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Classification of European *Illex coindetii* and *Loligo forbesii* Squid Stocks by Trace Element Analysis of Statoliths

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Received: 7 October 2024 | **Revised:** 11 August 2025 | **Accepted:** 21 August 2025

Funding: This project was funded by Evangelisches Studienwerk Villigst (Protestant Academic Foundation). The MEDITS surveys are co-funded by the European Union through the European Maritime and Fisheries Fund (EMFF) within the National Programme of collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy. Open Access funding was enabled and organized by Projekt DEAL.

Keywords: Loliginidae | Myopsida | Oegopsida | Ommastrephidae | statolith microchemistry analysis | stock structure

ABSTRACT

We investigated whether statolith microchemistry analysis could classify ommastrephid and loliginid squid species into fishery stocks. Statolith nucleus (early life stage) and edge (life stage at time before catch) of *Illex coindetii* (Verany, 1839) and *Loligo forbesii* (Steenstrup, 1856) from various areas of the North East Atlantic Ocean and Mediterranean Sea during 2021–2022 were analysed using laser ablation ICP-MS to measure values of 11 trace elements (Na, Mg, Mn, Fe Co, Cu, Zn, Sr., Ba, Pb and U) next to calcium. Four stocks were categorised for *I. coindetii* and five stocks for *L. forbesii* amongst sample areas. Common hatching areas and migration into distinct fishing regions were also identified. Our results provide substantial information to sustainably manage fisheries for both species in European waters by providing stock definitions, spawning periods and migration patterns.

1 | Introduction

Cephalopods have gained importance in European commercial fisheries due to abundance shifts and range expansions (Chen et al. 2006; van der Kooij et al. 2016; Oesterwind et al. 2022), whilst European finfish populations and fishery harvests have declined (Sabolić et al. 2021). Due to their rapid growth, high productive rates and adaptability, cephalopods are likely able to exploit ecological opportunities arising from the overfishing of commercial finfish stocks (Mangold and Boletzky 1988; Caddy and Rodhouse 1998). These features, along with their high market price, make cephalopods valuable harvest targets (Vaz-Pires et al. 2004). However, little is known about the stock structure of commercially important and highly mobile squid species in Europe (Pierce et al. 2025).

Two squid species that migrate extensively are the broadtail shortfin squid *Illex coindetii* and the veined squid *Loligo forbesii*. *I. coindetii*, an oceanic and neritic species, is widely distributed in the Atlantic and Mediterranean and plays an essential role in oceanic ecosystems by acting as an 'ecosystem accelerator' that converts food into energy-rich biomass which sustains higher

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†Klaus Peter Jochum, deceased 2024.

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Fisheries Management and Ecology, 2026; 33:181–200
https://doi.org/10.1111/fme.70016

trophic levels (González and Guerra 2013). Genetic analyses of *I. coindetii* from the Iberian Atlantic and the central Mediterranean revealed a homogenous population structure, albeit with moderate temporal and geographical variation (Martínez et al. 2005). However, statolith shape analysis revealed multiple stocks for *I. coindetii* in the North East Atlantic Ocean and Mediterranean Sea (Bobowski et al. 2024). *L. forbesii*, a demersal squid species that typically migrates ontogenetically, with juveniles moving offshore to feed and adults moving inshore to spawn, occurs primarily over the continental shelf (Pierce et al. 2013). However, around the Balearic Islands, adults have also been observed moving offshore to feed (Valls et al. 2015). Despite a lack of evidence for distinct stocks in European waters from morphometric and genetic analyses, isolated populations occur around the Azores and Rockall Bank (Shaw et al. 1999; Göpel et al. 2022; Sheerin et al. 2022). Statolith shape analyses, in contrast, indicated the presence of at least three stocks in the North East Atlantic Ocean and two stocks in the Mediterranean Sea (Bobowski et al. 2024).

Although squid species are currently not managed in Europe (Bobowski et al. 2023; Pierce et al. 2025), both species are important in European fisheries (Martínez et al. 2002; Pierce et al. 2013), especially as bycatch in trawls (Sánchez et al. 1998; Pierce et al. 2013). Furthermore, cephalopod fishing in Europe, especially for cuttlefish and squid, is increasing in the North East Atlantic Ocean. For example, Danish cephalopod landings from the northern North Sea and Skagerrak increased from 50 t in 2011–2014 to over 430 t in 2020 (Vinther 2021). Although cuttlefish and octopus are main contributors to cephalopod landings in Europe, landings of longfin squids (*L. forbesii*, *L. vulgaris*, *Alloteuthis* spp.) increased after 2017, with peak landings in 2022 (ICES 2023). In parallel, landings of short-finned squids (*I. coindetii*, *Todarodes sagittatus* and *Todaropsis eblanae*) increased significantly in 2021, with peak landings in 2022 (ICES 2023). Understanding population dynamics and defining management units or stocks (FAO Fishery Glossary, n.d.) is crucial for sustainable fishery assessment and management (Rodhouse et al. 2014).

Statolith microchemistry can be a valuable tool for defining stocks of cephalopod species and for identifying migration pathways or hatching grounds, to support their sustainable management (Zumholz, Hansteen, et al. 2007; Liu et al. 2015, 2016; Avigliano et al. 2020; Han et al. 2022). Statoliths are one of the few hard structures in cephalopods that consist mainly of aragonite, a polymorph of calcium carbonate (Dilly 1976). In addition to their use for age estimation based on statolith increments consisting of pairs of light (aragonite) and dark rings (organic material) that are laid down over time (usually daily) (Hanlon et al. 1989; Jackson 1994; Perez et al. 2006), statoliths can be used for estimating growth rates (Jackson and Choat 1992). Another important application of statoliths is stock discrimination based on statolith shape (Sheerin et al. 2022; Bobowski et al. 2024) or microchemistry analysis of trace elements in statoliths (Green et al. 2015). During cephalopod ontogeny, trace elements are absorbed into statoliths from surrounding water and ingested food that give rise to distinct elemental compositions caused by different habitats (water masses) occupied by individual squid, which can be used as a natural marker to distinguish cephalopod stocks (Avigliano et al. 2020). Besides stock identification, statolith element profiles can provide information on natal origin (Liu et al. 2015) or migration patterns of individuals (Liu et al. 2016; Han et al. 2022). Most trace elements are incorporated in squid statoliths during darkness when squids are at the sea surface, so sea surface temperature may have a more significant impact on the uptake of elements than deep water temperature (Liu et al. 2016).

With a concentration of ~400,000 ppm (Zumholz, Hansteen, et al. 2007; Han et al. 2022), calcium is the main component in cephalopod statoliths (Ikeda et al. 1998; Liu et al. 2013). Therefore, concentrations of key trace elements in statoliths are commonly expressed as a ratio in relation to calcium, including elemental ratios correlated with temperature, such as Barium/Calcium, Iodine/Calcium, Strontium/Calcium, Uranium/Calcium or salinity, such as Iodine/Calcium, Magnesium/Calcium, of surrounding water (Ikeda et al. 1998; Zumholz, Hansteen, et al. 2007; Liu et al. 2011). These ratios can be used as indicators of population migration and habitat (Han et al. 2022). Considering the complex relationship between statolith elemental composition and element availability in the environment, between elements and squid physiology, and the fact that no microchemical statolith studies of *I. coindetii* and *L. forbesii* have been conducted in Europe, as many of the relevant elements as possible should be examined.

Our objective was to determine if different stocks of *I. coindetii* and *L. forbesii* occur in the North East Atlantic Ocean and Mediterranean Sea, based on the elemental composition of statoliths. We also sought to determine which elements contributed most to stock differentiation. Two different spots on each statolith, the nucleus and the edge, were chemically analysed to provide complementary insights into stock structure: spawning origin (nucleus) and environmental history close to the capture date (edge). Age was also estimated to ascertain hatching periods and detect temporal overlap amongst stocks with respect to cohorts in the study area. We also determined if similar elemental ratios were present at different times (yearly quarters). Our findings provide a potential basis for developing sustainable fisheries management plans and actions for squids in European waters of the North East Atlantic Ocean and Mediterranean Sea.

2 | Material and Methods

Squid were collected using established protocols as part of ICES (International Council for the Exploration of the Sea) coordinated International Bottom Trawl Surveys (IBTS) and Mediterranean International Bottom Trawl Surveys (MEDITS) (ICES 2017, 2012). Additional squid were collected using standardised protocols as part of the Irish Anglerfish and Megrim Survey (IAMS) (Reid et al. 2007) and Scottish West Coast Groundfish Survey (SCOWCGFS) (ICES 2020). Squid were collected from the North East Atlantic Ocean in the North Sea in Q1 and Q3, 2021, Sea West of Scotland in Q4, 2021 and Celtic Sea in Q1, 2022. Squid were collected from the Mediterranean Sea in the Balearic Sea, Sea East of Sardinia, Sea West of Sardinia, South Adriatic Sea and Western Ionian Sea in Q3 of 2021 (Figure 1 and Table 1).

Dorsal mantle length (DML, mm) and total weight (W, 0.01 g) were measured, sex and maturity stage (ICES 2022) of *I.*

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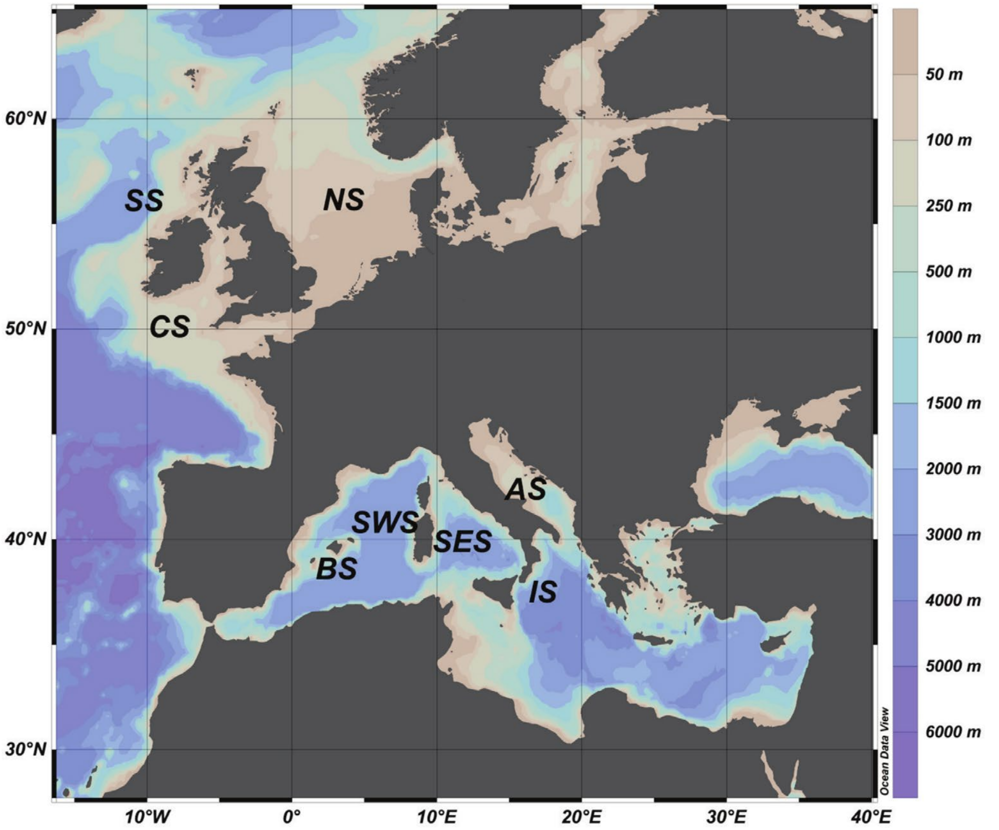

FIGURE 1 | Sampling areas for *Illex coindetii* and *Loligo forbesii* in the North Sea (NS), Sea West of Scotland (SS), Celtic Sea (CS), Balearic Sea (BS), Sea West of Sardinia (SWS), Sea East of Sardinia (SES), Western Ionian Sea (IS), South Adriatic Sea (AS) in the North East Atlantic Ocean and Mediterranean Sea during 2021–2022.

coindetii and *L. forbesii* were classified, and statoliths were extracted from the statocyst. Statoliths previously used for shape analysis (Bobowski et al. 2024) were cleaned with distilled water, affixed to a microscopic glass slide using a thermoplastic adhesive (Crystalbond), polished to the core with micro-mesh polishing paper (6000, 8000 and 12,000 grid) and rinsed with distilled water.

For age estimation, polished statoliths were photographed under transmitted light with an Axiocam 105 colour camera attached to an Olympus BX60 microscope and microscopy software Zen 2 blue edition (ver.2.0.0.0 by Carl Zeiss Microscopy GmbH, 2011). To minimise distortion and blurring caused by diffraction of the statolith that would cause miscounting of increments, a series of depth-focussed images was captured from the nucleus to the edge of the statolith. Increments were counted from the nucleus to the edge (dorsal dome) for *I. coindetii* and from the natal ring to the edge (dorsal dome) for *L. forbesii*. To estimate the precision of age estimates, increments on each statolith were counted twice by the same trained person. Only those age estimates with a standard deviation of less than 10 increments (days) were used for age estimation ($n=181$ *I. coindetii*; and $n=245$ *L. forbesii*). Based on the interpretation of statolith growth increments, we assumed that material at the nucleus corresponds to early life stages and material at the edge represents environmental conditions during the final weeks before capture.

Elemental composition of 453 polished statolith nuclei and edges (Figure 2) was quantified by laser ablation-inductively coupled plasma-mass spectrometry (LA-ICP-MS), using a New Wave Research UP213–LA paired with a Thermo Fisher Scientific ELEMENT2 ICP-MS. To ensure that measuring points were positioned as correctly as possible, microscopy images of polished statoliths taken by the same person were used as reference material. Statolith regions were ablated with a 40 μm spot size at 70% power, a pulse repetition rate of 10 Hz and ~14 J cm^{-2} energy density over ~40 s. Values were recorded every 0.836 s. A blank value was calculated from the first 16 measurements, and the average value for each corresponding measurement point was computed from the remaining 31 measurements. Reference materials for calibration included a synthetic silicate glass NIST612 (National Institute of Standards and Technology) and a calcium carbonate pressed powder pellet MACS-3 (United States Geological Survey) (Jochum et al. 2011). Both reference materials were measured in triplicate at the beginning and end of each laser session, with up to 14 samples between, and a dwell duration of 24 s.

Raw data were expressed as ratios to calcium (^{43}Ca). Raw concentration (ppm) was first corrected using relative sensitivity factors (RSFs) based on reference materials and then divided by calcium concentration in statoliths to express element-to-calcium ratios. Values below detection limits were excluded. Elements included sodium (^{23}Na), magnesium (^{25}Mg), manganese (^{55}Mn), iron (^{57}Fe), cobalt (^{59}Co), copper (^{65}Cu), zinc (^{66}Zn), strontium (^{88}Sr), barium (^{137}Ba), lead (^{208}Pb) and uranium (^{238}U). Crystalbond adhesive was also measured to ensure elements in the adhesive did not interfere with sample measurements.

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TABLE 1 | Dorsal mantle length (DML), weight, age and sex distribution (male = M, female = F, juvenile = J), capture period and hatch period of *Illex coindetii* and *Loligo forbesii* (n) sampled in the Balearic Sea, Celtic Sea, North Sea, Sea East of Sardinia, Sea West of Sardinia, Sea West of Scotland, South Adriatic Sea and Western Ionian Sea in the North East Atlantic and Mediterranean Sea during 2021–2022 (Q1 = January–March, Q2 = April–June, Q3 = July–September, Q4 = October–December; AuWiSS = Autumn–Winter spawning stock, SpSS = Spring spawning stock, SpSuSS = Spring–Summer spawning stock, SuSS = Summer spawning stock, WiSS = Winter spawning stock, WiSpSS: Winter–Spring spawning stock).

			DML (mm)		Weight (g)			Age (days)				
Species	**Spawning stock**	**Sex**	**Min-Max**	**Mean ± SD**	**Min-Max**	**Mean ± SD**	$n_{\text{DML+weight}}$	**Min-Max**	**Mean ± SD**	n_{age}	**Capture**	**Hatch**
Illex coindetii	Balearic WiSS	M	106–143	130 ± 14.36	58–104	86 ± 18.55	5	177–203	191 ± 12.38	4	Q3 2021	Q1 2021
		F	141–190	170 ± 16.61	106–184	135 ± 26.06	8	159–194	176 ± 14.02	8		
	Celtic SpSuSS	M	108–185	165 ± 16.19	28–200	125 ± 40.81	24	190–241	216 ± 13.86	20	Q1 2022	Q2/Q3 2021
		F	160–285	206 ± 27.57	73–549	191 ± 103.95	20	185–262	225 ± 26.39	17		
	North Sea SuSS Q1	M	79–157	114 ± 24.88	13–88	40 ± 25.66	19	128–167	148 ± 12.19	19	Q1 2021	Q3 2020
		F	90–158	116 ± 22.65	15–92	37 ± 23.55	18	116–165	147 ± 10.95	17		
	North Sea SuSS Q3	M	120–197	158 ± 21.74	92–232	143 ± 46.11	13	229–319	271 ± 28.26	11	Q3 2021	Q3 2020
		F	108–224	167 ± 40.39	33–331	143 ± 91.03	10	216–317	256 ± 36.81	10		
	Eastern Sardinian WiSS	M	142–152	147 ± 4.16	115–129	120 ± 6.29	4	195–195	195 ± 0	2	Q3 2021	Q1 2021
		F	140–209	176 ± 17.45	77–186	139 ± 31.69	12	182–213	192 ± 9.41	8		
	Western Sardinian WiSS	M	124–154	140 ± 8.13	67–158	114 ± 29.2	16	179–216	194 ± 13.67	12	Q3 2021	Q1 2021
		F	124–208	179 ± 24.78	49–222	139 ± 51.3	13	182–205	190 ± 7.77	10		
	South Adriatic WiSpSS	M	95–145	127 ± 13.87	26–123	86 ± 27.61	12	137–186	168 ± 16.52	9	Q3 2021	Q1/Q2 2021
		F	115–185	152 ± 16.85	43–186	107 ± 36.47	19	131–196	168 ± 18.23	15		
	Western Ionian WiSS	M	100–125	113 ± 7.99	44–81	61 ± 14.95	8	181–196	188 ± 7.51	3	Q3 2021	Q1 2021
		F	105–190	147 ± 17.5	31–193	106 ± 33.79	21	164–201	185 ± 10.39	16		
Loligo forbesii	Balearic WiSS	M	87–485	178 ± 131.57	32–1820	309 ± 519.38	14	166–218	184 ± 15.02	14	Q3 2021	Q1 2021
		F	74–365	181 ± 98.08	20–1057	264 ± 299.22	14	161–207	184 ± 11.67	14		
		J	78–225	152 ± 79.04	24–320	164 ± 152.32	4	174–193	183 ± 7.78	4		
	Celtic SuSS	M	72–250	150 ± 38.02	16–338	104 ± 67.98	19	157–204	180 ± 13.71	18	Q1 2022	Q3 2021
		F	82–182	142 ± 32.63	23–167	98 ± 50.03	7	145–190	171 ± 16	6		

(Continues)

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TABLE 1 | (Continued)

Species	Spawning stock	Sex	DML (mm) Min-Max	DML (mm) Mean ± SD	Weight (g) Min-Max	Weight (g) Mean ± SD	$n_{DML+weight}$	Age (days) Min-Max	Age (days) Mean ± SD	n_{age}	Capture	Hatch
	North Sea SpSuSS Q1	M	116–356	233 ± 83.63	61–704	291 ± 202.48	31	162–246	198 ± 23.03	31	Q1 2021	Q2/Q3 2020
		F	107–272	193 ± 40.01	44–525	227 ± 106.36	27	162–311	193 ± 31.81	26		
	North Sea AuWiSS Q3	M	87–298	173 ± 56.0	25–595	189 ± 150.06	45	148–244	180 ± 22.56	44	Q3 2021	Q4 2020/ Q1 2021
		F	95–199	148 ± 29.02	38–206	114 ± 49.52	23	151–230	174 ± 18.44	23		
	Western Scotland SpSS	M	144–424	231 ± 93.73	99–1533	418 ± 503.15	17	160–222	180 ± 18.57	16	Q4 2021	Q2 2021
		F	126–323	203 ± 56.23	79–885	277 ± 209.91	33	156–202	179 ± 12.08	30		
	South Adriatic AuWiSS	M	175–405	274 ± 92.49	185–1170	575 ± 411.51	6	233–268	247 ± 13.62	6	Q3 2021	Q4 2020/ Q1 2021
		F	180–215	201 ± 11.34	196–329	278 ± 41.06	13	204–284	234 ± 25.22	13		

A principal component analysis (PCA) was performed in R.4.2.2 (R Core Team 2022) using the prcomp() function from the base stats package. Missing values were imputed using the mice package (v3.14.0; van Buuren and Groothuis-Oudshoorn 2011). The first two principal components (PC1 and PC2) were used to describe spatial patterns of elemental ratios. Scatterplots of PC2 against PC1, with 95% confidence ellipses for grouped PCA scores, were plotted using the ggplot2 package (v3.3.6; Wickham 2016). Group means and standard errors were plotted as error bars to visualise central tendency and variation across sampling areas. Due to inhomogeneity of multivariate spatial variances, partitioning of variation amongst groups based on principal components was assessed by analysis of similarity (ANOSIM) using the vegan package (v2.5–7; Oksanen et al. 2020). To reduce Type I error, a Bonferroni correction was applied to *p*-values of multiple comparisons. For the correlation between observed and predicted classes, PCAs were classified using caret (v6.0–86; Kuhn 2020) and e1071 packages (v1.7–9; Meyer et al. 2021). To test for significant differences in element ratios between nucleus and edge measurements in each area, t-tests for normally distributed data or Mann–Whitney U tests for non-normally distributed data were computed using SigmaPlot 13 (Systat Software Inc. 2014).

3 | Results

3.1 | Biological Data

Biological data were collected from 475 squid, including 222 *I. coindetii* and 253 *L. forbesii* (Table 1). Fewer squid were analysed for statolith microchemistry, including 206 *I. coindetii* and 247 *L. forbesii*, and even fewer were analysed for age estimation (181 *I. coindetii*, 245 *L. forbesii*; Table 1).

All Mediterranean *I. coindetii* captured in Q3 of 2021 hatched in winter 2021, and four individuals from the South Adriatic Sea hatched in spring 2021 (April) (Table 1). *L. forbesii* from the Mediterranean also hatched in winter 2021, with some South Adriatic individuals hatched in autumn 2020. *I. coindetii* from the North Sea captured in Q1 and Q3 of 2021 hatched in summer of 2020, whereas *L. forbesii* from the North Sea differed in hatching periods between those caught in Q1 and Q3 of 2021. *L. forbesii* from the Sea West of Scotland hatched in spring 2021 and overlapped with spring–summer spawners in the North Sea that hatched in Q2 and Q3 of 2020.

For both *I. coindetii* and *L. forbesii*, microchemistry of the statolith nucleus deposited near the time of hatching and statolith edge deposited near the time of capture were divided into distinct groups that reflected different spawning and mating groups. However, groups differed between measurements at the nucleus and edge. For nucleus and edge measurements of both species, Co and Fe compositions explained greater variance in PC1 and PC2 than other elements, except Na at the *I. coindetii* nucleus (Figures 3B,D and 4B,D), for which a small angle of difference amongst elements indicated high similarity.

For microchemistry of *I. coindetii* at the statolith nucleus, the first two principal components explained 41% (PC1 = 26%; PC2 = 15%) of element variation, whereas at the statolith edge,

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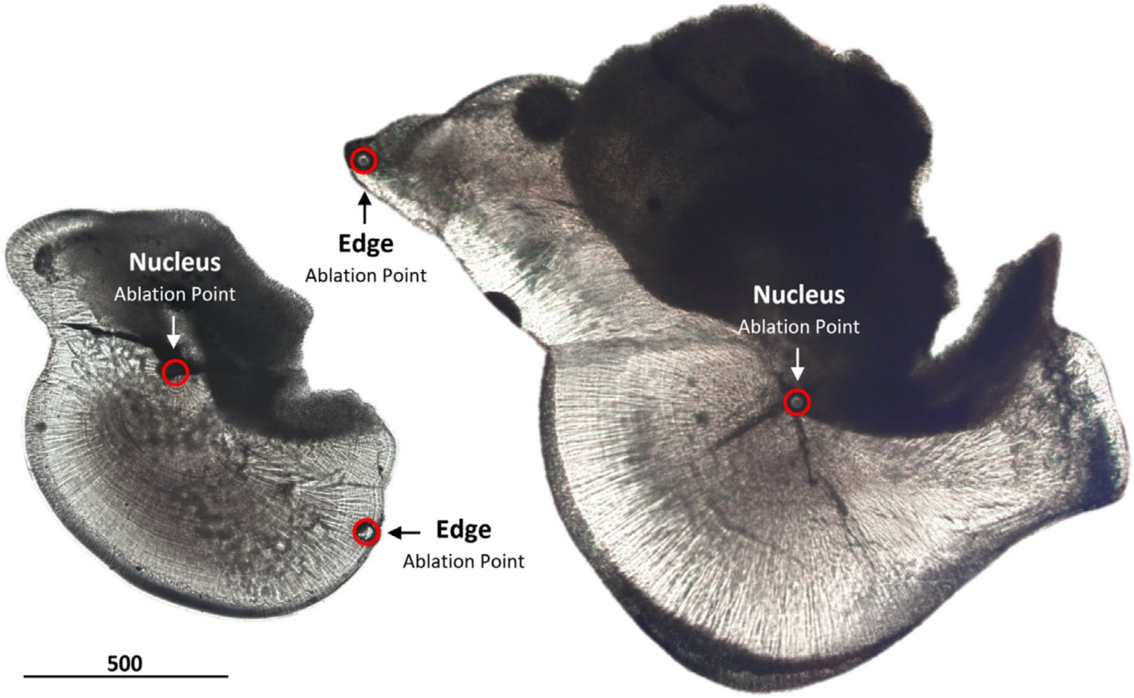

FIGURE 2 | Ablation point locations on a polished right-sided *Illex coindetii* (left) and *Loligo forbesii* (right) statolith from the North Sea. The nucleus represents the early life stage, and the edge represents the period of capture in developing, maturing or matured squid.

the first two principal components explained 45% (PC1 = 26%; PC2 = 19%) of element variation (Figure 3). For the Western Ionian winter spawning stock, element variation was highest at the statolith nucleus and highly influenced by Cu, Pb and Zn (Figure 3A,B). For Eastern Sardinian and Western Sardinian winter spawning stocks, element variation was highest at the statolith edge (Figure 3C,D). Element concentrations did not differ significantly between Balearic and each of the Eastern Sardinian winter spawning, South Adriatic winter–spring spawning, Ionian winter spawning and Celtic spring–summer spawning stocks, either at the nucleus or the edge (Table 2). Nucleus element concentrations did not differ significantly: (i) amongst Balearic winter spawning and Western Sardinian winter spawning stocks, (ii) between North Sea summer spawning groups (captured in Q1 and Q3) and (iii) between Eastern and each of Western Sardinian winter spawning, Adriatic winter spawning and Ionian winter spawning stocks. Element concentrations at the statolith edge did not differ significantly between Eastern and Western Sardinian winter spawning stocks.

For microchemistry of *L. forbesii* at the nucleus, the first two principal components explained 45% of element variation (PC1 = 24%; PC2 = 21%), with North Sea spring–summer, autumn–winter and Western Scotland spring spawning stocks strongly overlapping (Figure 4). Element concentrations overlapped for Celtic Sea summer spawning, Adriatic autumn–winter spawning and Balearic winter spawning stocks, which were more strongly influenced by Co and Fe than those of the North Sea and Scottish Sea stocks (Figure 4A,B). For element concentrations at the statolith edge, the first two principal components explained 54% of element variation (PC1 = 35%, PC2 = 19%). At the statolith edge, element profiles were strongly influenced by Co and Fe for Balearic winter spawning, Celtic summer spawning and South Adriatic autumn–winter spawning stocks and by Cu, Pb, Zn and Ba for the Western Scotland spawning stock (Figure 4C,D). Elemental composition at the statolith edge differed amongst sampled areas. In contrast, element concentrations at the statolith nucleus did not differ significantly: (i) amongst Balearic winter spawning and each of Celtic summer spawning and Adriatic autumn spawning stocks and (ii) between North Sea spring–summer spawning and North Sea autumn–winter spawning stocks (Table 2).

For *I. coindetii*, classification accuracy based on element ratios at the statolith nucleus was highest for the North Sea stock sampled in Q1 (100%), followed by the Celtic Sea stock (72%; Table 3). For Mediterranean Sea stocks, classification accuracy was less successful for Western Sardinian winter spawning, South Adriatic winter–spring and Western Ionian winter spawning (40%–69%), and stocks were completely misclassified for Balearic and Eastern Sardinian winter spawning stocks (0%). North Sea summer spawning squid captured in Q3 were completely misclassified based on element ratios at the statolith nucleus, but were assigned to the correct stock, albeit in a different quarter (NS Q1). Based on element composition at the statolith edge, classification was successful for squid from the North East Atlantic and Western Sardinian winter spawning stocks (80%–100%). Squid from other spawning stocks in the Mediterranean Sea were less correctly classified (33%–61%) or were completely misclassified to the Balearic winter spawning stock. Based on element ratios at the statolith nucleus and edge, Mediterranean Sea squid were mostly misclassified, with some misclassified to the Celtic Sea.

For *L. forbesii*, spawning stock classification for stocks in the North East Atlantic Ocean was higher based on element composition at the statolith edge, whereas those from the Mediterranean Sea were more correctly classified based on element composition

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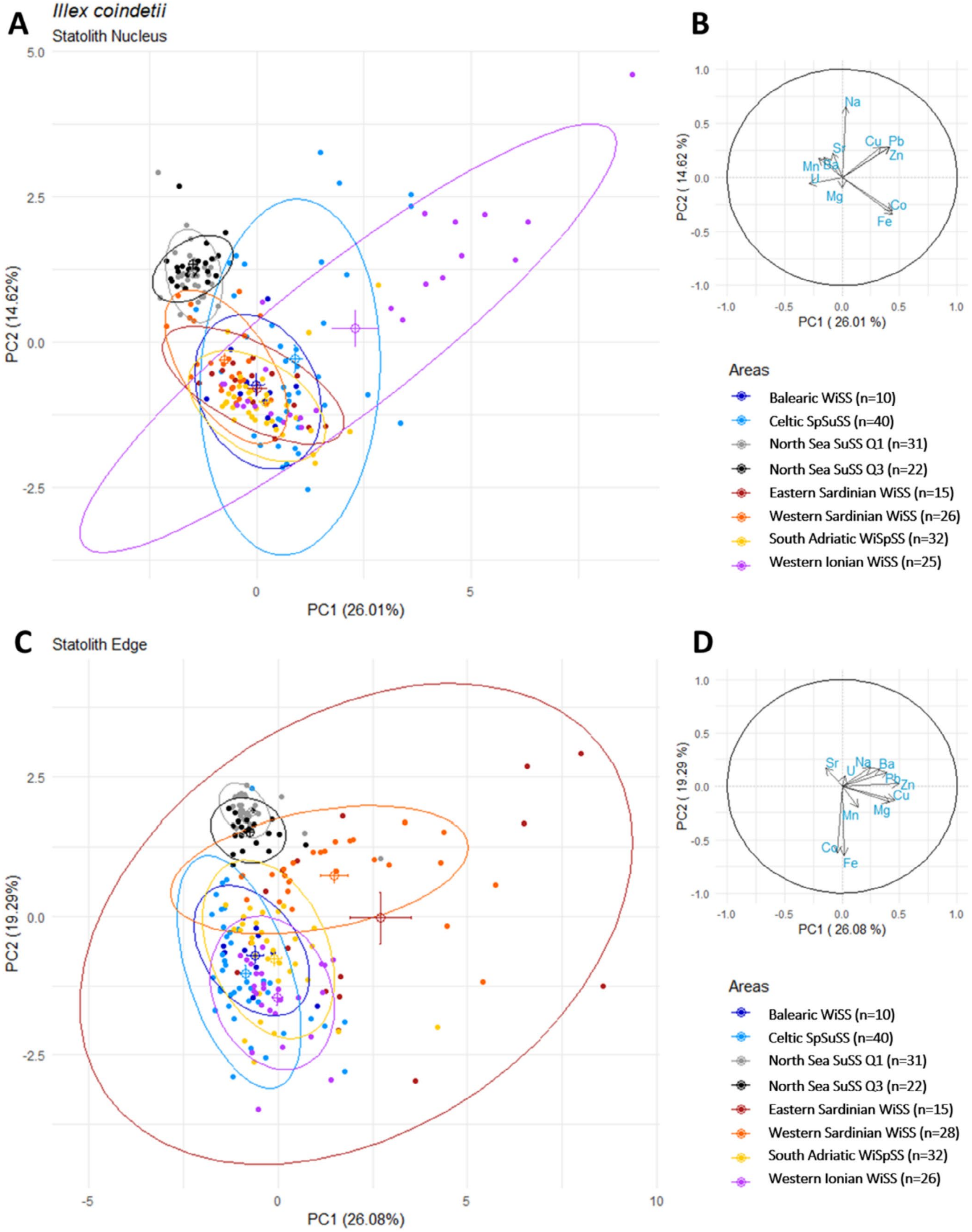

FIGURE 3 | Legend on next page.

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FIGURE 3 | Sample (A, C) and variable (B, D) biplots of the first two principal components (PC1, PC2) for statolith microchemistry of *Illex coindetii* spawning stocks sampled in the Balearic Sea (WiSS = dark blue), Celtic Sea (SpSuSS = light blue), North Sea (SuSS Q1 = grey, SuSS Q3 = black), Eastern Sardinian Sea (WiSS = red), Western Sardinian Sea (WiSS = orange), South Adriatic Sea (WiSpSS = yellow) and Western Ionian Sea (WiSS = purple) in the North East Atlantic Ocean and Mediterranean Sea during 2021–2022 (A, B = statolith nucleus, C, D = statolith edge; colours in A and C correspond to different spawning stocks: SuSS = Summer spawning stock, WiSS = Winter spawning stock, SpSuSS = Spring–Summer spawning stock, WiSpSS = Winter–Spring spawning stock). Open circles depict the mean (± standard error) and ellipses depict 95% of samples from each area.

at the nucleus (Table 3). Classification accuracy based on element concentrations at the statolith nucleus was higher for the North Sea autumn-winter spawning stock (> 90%) than for Balearic winter spawning, Celtic summer spawning, North Sea spring–summer spawning and South Adriatic autumn-winter spawning stock (50%–65%). Classification accuracy was lowest for the Western Scotland spring spawning stock (28%), with misclassified squid all classified to the North Sea. Based on element classification at the statolith edge, classification accuracy was higher for North Sea and Sea West of Scotland spawning stock (80%–96%) than for the Celtic summer spawning stock (67%) that were often classified to the North Sea autumn-winter spawning stock. Classification accuracy was low for Balearic winter spawning and South Adriatic autumn-winter spawning stocks (20%–48%).

Except for a few locations, element ratios of Sr, U and Zn differed between statolith nucleus and edge for both *I. coindetii* and *L. forbesii* (Table 4). For most sampling areas, Ba and Cu element ratios differed between statolith nucleus and edge for *I. coindetii*, whereas Na, Mg and Pb differed for *L. forbesii*. In contrast, whilst element ratios of Co and Fe discriminate sampling locations in the PCA, they did not differ much between the nucleus and edge of statoliths for both species, except *L. forbesii* from the Western Scotland spring spawning stock. For *I. coindetii* from the Western Ionian winter spawning stock, no element ratios differed significantly between statolith nucleus and edge.

4 | Discussion

Microchemical differences in statolith element ratios we observed have been previously linked to environmental factors, such as temperature, salinity or habitat use (Zumholz, Klügel, et al. 2007; Liu et al. 2016). For example, in combination with sea surface temperature, fluctuations in U/Ca ratios can indicate ontogenetic migration routes (Zumholz, Klügel, et al. 2007). Sr/Ca and Ba/Ca ratios can provide additional insights (Liu et al. 2016), with Ba/Ca correlated with water depth (Arkhipkin et al. 2004; Jones et al. 2018). Moreover, the Sr/Ca ratio as a temperature indicator seems more suitable to identify horizontal migration patterns (e.g., onshore-offshore) in loliginid species like *L. forbesii* than in oceanic ommastrephids like *I. coindetii*, whose horizontal movement is possibly masked by extensive diel-vertical migrations (Arkhipkin et al. 2004). However, elements like Fe and Zn, along with Sr, are related to temperature in the ommastrephid squid *Todarodes pacificus* (Ikeda et al. 1996). Whilst Mg/Ca is often used to indicate salinity variations due to its positive correlation with salinity in coral skeletons (Mitsuguchi et al. 1996), this correlation is not evident in cephalopods. Instead, Mg concentrations in cephalopod statoliths are linked to the deposition of organic matter and progressively decrease from the statolith nucleus to the edge as squid grow (Arkhipkin et al. 2004; Zumholz, Klügel, et al. 2007; Fan et al. 2023). Furthermore, I/Ca is positively correlated with temperature and negatively correlated with salinity in the common cuttlefish *Sepia officinalis* (Zumholz, Hansteen, et al. 2007). Non-biodegradable accumulating trace metals in statoliths, such as, Cd, Cr, Cu, Pb, Hg and Zn (Sharifuzzaman et al. 2016), can provide insight into residence at specific locations during ontogeny.

The ablation spot (40 μm) in our study corresponded to 25–30 daily increments in *I. coindetii* statoliths and 10–15 daily increments in *L. forbesii* statoliths, so elemental composition at the statolith nucleus represented early life stages, and the edge represented a few weeks before capture. Based on differences in element ratios at the nucleus and edge of statoliths, *I. coindetii* and *L. forbesii* were separated into seasonally and geographically distinct groups within the areas of the North East Atlantic Ocean and Mediterranean Sea that we interpret as stocks. Similar approaches using statolith element ratios have been successfully applied to discriminate squid stocks in other species (Fang et al. 2014; Green et al. 2015; Avigliano et al. 2020). Consistent with previous findings that statolith microchemistry reflects natal origin (Warner et al. 2009; Liu et al. 2015) differences in nucleus profiles here likely indicate hatching in different regions, whereas similar profiles suggest a shared origin. Differences in both nucleus and edge microchemistry, by contrast, suggest the presence of different stocks, consistent with previous studies demonstrating that variation in statolith element composition can delineate stock structure in squid (Fang et al. 2014; Avigliano et al. 2020). Alternatively, deposition of elements is influenced by abiotic factors and diet (Zumholz 2005), so squid from different areas that were temporally and spatially separated, but experienced similar abiotic conditions, could also have similar elemental ratios in their statoliths, thereby making their classification into distinct groups less accurate for some regions.

Combining our results with those from statolith shape analysis of the same individuals (Bobowski et al. 2024) allowed for the identification of potential cohorts of *I. coindetii* around southern Italy and possible common hatching or feeding grounds of both species that provided more detailed insight into European stock structures. For *I. coindetii*, microchemical analysis indicated that three distinct stocks and one mixed stock were found in Italian waters, thereby suggesting temporary ontogenetic separation, with overall connectivity, consistent with the 'middle course' situation proposed for the Mediterranean (Sánchez et al. 1998). This observation is consistent with the previously reported homogenous population structure (Martínez et al. 2005), highlighting that ecological separation does not imply genetic differentiation. Our analysis of *L. forbesii* revealed five distinct

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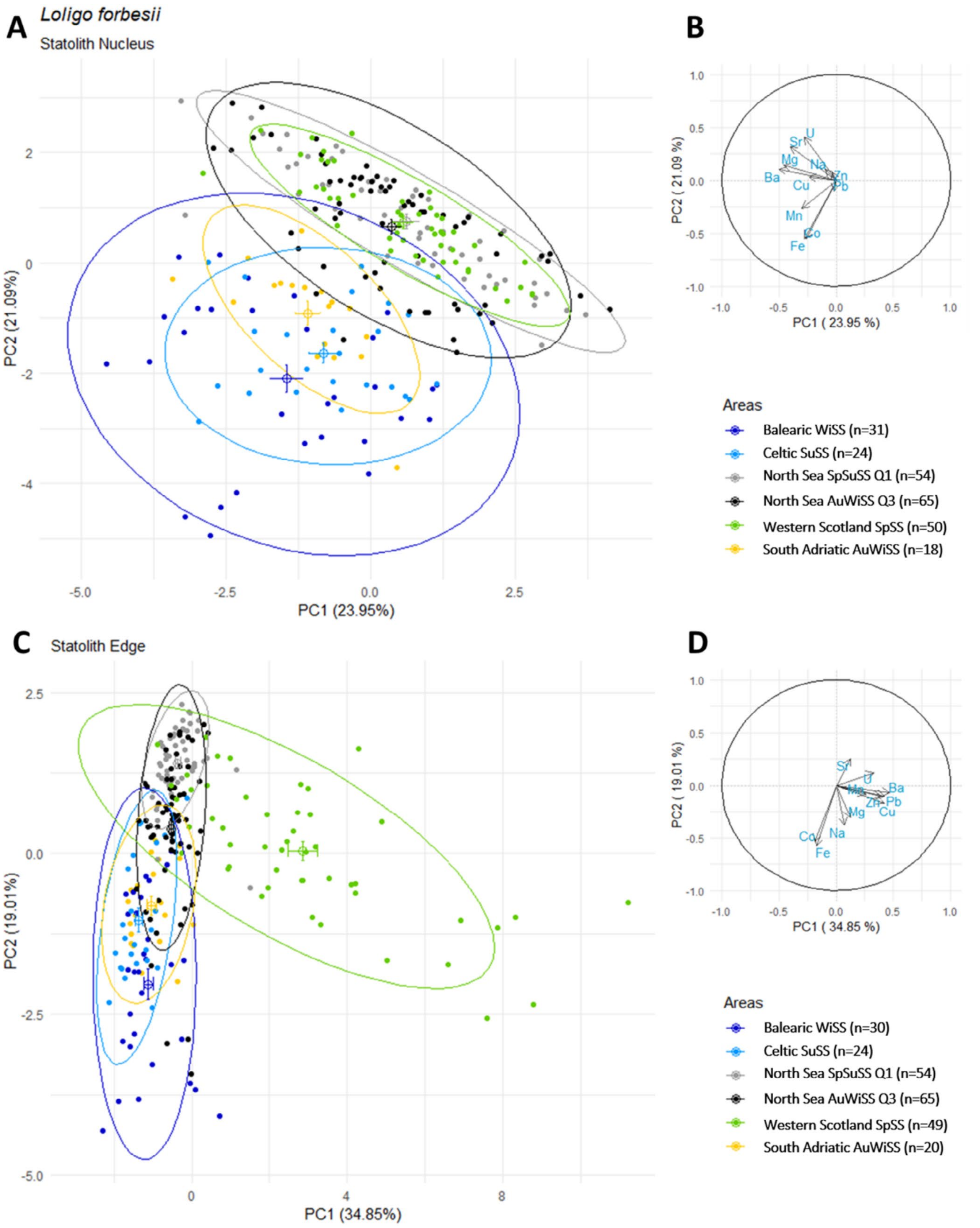

FIGURE 4 | Legend on next page.

stocks, with some connectivity amongst North East Atlantic stocks during different ontogenetic stages, contradicts a homogenous population structure inferred from genetic analysis (Göpel et al. 2022).

Our results are consistent with earlier studies that also found no evidence for temporally separated stocks of *I. coindetii* in the North Sea based on biological data (DML, maturity stage, hatching period) and statolith shape (Oesterwind et al. 2020;

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FIGURE 4 | Sample (A, C) and variable (B, D) biplots of the first two principal components (PC1, PC2) for statolith microchemistry of *Loligo forbesii* sampled in the Balearic Sea (WiSS = dark blue), Celtic Sea (SuSS = light blue), North Sea (SpSuSS Q1 = grey; AuWiSS Q3 = black), Western Scotland (SpSS = green) and South Adriatic Sea (AuWiSS = yellow) in the North East Atlantic Ocean and Mediterranean Sea during 2021–2022 (A, B = statolith nucleus, C, D = statolith edge; colours in A and C correspond to different spawning stocks: AuWiSS = Autumn–Winter spawning stock, SpSS = Spring spawning stock, SpSuSS = Spring–Summer spawning stock SuSS = Summer spawning stock, WiSS = Winter spawning stock). Open circles depict the mean (± standard error) and ellipses depict 95% of samples from each area.

Bobowski et al. 2024). Our findings, combined with observations of egg-spheres in the Norwegian Channel (Ringvold et al. 2021), support an assumption that *I. coindetii* in the North Sea complete their whole life cycle in the area as an independent North Sea stock (Oesterwind et al. 2010, 2015, 2020; Barrett et al. 2021). Based on element composition at the statolith nucleus and the edge, a proportion of the Celtic spring–summer spawning stock was assigned to the Mediterranean stock. Considering that water masses can have similar abiotic factors despite spatial and temporal separation, and the Celtic Sea and Mediterranean Sea areas around Italy are geographically distant areas, we assume that misclassified individuals inhabited environments with similar water conditions, which illustrates a limitation of our approach. Based on these considerations, and differences in statolith microchemistry (this study) and shape (Bobowski et al. 2024), we conclude that *I. coindetii* squid from the Celtic Sea belong to an Atlantic stock that originated from a different hatching area that was separated from stocks in the North Sea and Mediterranean Sea.

Stock identification by microchemistry analyses is more complex for *I. coindetii* in the Mediterranean Sea due to high misclassification and similarity amongst areas, similar to a statolith shape analysis (Bobowski et al. 2024). The Mediterranean *I. coindetii* population is complex, with multiple cohorts, micro-cohorts or heavily overlapping cohorts (Sánchez et al. 1998). *I. coindetii* does not attach its eggs to hard substrates, but lays floating gelatinous egg-spheres (Jereb and Roper 2010) that would facilitate exchange amongst areas. Because all squid we analysed were of similar age and part of the same spawning group, we conclude that squid from the Mediterranean Sea were exposed to *seasonally* similar water parameters during early life. Misclassified squid from the Mediterranean Sea were primarily classified for the Sea west of Sardinia and the south Adriatic Sea based on microelement composition of the statolith nucleus, whereas misclassification was lower based on statolith shape and squid did not differ amongst areas surrounding Italy (Bobowski et al. 2024). In contrast to microchemistry, statolith shape formation is a biologically regulated process that occurs over a longer period that involves proton and ion transporter control of endolymph composition and organic matrix and either promotes or inhibits crystal nucleation (Bettencourt and Guerra 2000). Consequently, shape analysis can indicate main areas of residence but provides no information about hatching areas or migration routes. Overall, our results indicated that squid around Italy might share a hatching region that splits into multiple cohorts thereafter, whilst also using similar feeding grounds.

Statoliths of *I. coindetii* from both Sardinian Sea areas were highest in concentrations of Cu, Pb and Zn at the edge, which suggests exposure to these trace metal elements near capture locations. The harbour at Cagliari (Sardinia, Italy) has an oil terminal with significant concentrations of trace metals in surface sediments throughout the area (Schintu et al. 2016). Additionally, soils and vegetation of the mining areas in southwest Sardinia have exceptionally high levels of Ca, Pb and Zn (Leita et al. 1989), which might enter surrounding seas through runoff that accumulates in statoliths of squid in this area. Accumulation might occur through direct deposition from water or through prey exposed to these metals. Early life stages of squid from the Western Ionian Sea had the highest value of Cu, Pb and Zn in their statoliths, so we assume that ommastrephid hatchlings incorporated such trace metals in their statoliths from surrounding water. These elements were not present or were lower in concentrations in early life stages of squid from East and West Sardinian Sea, so we infer that maturing and mature individuals from waters around Sardinia might have hatched outside the area and migrated into Sardinian Seas. Furthermore, all elements we measured did not differ between life stages of squid from the western Ionian Sea. Diets of *I. coindetii* change between early and late life stages (Sánchez et al. 1998; Schäfer et al. 2024), so we infer that both early and late life stages of these squid occupied the same area, or at least in regions with similar water parameters. However, some squid from the western Ionian Sea were misclassified to the Adriatic Sea in both life stages, which also supports an assumption that squid migrated amongst areas in southern Italy, similar to statolith shape analysis of the same samples of squid (Bobowski et al. 2024).

Mature female *L. forbesii* in the North East Atlantic are mainly found in the northern and central North Sea, northern and western Scotland and Ireland, and egg clusters attached to hard substrates have been found at coastal areas in northern Scotland and the Moray Firth (Laptikhovsky et al. 2022). A relatively high number of squid we sampled from the North Sea and the Western Scotland spring spawning stock were misclassified based on measurements at the statolith nucleus and edge, with higher misclassification of early life stages. High misclassification might indicate that paralarval stages were exposed to similar water conditions, perhaps due to a common spawning and hatching area. Whilst a potential migration was described from the West of Scotland into the North Sea (Waluda and Pierce 1998), routine migration was not evident between the two areas (Viana et al. 2009), so squid likely dispersed from a more northern region of Scotland. Nonetheless, these groups of squid likely have distinct feeding grounds because misclassification of individuals from the North Sea and Sea West of Scotland was lower based on element composition at the statolith edge as well as statolith shape comparisons (Bobowski et al. 2024). Moreover, early life stages did not differ significantly in statolith microchemistry between North Sea spring–summer and autumn–winter spawning stocks, which suggests that water conditions in areas inhabited by early life stages were relatively similar amongst different periods.

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TABLE 2 | Pairwise comparisons of statolith elemental composition of *Illex coindetii* and *Loligo forbesii* between spawning stocks in the Balearic Sea, Celtic Sea, North Sea, Sea East of Sardinia, Sea West of Sardinia, Sea West of Scotland, South Adriatic Sea and Western Ionian Sea in the North East Atlantic Ocean and Mediterranean Sea during2021 to 2022 (AuWiSS = Autumn–Winter spawning stock, SpSS = Spring spawning stock, SpSuSS = Spring–Summer spawning stock, SuSS = Summer spawning stock, WiSS = Winter spawning stock, WiSpSS: Winter–Spring spawning stock). Significant differences are in **bold** ($p < 0.05$, adjusted with Bonferroni method).

Illex coindetii		**Balearic WiSS**	**Celtic SpSuSS**	**North Sea SuSS Q1**	**North Sea SuSS Q3**	**Eastern Sardinian WiSS**	**Western Sardinian WiSS**	**South Adriatic WiSpSS**
Nucleus	Celtic SpSuSS	0.602	—	—	—	—	—	—
	North Sea SuSS Q1	**0.003**	**0.003**	—	—	—	—	—
	North Sea SuSS Q3	**0.003**	**0.003**	1.000	—	—	—	—
	Eastern Sardinian WiSS	1.000	**0.020**	**0.003**	**0.003**	—	—	—
	Western Sardinian WiSS	0.134	**0.003**	**0.003**	**0.003**	0.392	—	—
	South Adriatic WiSpSS	1.000	**0.003**	**0.003**	**0.003**	1.000	**0.003**	—
	Western. Ionian WiSS	1.000	**0.003**	**0.003**	**0.003**	0.224	**0.003**	**0.008**
Edge	Celtic Sea SpSuSS	0.666	—	—	—	—	—	—
	North Sea SuSS Q1	**0.003**	**0.003**	—	—	—	—	—
	North Sea SuSS Q3	**0.003**	**0.003**	**0.003**	—	—	—	—
	Eastern. Sardinian WiSS	0.210	**0.003**	**0.003**	**0.003**	—	—	—
	Western Sardinian WiSS	**0.011**	**0.003**	**0.003**	**0.003**	1.000	—	—
	South Adriatic WiSpSS	1.000	**0.003**	**0.003**	**0.003**	**0.007**	**0.003**	—
	Western Ionian WiSS	0.258	**0.003**	**0.003**	**0.003**	**0.003**	**0.003**	**0.003**

Loligo forbesii		**Balearic WiSS**	**Celtic SuSS**	**North Sea SpSuSS Q1**	**North Sea AuWiSS Q3**	**Western Scotland SpSS**
Nucleus	Celtic SuSS	0.065	—	—	—	—
	North Sea SpSuSS Q1	**0.002**	**0.002**	—	—	—
	North Sea AuWiSS Q3	**0.002**	**0.002**	0.558	—	—
	Western Scotland SpSS	**0.002**	**0.002**	**0.002**	**0.002**	—
	South Adriatic AuWiSS	0.372	**0.002**	**0.002**	**0.002**	**0.002**
Edge	Celtic Sea SuSS	**0.002**	—	—	—	—
	North Sea SpSuSS Q1	**0.002**	**0.002**	—	—	—
	North Sea AuWiSS Q3	**0.002**	**0.002**	**0.002**	—	—
	Western Scotland SpSS	**0.002**	**0.002**	**0.002**	**0.002**	—
	South Adriatic AuWiSS	**0.006**	**0.002**	**0.002**	**0.002**	**0.002**

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TABLE 3 | Classification matrix for *Illex coindetii* and *Loligo forbesii* microchemistry from the Balearic Sea, Celtic Sea, North Sea, Sea East of Sardinia, Sea West of Sardinia, Sea West of Scotland, South Adriatic Sea and Western Ionian Sea in the North East Atlantic Ocean and Mediterranean Sea during 2021–2022 (AuWiSS = Autumn–Winter spawning stock, SpSS = Spring spawning stock, SpSuSS = Spring–Summer spawning stock, SuSS = Summer spawning stock, WiSS = Winter spawning stock, WiSpSS: Winter–Spring spawning stock). Predicted versus observed spawning stocks with correctly assigned individual numbers are shown in **bold**. Correct classification is shown as classification success rate in percentage, with a second value in parenthesis for North Sea (captured in Q1 and Q3) combined.

		Predicted area								
***Illex coindetii* NUCLEUS**		**Balearic WiSS**	**Celtic SpSuSS**	**North Sea SuSS Q1**	**North Sea SuSS Q3**	**Eastern Sardinian WiSS**	**Western Sardinian WiSS**	**South Adriatic WiSpSS**	**Western Ionian WiSS**	**Classification success rate (%)**
Observed area	Balearic WiSS	**0**	4	0	0	0	2	4	0	0.00
	Celtic SpSuSS	0	**29**	3	0	0	3	3	2	72.50
	North Sea SuSS Q1	0	0	**31**	0	0	0	0	0	100.00 (100.00)
	North Sea SuSS Q3	0	0	22	**0**	0	0	0	0	0.00 (100.00)
	E. Sardinian WiSS	0	5	0	0	**0**	8	2	0	0.00
	W. Sardinian WiSS	0	1	3	0	0	**18**	4	0	69.23
	S. Adriatic WiSpSS	0	9	0	0	0	3	**19**	1	59.38
	W. Ionian WiSS	0	6	0	0	0	1	8	**10**	40.00

		Predicted area								
***Illex coindetii* EDGE**		**Balearic WiSS**	**Celtic SpSuSS**	**North Sea SuSS Q1**	**North Sea SuSS Q3**	**Eastern Sardinian WiSS**	**Western Sardinian WiSS**	**South Adriatic WiSpSS**	**Western Ionian WiSS**	**Classification success rate (%)**
Observed area	Balearic WiSS	**0**	3	0	0	0	0	4	3	0.00
	Celtic SpSuSS	0	**32**	1	0	0	0	1	6	80.00
	North Sea SuSS Q1	0	0	**28**	1	0	2	0	0	90.32 (93.55)
	North Sea SuSS Q3	0	0	15	**7**	0	0	0	0	31.82 (100.00)
	E. Sardinian WiSS	0	2	0	0	**5**	3	1	4	33.33
	W. Sardinian WiSS	0	3	0	0	0	**23**	2	0	85.14
	S. Adriatic WiSpSS	0	11	0	0	1	0	**14**	6	43.75
	W. Ionian WiSS	0	7	0	0	0	0	3	**16**	61.54

(Continues)

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TABLE 3 | (Continued)

Loligo forbesii NUCLEUS		Predicted area						
		Balearic WiSS	**Celtic SuSS**	**North Sea SpSuSS**	**North Sea AuWiSS**	**Western Scotland SpSS**	**South Adriatic AuWiSS**	**Classification success rate (%)**
Observed area	Balearic WiSS	**20**	5	0	2	0	4	64.52
	Celtic SuSS	5	**15**	0	3	0	1	62.50
	North Sea SpSuSS	0	0	**19**	25	10	0	35.19 (62.96)
	North Sea AuWiSS	0	1	18	**41**	3	2	63.08 (90.77)
	W. Scotland SpSS	0	0	12	24	**14**	0	28.00
	S. Adriatic AuWiSS	3	5	0	1	0	**9**	50.00

Loligo forbesii EDGE		Predicted area						
		Balearic WiSS	**Celtic SuSS**	**North Sea SpSuSS**	**North Sea AuWiSS**	**Western Scotland SpSS**	**South Adriatic AuWiSS**	**Classification success rate (%)**
Observed area	Balearic WiSS	**15**	9	0	2	0	4	48.39
	Celtic SuSS	1	**16**	0	6	0	1	66.67
	North Sea SpSuSS	0	0	**45**	7	2	0	83.33 (96.30)
	North Sea AuWiSS	4	0	16	**41**	0	4	63.08 (87.69)
	W. Scotland SpSS	0	0	5	5	**39**	0	79.59
	S. Adriatic AuWiSS	1	8	0	7	0	**4**	20.00

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TABLE 4 | Differences in element concentration between statolith nucleus and edge (*t*-test or Mann–Whitney *U*-test) of *Illex coindetii* and *Loligo forbesii* from Balearic Sea, Celtic Sea, North Sea, Sea East of Sardinia, Sea West of Sardinia, Sea West of Scotland, South Adriatic Sea and Western Ionian Sea in the North East Atlantic Ocean and Mediterranean Sea during2021 to 2022 (SpSS = Spring spawning stock, SuSS = Summer spawning stock, WiSS = Winter spawning stock, AuWiSS = Autumn–Winter spawning stock, SpSuSS = Spring–Summer spawning stock, WiSpSS = Winter–Spring spawning stock). Significant differences ($p < 0.05$) are in **bold**.

		Balearic WiSS	Celtic SpSuSS	North Sea SuSS Q1	North Sea SuSS Q3	Eastern Sardinian WiSS	Western Sardinian WiSS	South Adriatic WiSpSS	Western Ionian WiSS
Illex coindetii	Na	0.116	0.292	**0.047**	**0.005**	**<0.001**	**<0.001**	**<0.001**	0.223
	Mg	**0.009**	**<0.001**	**<0.001**	**<0.001**	0.648	0.061	**<0.001**	0.224
	Mn	0.216	0.307	**<0.001**	0.054	0.973	0.448	**0.039**	0.110
	Fe	0.648	0.851	0.601	0.846	0.818	0.568	0.587	0.992
	Co	0.515	0.864	0.530	0.231	0.320	0.815	0.712	0.604
	Cu	**0.013**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.618
	Zn	**0.006**	**0.006**	**0.022**	**0.021**	**<0.001**	**<0.001**	**<0.001**	0.807
	Sr	**<0.001**	**<0.001**	0.139	**<0.001**	**0.007**	**<0.001**	**<0.001**	0.658
	Ba	**0.046**	**<0.001**	**0.001**	**<0.001**	**0.002**	**0.001**	**0.033**	0.164
	Pb	**0.010**	**<0.001**	0.265	0.245	**<0.001**	**<0.001**	**<0.001**	0.957
	U	**<0.001**	**<0.001**	**<0.001**	**0.001**	0.073	**<0.001**	**<0.001**	0.456

		Balearic WiSS	Celtic SuSS	North Sea SpSuSS Q1	North Sea AuWiSS Q3	Western Scotland SpSS	South Adriatic WiSS
Loligo forbesii	Na	**0.003**	**0.014**	**0.004**	**0.011**	**<0.001**	**0.406**
	Mg	**<0.001**	**0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**
	Mn	**<0.001**	**0.012**	**<0.001**	**<0.001**	0.718	0.391
	Fe	0.960	0.714	0.647	0.989	**<0.001**	0.808
	Co	0.805	0.342	0.953	0.964	0.909	0.547
	Cu	**<0.001**	**0.011**	0.152	0.574	**<0.001**	**0.011**
	Zn	**0.001**	**<0.001**	**0.017**	0.236	**<0.001**	**0.005**
	Sr	**0.005**	**<0.001**	**<0.001**	0.412	**<0.001**	**0.013**
	Ba	**<0.001**	0.671	**<0.001**	**<0.001**	**<0.001**	0.179
	Pb	**0.004**	**<0.001**	**0.002**	**0.006**	**<0.001**	**0.035**
	U	**0.011**	**<0.001**	**<0.001**	**<0.001**	**0.027**	0.221

L. forbesii from the Sea West of Scotland had the highest concentrations of Cu, Pb and Zn at the edge of the statolith, although the source of these elements was not clear, which suggests the use of feeding grounds separated from the hatching area that potentially included prey that had already accumulated these metals in tissues. *L. forbesii* hatches in the western English Channel and Celtic Sea (Laptikhovsky et al. 2022), before migrating through the English Channel into the southern North Sea and returning to the Celtic Sea to spawn (Holme 1974). Alternatively, migration into the North Sea could also be from northern Ireland or the Sea West of Scotland into the northern North Sea (Waluda and Pierce 1998). A relatively high number of squid from the Celtic spring–summer spawning stock (25%) were misclassified to the North Sea autumn-winter spawning stock, based on element composition at the statolith edge. These squid did not likely migrate from the North Sea back into the Celtic Sea, because the shortest migration route through the English Channel spans over 560 km (López Solano et al. 2022), which is impossible for *L. forbesii* to cover in 2 weeks (statolith edge ablation point) at the average swimming speed of 3.0 km/day for *L. reynaudii* (Sauer et al. 2000). Furthermore, Celtic Sea squid that were misclassified based on statolith microchemistry to the North Sea autumn-winter spawning stock were not the same as those misclassified to the North Sea based on statolith shape analysis (Bobowski et al. 2024). Consequently, these squid more likely stayed in a region with water parameters similar to the North Sea where squid hatched in autumn-winter, perhaps separated from correctly classified squid that were primarily

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found in a considerably more southern area than misclassified squid in the Celtic Sea. However, seasonal or annual differences in element incorporation could affect classification.

Microelement composition at the edge of *L. forbesii* statoliths suggested that squid caught in the southern Adriatic Sea differed from those caught in the Balearic Sea, with two separate stocks and hatching areas, similar to results of statolith shape analysis (Bobowski et al. 2024). In contrast, the similar microelement composition of the statolith nucleus we found supported the possibility of a common stock, like an earlier genetic analysis that showed a linkage between the two regions (Göpel et al. 2022). However, squid from the two areas may be separate stocks, with paralarval stages that may have been exposed to similar abiotic conditions after hatching in winter, which aligns with the November to July period when most *Loligo* spp. eggs are typically found in the Mediterranean (Laptikhovsky et al. 2025). Additionally, squid from the Adriatic winter spawning stock were the least correctly classified (20%), based on the elemental composition at the statolith edge, with 75% misclassified to the Celtic summer spawning and North Sea autumn-winter spawning stocks combined. Squid from the Balearic winter spawning stock were also misclassified (37%) for the same North East Atlantic areas based on element composition of the statolith edge. The Adriatic Sea is relatively narrow, bordered by land on three sides and influenced by the river Po, which may have influenced inputs of elements to cause high variability in nearshore seawater composition. For instance, harbours and estuaries in coastal areas of the southern Adriatic are critical hotspots for Zn, Cu, Mn and Ni (Accornero et al. 2004). Moreover, the Adriatic is an upwelling area (Vilibić and Orlić 2002) and this hydrographic element could further concentrate microelements mentioned above. Elevated concentrations of Cu and Zn at the statolith edge of *L. forbesii* from the Adriatic Sea reflect this pollution. However, squid from the North Sea had lower values of these trace metals in their statolith edge, whilst squid from the Adriatic winter spawning stock ranged widely. This suggests that misclassification between these two spawning stocks was caused by squid with low trace metal concentrations in the Adriatic Sea or by similar element concentrations as in squid from the North Sea. Misclassification of squid from both Mediterranean areas was lower in early life stages, but they were misclassified as Celtic summer spawning or North Sea autumn-winter spawning stocks. A small number of squid from Celtic summer spawning and North Sea autumn-winter spawning stocks were also misclassified to the Balearic and Adriatic winter spawning stocks based on microchemical analysis. Misclassification of squid between areas in the North East Atlantic Ocean and Mediterranean Sea based on statolith nucleus microelements may have been linked to depth differences of eggs because similar water parameters could exist at different depths in these areas. However, because only squid from areas in the Mediterranean Sea and North Sea did not differ at early life stages, the effect of depth was likely negligible. Furthermore, misclassification of elemental composition was higher at the statolith edge than at the nucleus, so early life stages may reside at more specific locations with less seawater element variability (possibly caused by pollution) than maturing and mature individuals. Last, misclassification of *L. forbesii* between North East Atlantic and Mediterranean may have been caused by the tendency of cephalopods to accumulate certain environmental microelements (e.g., Zn, Cu, Fe and Sr.; Lourenço et al. 2009). In polluted environments, such accumulation could further obscure differences amongst areas. Overall, results of our study were similar to results of shape analysis of the same individuals (Bobowski et al. 2024), with higher or similar correct classification to most areas for both species in the life stage before capture (i.e., statolith edge).

5 | Conclusions

Our study clearly showed the potential and limitations of statolith microchemistry for stock discrimination. Stock discrimination in squid is highly complex, and a single approach is likely insufficient to comprehensively discriminate all stocks. Microchemistry of the statolith edge reflects the influence of water parameters or diet close to the time of capture, but provides no information about primary habitat prior to the time of capture. Nevertheless, in combination with elemental ratios at the statolith nucleus and age estimates, statolith edge microchemistry provided a good indication of whether individuals from the same capture area shared the same hatching area. However, to accurately determine the primary habitat of squid, shape analysis is preferable to microchemical analysis based solely on nucleus and edge measurement. Of all elements we measured, Co and Fe best separated capture areas. However, when all elements were considered, both species were incorrectly classified to some areas, especially the squid in the Mediterranean Sea. Therefore, we recommend that for a correct and detailed stock differentiation, including hatching area, migration pathway and the main residence area, microchemistry analysis of transect measurements from nucleus to edge be combined with shape analysis and age estimation. Additionally, based on high concentrations of statolith trace metals in some life stages and areas, we assume that microchemistry could be used as an indicator for trace metal pollution in marine areas or prey organisms.

Acknowledgements

B.T.C.B. thanks Dr. Anne Sell and the technical assistant Samira Peter for their support in the laboratory as well as Brigitte Stoll and Ulrike Weis for their supervision and support with the microchemistry analysis. She would also like to thank Marilena Donnaloia for providing individuals from the Adriatic Sea as well as their associated biological data. Furthermore, thanks to the crew and scientific officers of the *RV Dana* and *RV Celtic Explorer* who supplied samples, especially Susan Maersk Lusseau and Dr. Eoghan Kelly. Last but not least, we thank the anonymous reviewers and Michael J Hansen for their comments, which have improved the manuscript. Open Access funding enabled and organized by Projekt DEAL.

Ethics Statement

The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Appendix A

Figures A1 and A2

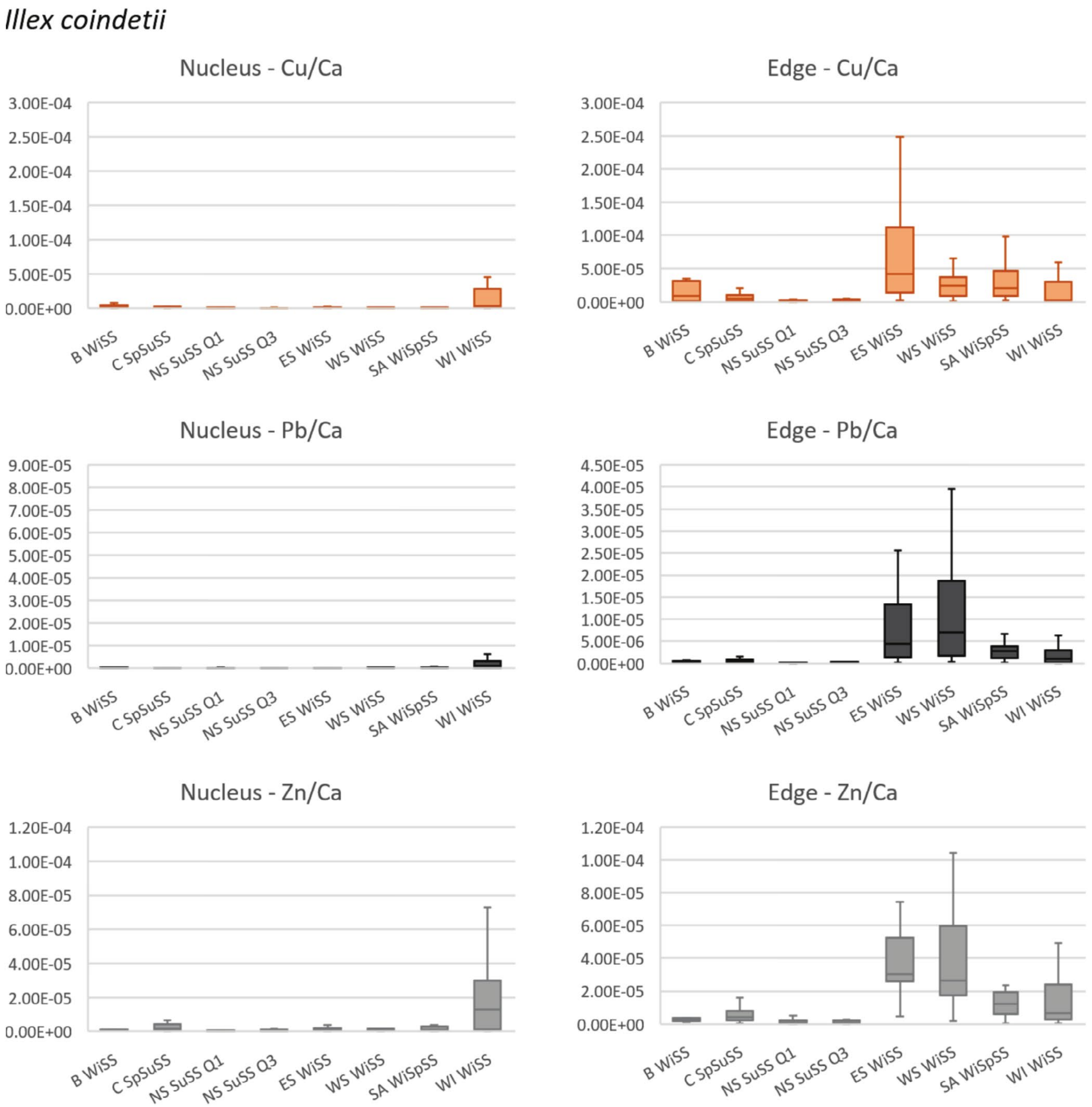

FIGURE A1 | Concentration of copper (Cu), lead (Pb) and zinc (Zn) at the nucleus and edge of statoliths from *Illex coindetii* sampled in the Balearic Sea (B WiSS), Celtic Sea (C SpSuSS), North Sea (NS SuSS Q1 = captured in Q1; NS SuSS Q3 = captured in Q3), Sea East of Sardinia (ES WiSS), Sea West of Sardinia (WS WiSS), South Adriatic Sea (AS WiSpSS) and Western Ionian Sea (WI WiSS) in the North East Atlantic Ocean and Mediterranean Sea during 2021–2022 (AuWiSS = Autumn–Winter spawning stock, SpSS = Spring spawning stock, SpSuSS = Spring–Summer spawning stock, SuSS = Summer spawning stock, WiSS = Winter spawning stock, WiSpSS = Winter–Spring spawning stock). Data distributions with quartiles; box for Q1 to Q3 whiskers extend to minimum and maximum values within 1.5 times the interquartile range.

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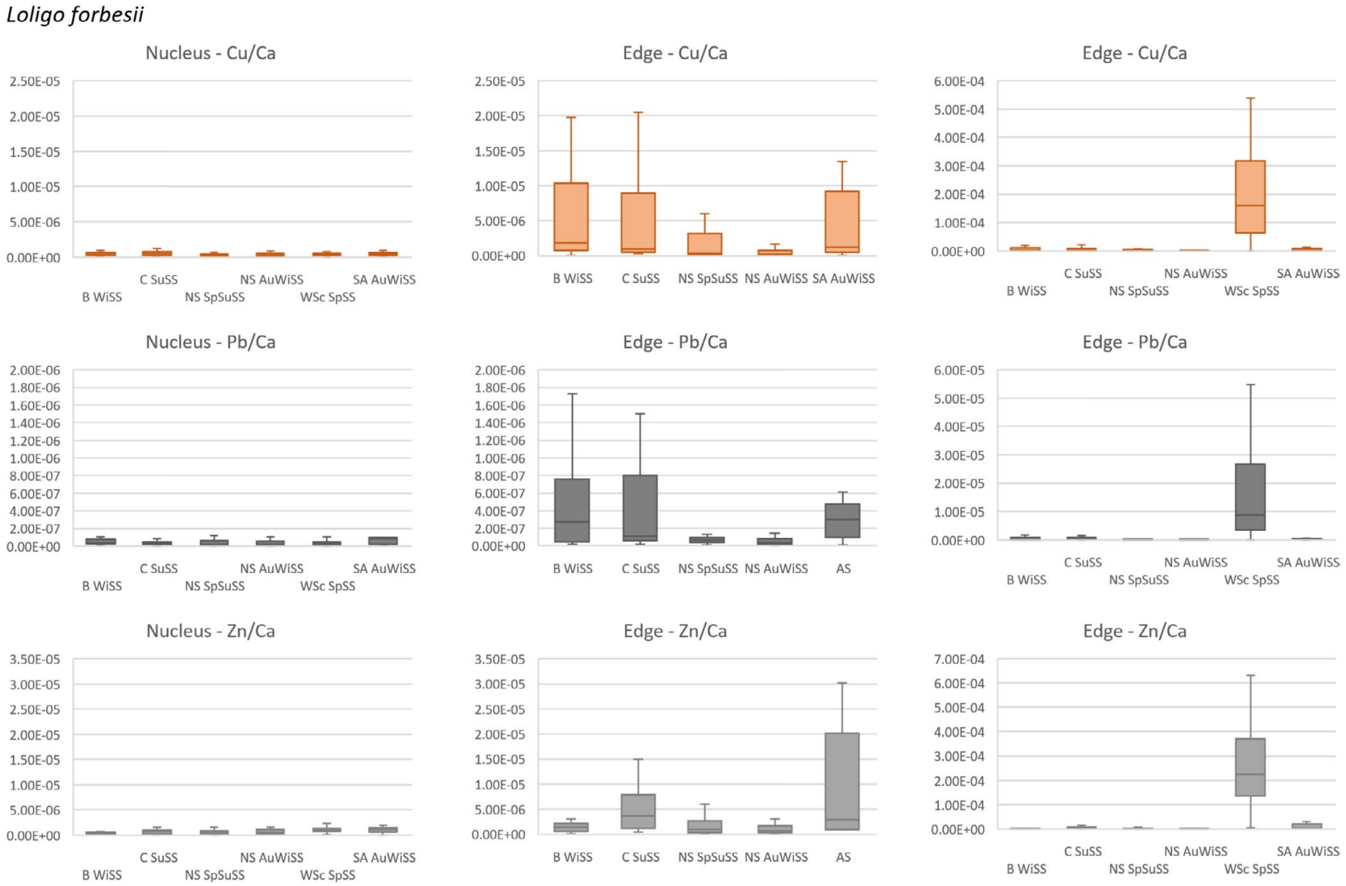

FIGURE A2 | Concentration of copper (Cu), lead (Pb) and zinc (Zn) at the nucleus and edge of statoliths from *Loligo forbesii* sampled in the Balearic Sea (B WiSS), Celtic Sea (C SuSS), North Sea (NS SpSuSS = captured in Q1, NS AuWiSS = captured in Q3), Sea West of Scotland (WSc SpSS), South Adriatic Sea (SA AuWiSS) in the North East Atlantic Ocean and Mediterranean Sea during 2021–2022 (AuWiSS = Autumn–Winter spawning stock, SpSS = Spring spawning stock, SpSuSS = Spring–Summer spawning stock, SuSS = Summer spawning stock, WiSS = Winter spawning stock). Data distributions with quartiles; box for Q1 to Q3 whiskers extend to minimum and maximum values within 1.5 times the interquartile range. Two visualisations for microchemical edge data: right column = all sampled areas, and middle column = excluding West Scotland Spring spawning stock, where extreme values were recorded.

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