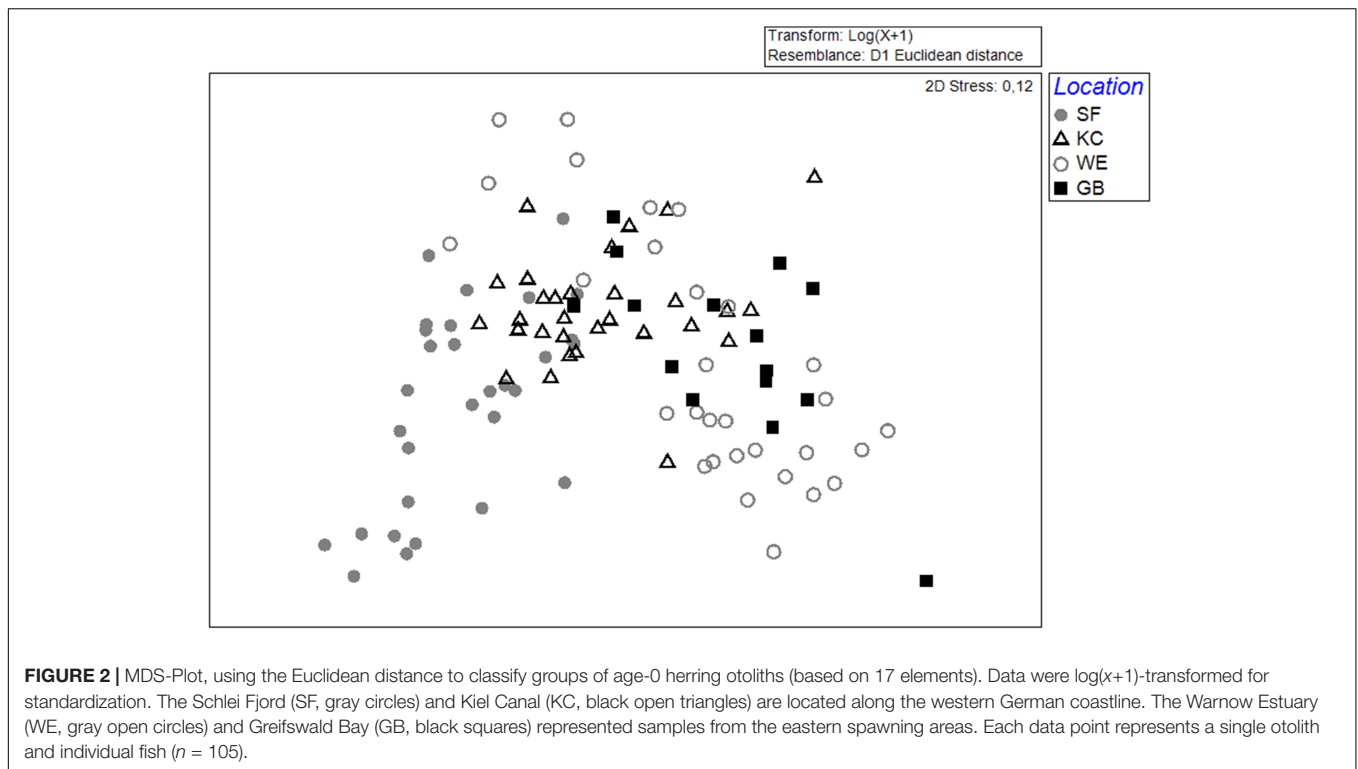
Chemical Signatures in Herring Otoliths

In total, 39 elements could be determined in young-of-the-year otolith samples from different inshore spawning areas. Altogether, 17 elements were used to distinguish the chemical otolith signatures from different sampling sites. The mean elemental concentrations are given in **Supplementary Table 2**. The element concentrations found in all 105 individuals were included in an MDS-plot for visualizing the differences in chemical signatures for each sampling area (**Figure 2**). Otolith signals from the western sampling areas Schlei Fjord (SF) and Kiel Canal (KC) are more similar in their elemental concentrations compared to the eastern sampling areas Warnow Estuary (WE) and Greifswald Bay (GB) with some intermingling signals from KC, GB and WE. Elemental otolith compositions from WE showed a higher variability in individual element concentration. However, a clear separation between the western and eastern spawning areas is discernible (**Figure 2**).

Significant Differences in Elemental Compositions

We found continuously high significant differences ($p \leq 0.001$) in element concentrations between all four sampling areas and significant differences ($p = 0.008$) for tin (Sn) (**Table 2**). Based on these results we performed *post-hoc* tests for single elements to identify habitat-specific significant differences between single sampling areas. Detailed information on the results for each element is given in **Table 3**. We found 13 elements to be significantly different between SF-WE comparison. The comparisons SF-KC and SF-GB revealed significant differences of 11 elements with uranium (U), being significantly different between SF-GB. Ten elements were significantly different within the KC-WE comparison. Furthermore, 7 elements were significantly different between KC-GB. The comparison WE-GB revealed significant differences in 6 elements (**Table 3**).

Elemental Fingerprinting Indices (*EFI*)

The entire chemical otolith inventory for each inshore coastal spawning area revealed 4 habitat-specific fingerprint plots with similarities in the generally dominance of single elements, but clear differences in their relative element ratio (**Figure 3**). We conducted multi-elemental concentration pairwise comparisons for individuals within one sampling site and pairwise comparisons of individuals between different sampling

FIGURE 2 | MDS-Plot, using the Euclidean distance to classify groups of age-0 herring otoliths (based on 17 elements). Data were log(x+1)-transformed for standardization. The Schlei Fjord (SF, gray circles) and Kiel Canal (KC, black open triangles) are located along the western German coastline. The Warnow Estuary (WE, gray open circles) and Greifswald Bay (GB, black squares) represented samples from the eastern spawning areas. Each data point represents a single otolith and individual fish (n = 105).

sites, using *EFI* to identify similarities in element concentrations within one group and differences between groups. Elemental concentrations of individuals within each of the SF, KC and GB sample groups were rather stable, whereas WE samples were

TABLE 2 | Results of ANOVA with Welch correction to identify statistical differences in age-0 herring otolith element concentration between the four juvenile inshore areas [Schlei Fjord, Kiel Canal, Warnow Estuary (n = 30) and Greifswald Bay (n = 15)], with degrees of freedom (*df1* and *df2*), *F*-value and significance level (*p*) for each single element.

	df1	*df2*	*F*	*p*
Li	3	41.22	18.92	<0.001
B	3	43.43	70.19	<0.001
Na	3	43.66	27.65	<0.001
Mg	3	40.56	41.25	<0.001
Si	3	44.82	26.65	<0.001
Mn	3	43.29	7.77	<0.001
Fe	3	43.47	61.25	<0.001
Co	3	45.00	19.41	<0.001
Cu	3	39.31	14.91	<0.001
Zn	3	37.42	12.62	<0.001
Rb	3	39.57	16.79	<0.001
Sr	3	45.61	12.98	<0.001
Sn	3	37.89	4.59	0.008
Ba	3	46.95	12.98	<0.001
Pb	3	35.28	10.93	<0.001
Tl	3	52.02	61.11	<0.001
U	3	35.36	6.87	0.001

slightly more variable in their multi-element composition (lower mean *EFI*). Comparisons of individual fingerprints between two sampling groups revealed clear differences between WE and SF, whereas comparisons between SF-KC and KC-GB were more similar in their element signatures (**Table 4**). *EFI* values for comparisons of SF-GB, WE-KC and WE-GB were smaller than *EFI* values of within-group comparisons, indicating that elemental concentrations between all four groups are more different than within groups (**Table 4**). Regarding statistical differences between two group comparisons, the *EFI* values showed highly significant differences for all comparisons (GB-KC: $F_{(2,288.7)}$ = 253.2, p < 0.001; GB-WE: $F_{(2,345.1)}$ = 144.8, p < 0.001; GB-SF: $F_{(2,289.1)}$ = 410.8, p < 0.001; WE-KC: $F_{(2,1767)}$ = 959.5, p < 0.001; WE-SF: $F_{(2,1013.4)}$ = 1413.6, p < 0.001; SF-KC: $F_{(2,975.5)}$ = 563.2, p < 0.001). *Post-hoc* test results are shown in **Supplementary Table 3**.

DISCUSSION

The successful outcome of otolith microchemistry studies strongly depends on spatial variability of elemental concentrations between investigated habitats. There is abundant evidence that fish otoliths from different basins and even sites within basins show spatial variability in their elemental composition (De Pontual et al., 1999; Rooker et al., 2001; Yamane et al., 2010). Our approach included the entire inventory of otolith-core elements summarized by a unique *EFI*, based on 17 elements. To our best knowledge, this approach allows comparing multi-elemental chemical composition of otoliths

TABLE 3 | Results of Games Howell *post-hoc* test to identify site-specific significant differences for each element with respective significant levels ($p \leq 0.05$), including sample sizes of $n = 30$ for Schlei Fjord (SF), Kiel Canal (KC) and Warnow Estuary (WE) and $n = 15$ for Greifswald Bay (GB).

Element	Site comparisons					
	SF-KC	SF-WE	SF-GB	KC-WE	KC-GB	WE-GB
Li	**0.001**	**<0.001**	**0.006**	**<0.001**	0.107	0.110
B	**<0.001**	**<0.001**	0.070	**<0.001**	**<0.001**	**<0.001**
Na	**<0.001**	**<0.001**	**<0.001**	**0.011**	0.419	0.523
Mg	**0.003**	**<0.001**	**<0.001**	**0.001**	0.486	**0.028**
Si	0.634	**0.002**	**<0.001**	**0.038**	**<0.001**	**0.002**
Mn	**0.001**	**0.006**	**0.001**	0.108	0.873	0.083
Fe	**<0.001**	0.202	0.547	0.207	**<0.001**	0.337
Co	**<0.001**	**0.045**	0.990	0.824	**<0.001**	**0.040**
Cu	0.118	**0.001**	**0.001**	**0.003**	**0.005**	0.536
Zn	**0.023**	**<0.001**	0.077	**0.003**	0.132	0.691
Rb	**<0.001**	**0.046**	**0.012**	0.632	0.968	0.810
Sr	0.938	**<0.001**	**0.038**	**<0.001**	0.088	0.095
Sn	0.736	**0.005**	1.000	0.907	0.738	**0.007**
Ba	**<0.001**	0.898	0.203	**<0.001**	**0.017**	0.052
Pb	0.234	**<0.001**	**0.047**	**0.001**	0.370	**0.009**
Tl	**<0.001**	0.152	**<0.001**	0.645	**<0.001**	0.282
U	0.158	0.175	**0.016**	0.189	0.051	0.280

Significant p-values are given in bold type.

within and between herring juvenile areas for the first time. Our results show significantly distinct chemical "fingerprints" on the scale of particular bays and estuaries providing a chemical "birth certificate" of their natal origin.

Environmental Factors

The incorporation of elements into the growing surface of fish otoliths is related to environmental variables, such as water temperatures, salinity and the availability of specific elements in the water (Tzeng et al., 1997; Elsdon and Gillanders, 2003). In addition, endogenous factors (such as physiology, genetics and growth effects) control incorporation processes (Fowler et al., 1995; Martin and Thorrold, 2005; Barnes and Gillanders, 2013). Elemental uptake by prey digestion might be marginal, at least for some species (Farrell and Campana, 1996; Milton and Chenery, 2001; Buckel et al., 2004). The impact of environmental variables on element incorporation is sufficiently studied, but results are rather contradictory (Kalish, 1989; Radtke et al., 1990; Townsend et al., 1992; Hoff and Fuiman, 1995), indicating that interactions between environmental and endogenous factors might be species-specific. However, it is stated that non-physiologically regulated elements (such as Sr, Ba, Mn) are usable for life history studies (Elsdon and Gillanders, 2003). Woodcock et al. (2012) indicated that Mg, an element often used in microchemistry studies, might also be physiologically regulated in fish otoliths. Hence, validation experiments for the species of interest are highly recommended to verify interpretations (Kalish, 1989).
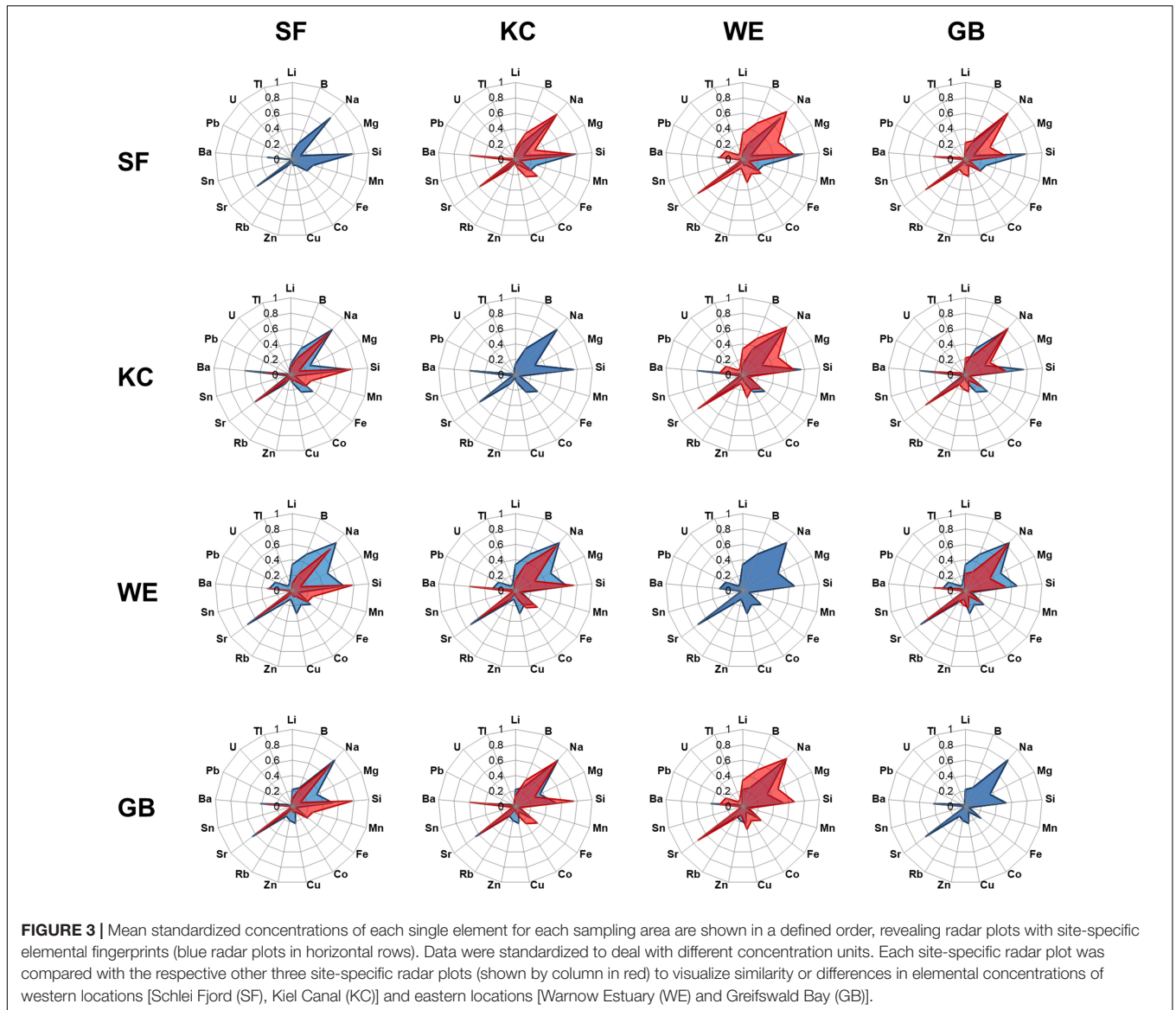
Whereas studies on the elemental uptake are almost entirely focused on single elements (see review in Elsdon and Gillanders, 2003), multi-element investigations are rather scarce (Fowler et al., 1995; Elsdon and Gillanders, 2002). With our multi-element approach, including also heavy metals, we assume that observed chemical patterns are more related to habitat-specific differences than affected by endogenous factors. However, more research is required to understand the impact and interaction of different factors on elemental incorporation in herring otoliths.

Potential temporal variability of element concentrations is one important aspect to be considered in future connectivity studies (Milton et al., 1997; Hamer et al., 2003; Swearer et al., 2003; Arkhipkin et al., 2009). Although some studies showed high temporal variability in elemental concentrations, other studies revealed inter-annual consistency of elements (Patterson et al., 1999; Rooker et al., 2001), indicating that variability might be habitat-specific. Gillanders (2002b) stated to build up a library of elemental fingerprints over several years for each study area to increase the interpretation success of fingerprint patterns from juvenile fish, regarding contribution estimates of single reproduction areas to the overall fish population. A multi-year sampling should be considered in the future to investigate temporal consistency of the found habitat-specific signals.

Element Concentrations in Herring Otoliths

The concentrations levels found in YOY herring otoliths corresponded to levels for single elements (Mg, Zn, Sr, Ba, Pb) from a study by Brophy et al. (2003), except for the two elements Sr and Ba. Those in particular are marker elements for an origin relative to certain salinity conditions, with higher Sr concentrations in marine habitats and higher Ba concentrations in freshwater habitats (Tzeng and Tsai, 1994; Elsdon and Gillanders, 2005). The concentrations found in otolith samples from inshore juvenile areas were generally

FIGURE 3 | Mean standardized concentrations of each single element for each sampling area are shown in a defined order, revealing radar plots with site-specific elemental fingerprints (blue radar plots in horizontal rows). Data were standardized to deal with different concentration units. Each site-specific radar plot was compared with the respective other three site-specific radar plots (shown by column in red) to visualize similarity or differences in elemental concentrations of western locations [Schlei Fjord (SF), Kiel Canal (KC)] and eastern locations [Warnow Estuary (WE) and Greifswald Bay (GB)].

lower in Sr and higher in Ba, compared to herring otoliths from the North Sea (Brophy et al., 2003), reflecting the brackish Baltic Sea ecosystem, with high salinity gradients (from rather marine salinities of ∼30 PSU) in adult herring feeding areas up North in the Kattegat and Skagerrak to more brackish conditions within the Western Baltic Sea. In addition to the overall Baltic Sea salinity gradient from Southwest to Northeast, there are multiple local inshore-offshore salinity gradients composed by river estuaries or other transitional waters, making it difficult to interpret results solely based on these salinity signatures. Hence, we focused on the multiple-element approach to find differences in elemental composition of herring otolith from different coastal spawning grounds.

Sampling in four historically known juvenile areas was performed in summer 2016. Due to sampling site-specific time of spawning and larval growth, we were not able to sample YOY herring otoliths of the same size. However, high

concentration variations between different otolith sizes could not be observed during our measurements. Using the LA-ICP-MS approach for unpolished herring otoliths within a specific size-range was applicable, at least for the Western Baltic Sea, since all herring samples were collected within their inshore coastal reproduction areas. Moreover, the approach of solution-based ICP-MS is an approved method, where whole otoliths are dissolved in nitric acid to analyze chemical signatures and habitat-specific patterns (Patterson et al., 1999; Rooker et al., 2003). However, the choice of sample processing and analytical methods is depending on single fish species and their particular habitat utilization.

Multi-Element Approach

Although we were able to detect concentration values of 39 elements in total with the LA-ICP-MS approach, we had to exclude all rare earth metals and some heavy metals

TABLE 4 | Elemental fingerprinting indices {mean *EFI* [with standard deviation (±SD)] and median *EFI*} with number of comparisons for each sampling area (upper table) and results of comparisons between respective groups (lower table) with number of comparisons.

	Comparisons within one group		
Area 1	No. comparisons	Mean *EFI* (±SD)	Median *EFI*
SF	435	0.877 (±0.039)	0.879
KC	435	0.858 (±0.043)	0.861
WE	435	0.755 (±0.074)	0.762
GB	105	0.845 (±0.048)	0.850

		Comparisons between two groups		
Area 1	Area 2	No. comparisons	Mean *EFI* (±SD)	Median *EFI*
SF	KC	900	0.799 (±0.048)	0.802
SF	WE	900	0.705 (±0.086)	0.703
SF	GB	450	0.777 (±0.062)	0.784
KC	GB	450	0.792 (±0.046)	0.795
WE	KC	900	0.737 (±0.059)	0.739
WE	GB	450	0.759 (±0.067)	0.764

The EFI ranges from 0 to 1, where a value of 0 indicates that two compared individuals are most different in otolith elemental composition, whereas a value of 1 indicating the highest similarity in elemental composition of two comparing individuals.

(such as Cd and Hg), due to concentration levels below the instrument detection threshold. All together 17 elements could be used for data analysis, which is still an appreciable element number. In most studies, differences in elemental compositions were mainly based on a few established elements (e.g., Ba, Mg, Mn, Sr) (see Thorrold et al., 1998; Campana et al., 2000) with some exceptions, focusing also on multiple elements (Edmonds et al., 1991; Leakey et al., 2009). For our interdisciplinary multiple-element approach, we created a unique and innovative *EFI* to describe differences and similarities of the otolith chemical inventory. The *EFI*s were more similar within one group/sampling area than between different sampling areas, indicating that habitat-specific chemical signatures were more stable within a particular area and more variable between different sampling areas, except for the comparison GB-WE, due to higher variability in chemical composition of WE samples. Our results show a clear separation between the western and eastern spawning areas, based on site-specific water chemistry, including salinity and pollutant signals. We can only speculate, if these patterns reflect the historical pollutant signals of different water management strategies, caused by the boundary of the "German Wall," since pollutants are known to accumulate into the sediment over decades (Deely and Fergusson, 1994; Ruiz, 2001; Buccolieri et al., 2006) or if different elemental signals are based on site-specific alterations (ship traffic, industrial and agricultural discharge).

The lack of knowledge on the quantitative contribution of single reproduction areas to the overall herring population is problematic, since herring show a distinct homing behavior to their traditional spawning areas. If important nursery areas are affected by human-induced habitat degradation and environmental conditions of important nurseries become unfavorable for successful herring reproduction, but herring continue their migrations to these specific anthropogenic-stressed habitats, this might have severe impacts for the population persistence. This unknown habitat dependency demonstrates the relevance of our results, which set the baseline for future estimates on habitat productivity, which could lead to a more directed coastal zone management of important spawning grounds and coastal nursery areas in the future.

AUTHOR CONTRIBUTIONS

DM, PK, LvN, and PP conceptualized the study. DM wrote the manuscript, performed the sampling and was responsible for laboratory processing and sample preparation. KJ and DM performed the measurements with the LA-ICP-MS. DM and PK analyzed the data. PK contributed the *EFI* calculations and *EFI* statistical analyses. PK, LvN, PP, and KJ revised the manuscript.

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