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ARTICLE

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Stock discrimination of two European squids (*Illex coindetii*, *Loligo forbesii*) by statolith shape analysis

Bianca T. C. Bobowski[1,2] | **Anne Marie Power**[3] | **Finlay Burns**[4] | **Pierluigi Carbonara**[5,6] | **Danila Cuccu**[7] | **Marilena Donnaloia**[6] | **Maria Cristina Follesa**[7] | **Ana Moreno**[8] | **Inna M. Sokolova**[2] | **Maria Valls**[9] | **Daniel Oesterwind**[1]

[1]Thünen Institute of Baltic Sea Fisheries, Rostock, Germany
[2]Department of Marine Biology, University of Rostock, Rostock, Germany
[3]Ryan Institute, School of Natural Sciences, University of Galway, Galway, Ireland
[4]Marine Directorate – Scottish Government, Marine Laboratory, Aberdeen, UK
[5]Fondazione COISPA ETS, Bari, Italy
[6]COISPA Tecnologia & Ricerca, Bari, Italy
[7]Department of Life and Environmental Science, University of Cagliari, Cagliari, Italy
[8]IPMA, Instituto Português do Mar e da Atmosfera, Lisbon, Portugal
[9]Oceanographic Center of the Balearic Islands (COB-IEO, CSIC), Palma, Spain

Correspondence
Daniel Oesterwind, Thünen Institute of Baltic Sea Fisheries, Alter Hafen Süd 2, 18069 Rostock, Germany.
Email: daniel.oesterwind@thuenen.de

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Abstract

We evaluated the feasibility of classifying ommastrephid and loliginid squid species by statolith shape analysis into fisheries management units or stocks. Statoliths of *Illex coindetii* (Verany, 1839) and *Loligo forbesii* (Steenstrup, 1856) were studied from multiple areas of the North East Atlantic and Northern Mediterranean Sea during 2021–2022. *I. coindetii* and *L. forbesii* individuals were categorized into multiple stocks across the areas studied. Stocks migrating between fishing areas as well as multiple stocks in the same area, as identified for *L. forbesii* in this study, need to be considered for sustainable fisheries management.

KEYWORDS

broadtail shortfin squid, Loliginidae, Myopsida, Oegopsida, Ommastrephidae, statolith shape analysis, stock structure, veined squid

1 | INTRODUCTION

Cephalopods are increasingly important in commercial fisheries due to changes (extending or expanding) in their global distribution (Chen et al., 2006; Kooij et al., 2016; Oesterwind et al., 2022) and because finfish populations are declining worldwide (Sabolić et al., 2021). The landed biomass of squid, cuttlefish and octopus has steadily increased (Doubleday et al., 2016), from 2.7 million tonnes (Mt) in 1993 to a record high of 4.9 Mt in 2014 (FAO, 1998, 2022). Since 1980, East Asia and South America (Peru and Argentina) are main contributors to these landings (Ospina-Alvarez et al., 2022).

The veined squid *Loligo forbesii* is important in European fisheries and one of the most commonly caught myopsid squid in the North East Atlantic fishery (Pierce et al., 2013). Although Scotland and France target squid fishing (Marchal & Vermard, 2023; Young et al., 2006), *L. forbesii* is usually caught as bycatch in trawl nets that primarily target demersal fish species (Pierce et al.,2013). European Atlantic annual landings of loliginid squid species (which include *L. forbesii*, *L. vulgaris*, *Alloteuthis media*, *A. subulata*) ranged 8000–12,000 tonnes in the last 5 years, with highest yields from the North Sea and English Channel (ICES, 2023). The broadtail shortfin squid, *Illex coindetii*, is another commercially important species found throughout the Atlantic Ocean that is among the most important commercial species of its genus (Martínez et al., 2002). In Europe, this species is predominantly caught as bycatch in demersal and pelagic trawl fisheries (Sánchez et al., 1998) with landings of 5000–7000 tonnes per year (since 2018), mostly by Spanish Fisheries (ICES, 2023). For effective fisheries management and assessment, understanding population dynamics and defining management units (stocks) is crucial (Rodhouse et al., 2014). Fish stocks encompass the living resources within a population used for fishing, typically implying a self-sustaining population isolated from other stocks of the same species (FAO Fishery Glossary, n.d.). To support effective management, statolith shape analysis is a promising method for defining different stocks of a species, including squids (Fang et al., 2014; Green et al., 2015; Sheerin et al., 2022).

Like other hard structures (beak, gladius or cuttlebone), statoliths can provide valuable information for species identification (Guo et al., 2021) and delineation of stocks (Green et al., 2015; Sheerin et al., 2022). Statoliths are paired calcified structures (Jackson, 1994) composed of aragonite crystals and organic matter (Liu et al., 2016). Several substances in a mineral structure inhibit, or favour, primary or secondary nucleation and control crystalline structure formation. These regulatory factors, in combination with the limited available space, lead to a certain mineral structure (Bettencourt & Guerra, 2000). Moreover, statolith size can vary among different cephalopod species and may be influenced by their locomotion patterns. In slow-moving cephalopods, larger statoliths can be advantageous for detecting and responding to slow movements. Larger statoliths provide a greater inertial mass within the statocyst that potentially increases sensitivity to changes in acceleration and movement (Budelmann, 1988). Ommastrephid species, including *I. coindetii*, commonly known as flying squids or arrow squids, are highly active and agile swimmers (Muramatsu et al., 2013). In contrast, loliginid squids are slower swimmers (O'Dor et al., 1995). Consequently, the behaviour of *I. coindetii* is associated with significantly smaller statoliths than those of *L. forbesii* (Figure 1). Furthermore, bathymetry is assumed to affect behaviour and thereby influence statolith development and shape (Ching et al., 2022; Fang et al., 2018). Statolith growth, shape, and microstructure are also affected by temperature (Chemshirova et al., 2023; Moreno et al., 2012). In particular, the four main areas of statolith shape (dorsal dome, lateral dome, rostrum and wing; Figure 1) have distinguishing characteristics that can be used to differentiate among species within the same family (Fang & Chen, 2017). Furthermore, statolith shape can differentiate individuals from different stocks of the same species. For instance, a combination of genetic analysis and statolith shape analysis for *L. forbesii* revealed variations in statolith shape among individuals from different areas of the Irish Shelf (Sheerin et al., 2022), while microsatellites of *L. forbesii* from the North East Atlantic and Mediterranean Sea differed at a larger geographical scale (Göpel et al., 2022). Hence, genetic traits alone may not consistently differentiate stocks, but rather define isolated breeding groups. Populations may share spawning grounds (or partially exchange breeding individuals), but exist as distinct entities outside the spawning season, and consequently differ biologically, such as growth and maturity, and different seasonality patterns (Arvanitidis et al., 2002; Moreno et al., 2002). Therefore, a comprehensive understanding of the "stock concept" requires additional approaches (Begg et al., 1999) in some cases.

For sustainable use of fishery resources, management based on previously defined stocks is necessary. For example, along

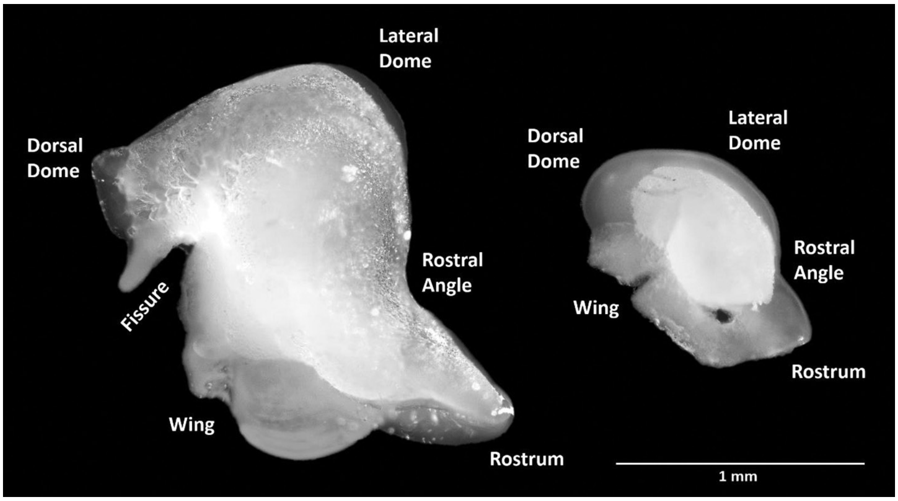

FIGURE 1 Photomicrograph of right-side statoliths from mature Q1 2021 North Sea *Loligo forbesii* (left) and Q3 2021 North Sea *Illex coindetii* (right) individuals with labelled key morphological features.

the northwest coast of Africa, the common octopus (*Octopus vulgaris*) is heavily exploited, with its three stocks already considered overfished (FAO, 2012). Management measures implemented to reduce fishing pressure on this species include fishing licences, closed seasons, minimum landing size limits and prohibitions on trawling in waters shallower than 20m (FAO, 2012; Fernández-Rueda & García-Flórez, 2007). However, octopuses are benthic species that migrate little, so their stock definition should be more straightforward than squid, which are known for migratory behaviour over medium to long distances, which might contribute to inadequate stock discrimination by genetic analysis (Göpel et al., 2022). Cephalopod management measures implemented by non-EU countries, Australia, New Zealand and Iceland, include licenced commercial fishing vessels, assessment of key stocks, catch restrictions and input controls (Marchal et al., 2016). The Magnuson-Stevens Fishery Conservation and Management Act of the United States also requires states to meet standards for fishing effort and management (NOAA, 2007). However, this management is either based on stock definition by species distribution, including timing and occurrence of larval and juvenile stages (for *I. illecebrosus*; Dawe & Hendrickson, 1998), or genetic analysis of *L. pealeii* (Shaw et al., 2012). For European cephalopods, no such management measures have been implemented (Bobowski et al., 2023), and cephalopod stocks are not currently differentiated based on biological characteristics for fisheries management. Therefore, stock differentiation is needed for commercially used cephalopod species (Jereb et al., 2015; Lishchenko et al., 2021) to ensure a sustainable fishery.

We evaluated the potential of statolith shape analysis to delineate loliginid and ommastrephid squid stocks across their distribution in European waters. We hypothesized that shape analysis would provide a more detailed view of spatial and temporal discrimination of stocks than genetic analysis. Our findings would provide relevant information for fisheries management and contribute to the development of more sustainable fishing of European squids.

2 | MATERIALS AND METHODS

2.1 | Sample collection and preparation

Squid samples were collected during ICES (International Council for the Exploration of the Sea) co-ordinated International Bottom Trawl Surveys (IBTS) and Mediterranean International Bottom Trawl Surveys (MEDITS), following standardized protocols (ICES, 2012, 2017). Samples were also collected during the Irish Anglerfish and Megrim Survey (IAMS) using standardized protocols (Reid et al., 2007) and the Scottish West Coast Groundfish Survey (SCOWCGFS) (ICES, 2020a). Samples were collected within a one-year period, but in different quarters (Q) encompassing eight areas in the North East Atlantic and Northern Mediterranean Sea, including North Sea, Sea West of Scotland, Celtic Sea, Balearic Sea, Sea West of Sardinia, Sea East of Sardinia, Western Ionian Sea and South Adriatic Sea (Figure 2). Mediterranean samples were collected in Q3 2021, whereas North East Atlantic samples were collected in different year quarters (North Sea: Q1, Q3 2021; Sea West of Scotland: Q4 2021, Celtic Sea: Q1 2022).

Dorsal mantle length (DML, mm), total weight (*W*, 0.01g), sex and maturity stage (ICES, 2022) of *I. coindetii* and *L. forbesii* were measured or classified, and statoliths were extracted from the statocyst. Statoliths were cleaned with distilled water, affixed to a microscope slide using a thermoplastic adhesive (Crystalbond™) and photographed under reflected 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). Images of dust particles and fibres were removed from photographs to ensure that statolith outlines were suitable for Fourier shape analysis. To avoid ontogenetic bias due to development of the statolith wing (similar to *I. illecebrosus*, see Morris & Aldrich, 1984), only statoliths from adult *I. coindetii* (Maturity stage 2a-3b (Table 1)) were included. Broken statoliths were excluded. Of 441 total right-side statoliths, 187 statoliths were from *I. coindetii* and 254 statoliths were from *L. forbesii*. Due to the availability of two different seasonal data sets (Q1 and Q3) for each species from the North Sea (Table 1), seasonal differences were tested for this area.

2.2 | Statistical analyses

Statolith shape (contour) of *I. coindetii* and *L. forbesii* was extracted from a bitmap image, described with Elliptic Fourier Descriptors (EFDs) and principal component analysis (PCA) of EFDs, using SHAPE (ver.1.3 by Iwata & Ukai, 2002) software. Statolith shapes were normalized based on the first harmonic ellipse that corresponds to the first Fourier approximation to the contour information with a standardized size and orientation of the contour in accordance with the size and alignment of the major axis of the ellipse (Iwata & Ukai, 2002). A scatterplot was used to represent statolith shape differences for each sampled area (Q1 and Q3 North Sea samples combined) in the plane of first two principal components (PC1 and PC2) using the ggplot2 package in RStudio (ver.4.2.2 by Posit PBC, 2022). Partitioning of variation among groups, based on principal components, was assessed through permutational multivariate analysis of variance (PERMANOVA) using the vegan package in RStudio. A Bonferroni correction was implemented on *p*-values of multiple comparisons to reduce Type I errors. If multivariate spatial dispersions of variances were not homogenous, an analysis of similarities (ANOSIM) was used instead of PERMANOVA. To test for correlation between observed and predicted classes, PCAs were classified and analysed in Statistica (ver.14.0.1.25 by TIBCO, 2020). Maps of individuals in areas were created in Ocean Data View version 5.6.5 (Schlitzer, 2023). Additionally, an MDS plot was created in Primer v6.1.13 to visualize proximity of maturity stage 1 of *L. forbesii* in different areas.

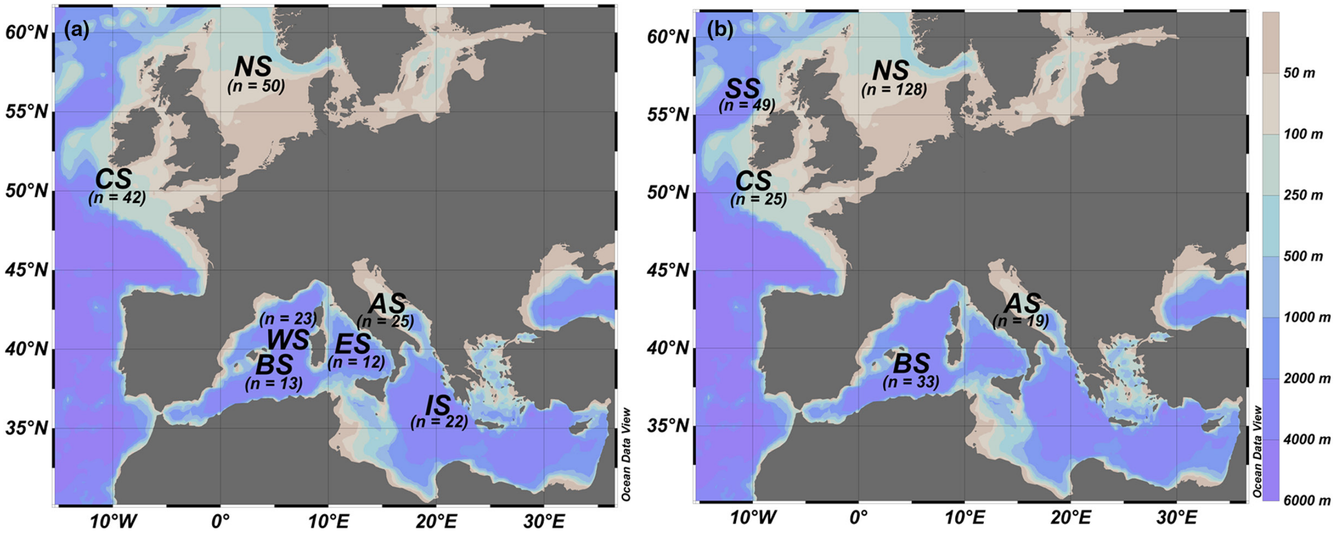

FIGURE 2 Sampling areas of *Illex coindetii* (a) and *Loligo forbesii* (b), with number of individuals analysed (*n*), in the North Sea (NS), Sea West of Scotland (SS), Celtic Sea (CS), Balearic Sea (BS), Sea West of Sardinia (WS), Sea East of Sardinia (ES), Western Ionian Sea (IS), South Adriatic Sea (AS) in the North East Atlantic and Northern Mediterranean Sea during 2021–2022.

TABLE 1 Biological characteristics of *Illex coindetii* and *Loligo forbesii* and quarters sampled for the North Sea in the North East Atlantic and Northern Mediterranean Sea during 2021–2022.

		DML (mm)			Weight (g)				
Species	**Sex**	**Min.**	**Max.**	**Mean ± SD**	**Min.**	**Max.**	**Mean ± SD**	**Individuals (*n*)**	**Maturity stage**
I. coindetii	All males	79	197	144 ± 24.85	13	232	104 ± 45.94	85	
	All females	92	285	169 ± 33.37	16	549	132 ± 72.21	102	
	Q1 NS	79	158	122 ± 23.37	13	158	46 ± 24.39	27	2a, 2b
	Q3 NS	108	224	162 ± 30.77	33	331	143 ± 67.45	23	3a, 3b
L. forbesii	All juveniles	78	225	152 ± 79.04	24	320	164 ± 152.3	4	
	All males	72	485	195 ± 85.14	16	1820	256 ± 308.6	135	
	All females	74	365	184 ± 55.42	20	1057	223 ± 174.3	115	
	Q1 NS	107	356	214 ± 69.37	44	704	261 ± 166.7	58	2a, 2b, 3a
	Q3 NS	87	298	165 ± 49.81	25	595	164 ± 129.9	68	2a, 2b, 3a

Abbreviations: DML, dorsal mantle length; NS, North Sea; Q1, Sampling period Quarter 1 (25.01.2021–26.02.2021); Q3, Sampling period Quarter 3 (19.07.2021–17.08.2021).

3 | RESULTS

3.1 | Biological data

Mean dorsal mantle length (DML) of *I. coindetii* was shorter for males than females (Mann–Whitney *U*-test, $p \leq 0.001$, Table 1). Mean DML of mature *L. forbesii* males did not differ from mature females (Mann–Whitney *U*-test, $p = 0.825$). For *I. coindetii* from the North Sea, mean DML was shorter (*t*-test, $p \leq 0.001$), mean wet weight was lighter (Mann–Whitney *U*-test, $p \leq 0.001$), and mean maturity stage was lower (Mann–Whitney *U*-test, $p \leq 0.001$) in Q1 (including developing and maturing individuals) than in Q3 (including mature and spent individuals). Conversely, for *L. forbesii* from the North Sea, mean DML was longer (*t*-test, $p \leq 0.001$), mean wet weight was heavier (Mann–Whitney *U*-test, $p \leq 0.001$), and mean maturity stage was higher (Mann–Whitney *U*-test, $p \leq 0.001$) in Q1. However, both quarters included the same maturity categories: developing, maturing and mature individuals (Table 1).

3.2 | Statolith shape differences

For *I. coindetii*, mean statolith shape from the North Sea (Q1 and Q3 combined) differed more than from other regions (Mediterranean areas: Q3 2021, CS: Q1 2022). Compared to other areas, statoliths were more rounded, with a prominent wing and wide rostral angle (Figure 3). The first two principal components explained 63.61% (PC1: 38.54%; PC2: 25.07%) of statolith shape variation. Statolith shape grouped together in geographical distance-dependent groups (Figure 4). To achieve homogenous multivariate dispersion

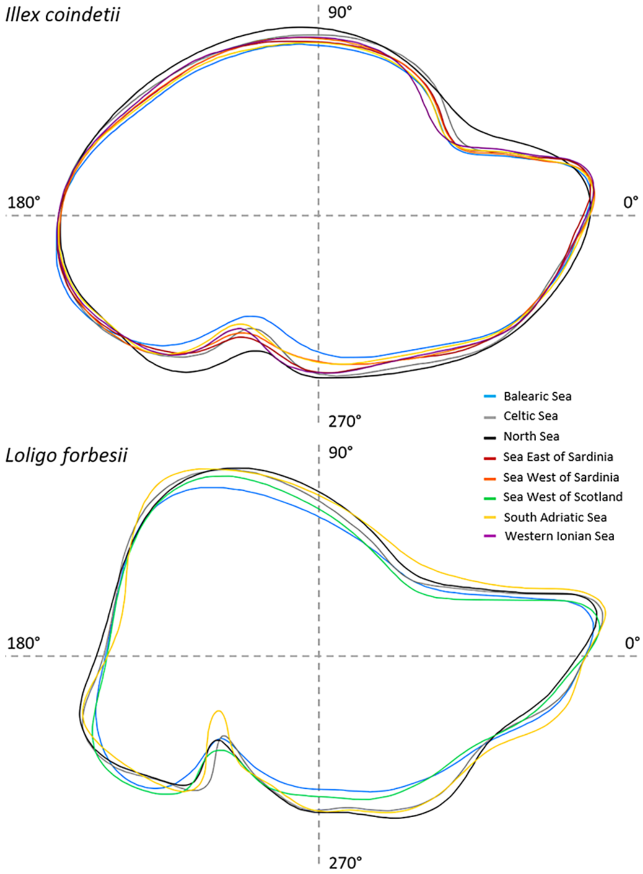

FIGURE 3 Mean statolith shapes of *Illex coindetii* and *Loligo forbesii* (all maturity stages and sexes) from the Balearic Sea (blue), Celtic Sea (grey), North Sea (Q1 & Q3 combined; black), Sea East of Sardinia (red), Sea West of Sardinia (orange), Sea West of Scotland (green), South Adriatic Sea (yellow), Western Ionian Sea (purple) of the North East Atlantic and Northern Mediterranean Sea during 2021–2022. Intersection of coordinate lines corresponds to the statolith centroid.

in space among areas, North Sea samples were excluded from PERMANOVA analysis (homogeneity when North Sea excluded: $p = 0.4175$, $F_{5,131} = 1.005$). Excluding the North Sea, statolith shape differed among all areas and the Balearic Sea, except South Adriatic Sea, and between the Celtic Sea and all areas, except the Sea East of Sardinia. Furthermore, Sardinian Seas and South Adriatic Sea did not differ in statolith shape; similarly, statolith shape from the North Sea did not differ from those from the Sea East of Sardinia (Table 2).

For *L. forbesii*, mean statolith shape from the North Sea (Q1 and Q3 combined) had a more pronounced dorsal dome and wing structure than from other areas (Mediterranean areas: Q3 2021, SS: Q4 2021, CS: Q1 2022) and were less pronounced from the Balearic Sea (Figure 3). PC1 (50.28%) and PC2 (12.77%) accounted for 63.05% of statolith shape variation (Figure 4). Statolith shape of individuals from North Sea and Celtic Sea was similar, whereas statolith shape of individuals from Scottish waters differed from these regions. Statolith shape of individuals from the Balearic Islands (part of the Mediterranean) was closer to that of Scottish individuals and differed from those in the Southern Adriatic Sea. Due to non-homogenous multivariate dispersion in space of individual areas, a one-way ANOSIM was used for *L. forbesii* (Table 2). Statolith shape differed among all areas, except between the North Sea and Celtic Sea (Table S1).

3.3 | Area classification

Classification of *I. coindetii* to sample areas based on statolith shape was highly accurate, with >80% of specimens from the North East Atlantic and >50% overall from the Mediterranean correctly classified (Table 3). Within the Mediterranean, however, only ~33% of individuals from the Sea East of Sardinia were correctly classified. Classification of *L. forbesii* to sample areas based on statolith shape was also highly accurate, with 80%–90% of specimens classified to correct areas (Table 3), although only 44% from the Celtic Sea were correctly classified.

Within the North Sea, statolith shape did not differ significantly between FAO areas (https://www.fao.org/fishery/en/area/27/en) in both *I. coindetii* ($F_{1,48} = 0.2108$, $p = 0.64852$) and *L. forbesii* ($F_{2,125} = 0.5193$, $p = 0.5962$) (Table S8). However, statolith shape differed significantly between samples from Q1 and Q3 for both species (*I. coindetii* ANOSIM: $p = 0.006$; *L. forbesii* PERMANOVA; $p = 0.006$).

4 | DISCUSSION

We found that statolith shape variation of *I. coindetii* and *L. forbesii* distinguished among geographically and seasonally separated groups within the North East Atlantic and the Mediterranean, which we interpreted as stocks, in contrast to stock identification studies based on genetic variation (ICES, 2020b) that only revealed differences at a larger geographical scale for *L. forbesii* in European waters due to high migration rate (Göpel et al., 2022; Sheerin et al., 2022). Genetic stock discrimination may be limited for highly mobile species with large gene flow, whereas the present and other studies illustrate the use of statolith shape analysis to distinguish stocks of squid species on a smaller geographic scale (shape markers may indicate ecologically separate groups of species with similar migration patterns; Fang & Chen, 2017; Green et al., 2015; Guo et al., 2021; Sheerin et al., 2022).

High accuracy of correct area classification for North Sea and Celtic Sea and differences in statolith shape between areas, in the present study, suggests the presence of at least two distinct *I. coindetii* stocks in the North East Atlantic. Previously, single adult individuals without any evidence of reproduction occurred in the North Sea, which were thought to have migrated into the North Sea from adjacent waters (Oesterwind et al., 2020). The current reproductive success in the North Sea (first observed in 2016) probably results from rising temperatures and prevailing currents (Barrett et al., 2021; Oesterwind et al., 2022) and has led to an independent stock. The

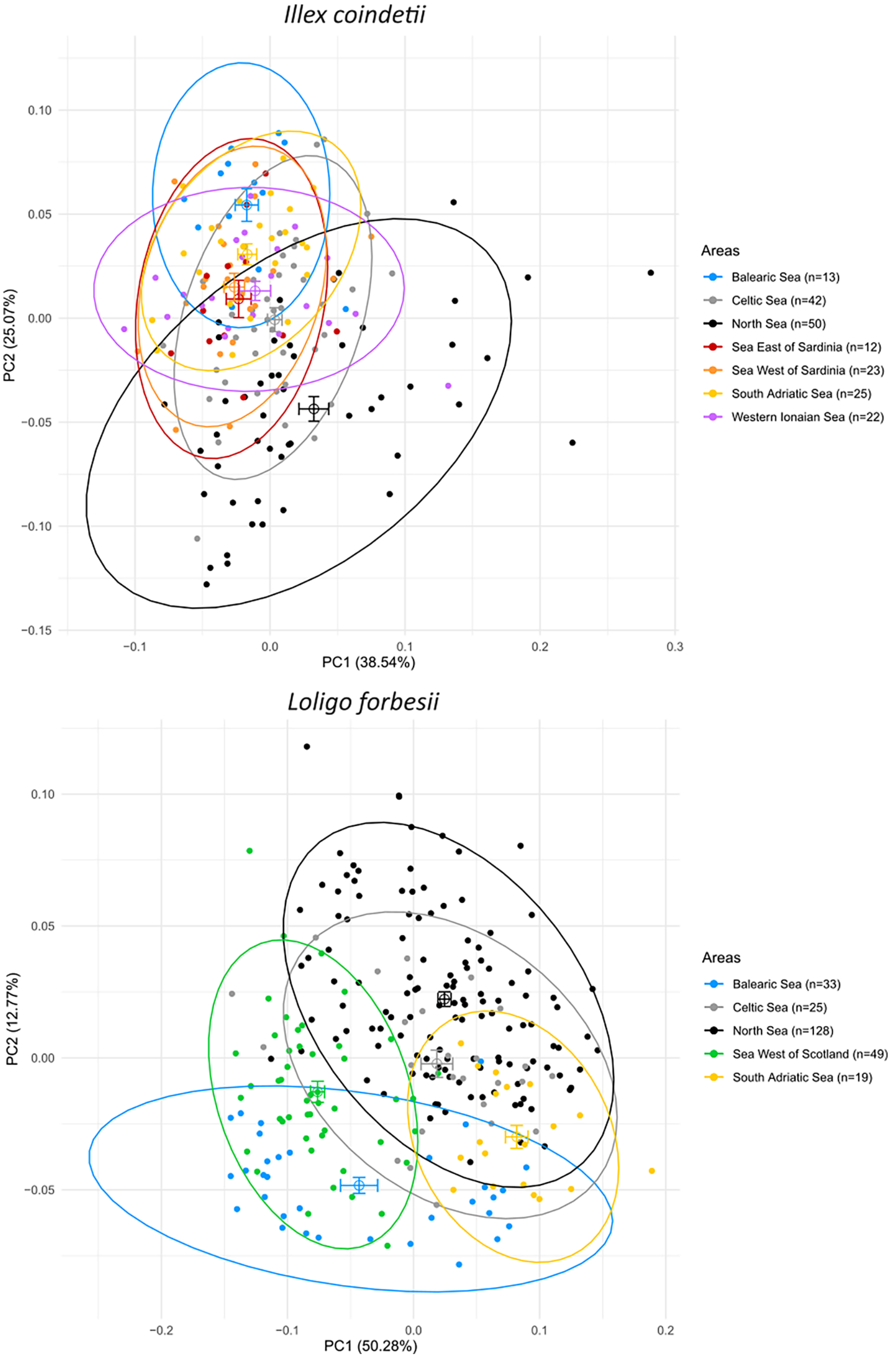

FIGURE 4 Principal components one and two of *Illex coindetii* and *Loligo forbesii* statolith shape from the Balearic Sea (blue), Celtic Sea (grey), North Sea (Q1 & Q3 combined; black), Sea East of Sardinia (red), Sea West of Sardinia (orange), Sea West of Scotland (green), South Adriatic Sea (yellow), and Western Ionian Sea (purple) of the North East Atlantic and Northern Mediterranean Sea during 2021–2022. Open circles represent the mean (± standard error) and ellipses encompass 95% of specimens from each area.

North Sea appears to be the northernmost breeding area, with main spawning grounds in the Central and Northern North Sea (Barrett et al., 2021), while floating egg masses have been observed in the Norwegian Channel (Ringvold et al., 2021). The bathymetry and hydrology of the North Sea, as a shelf sea with an average depth of 90m and a relatively narrow connection to the Atlantic Ocean (ESaTDOR, 2013), could prevent emigration from this area by passive drifting egg spheres and hatchlings of *I. coindetii*. Despite our observed differences in *I. coindetii* statolith shape between two sampling periods within the North Sea, this species has only one spawning season in the area (Oesterwind et al., 2020) and statolith shape did not differ among maturity stages (Q1: 2a, 2b; Q3: 3a, 3b) (Table S4). Therefore, we assume only one stock is present in this region. Factors responsible for statolith shape differences between sampling quarters need to be studied in the future. Based on genetic homogeneity, Pierce et al. (2010) concluded that only one stock of *I. coindetii* occurs throughout the North East Atlantic, which could be interpreted as a single breeding stock with ecologically distinct sub-units (e.g., due to separate migration patterns). However, as mentioned above, a new stock of *I. coindetii* reproduced since at least 2016 in the North Sea (Barrett et al., 2021; Oesterwind et al., 2020). Hence, the North Sea stock was likely established since the study by Pierce et al. (2010), primarily due to the previously limited number of *I. coindetii* individuals found in this region (Oesterwind et al., 2010, 2015).

TABLE 2 Pairwise comparisons of *Illex coindetii* and *Loligo forbesii* statolith shape from the Balearic Sea, Celtic Sea, North Sea (Q1 & Q3 combined), 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 Northern Mediterranean Sea during 2021–2022 using permutation MANOVAs, respectively one- way ANOSIM on Euclidian distance matrix.

		Balearic Sea	**Celtic Sea**	**Sea east of Sardinia**	**Sea west of Sardinia**	**South Adriatic Sea**
Illex coindetii MANOVA	Celtic Sea	**0.001**	–	–	–	–
	S. E. o. Sardinia	**0.033**	0.601	–	–	–
	S. W. o. Sardinia	**0.049**	**0.010**	1.000	–	–
	S. Adriatic Sea	0.845	**0.001**	1.000	1.000	–
	W. Ionian Sea	**0.025**	**0.042**	1.000	0.735	1.000

		Balearic Sea	Celtic Sea	North Sea	Sea East of Sardinia	Sea West of Sardinia	South Adriatic Sea
Illex coindetii ANOSIM	Celtic Sea	**0.001**	–	–	–	–	–
	North Sea	**0.004**	**0.001**	–	–	–	–
	S. E. o. Sardinia	**0.005**	0.272	0.287	–	–	–
	S. W. o. Sardinia	**0.027**	**0.021**	**0.011**	0.434	–	–
	S. Adriatic Sea	0.238	**0.001**	**0.001**	0.224	0.178	–
	W. Ionian Sea	**0.009**	**0.003**	**0.003**	0.600	0.240	0.118

		Balearic Sea	Celtic Sea	North Sea	Sea West of Scotland
Loligo forbesii ANOSIM	Celtic Sea	**0.001**	–	–	–
	North Sea	**0.001**	0.654	–	–
	S. W. o. Scotland	**0.001**	**0.001**	**0.001**	–
	S. Adriatic Sea	**0.001**	**0.001**	**0.027**	**0.001**

Note: Significant comparisons ($p < 0.05$, adjusted with Bonferroni method) are shown in bold.

The Mediterranean *I. coindetii* population structure is described as a middle-course situation, involving a combination of C-type (multiple cohorts or microcohorts) and D-type (multiple, heavily overlapping cohorts) population structures (Sánchez et al., 1998). This conclusion corresponds with our findings, as the stock interpretation by statolith shape analysis in this area was more complex than in the North East Atlantic. The complexity was because of a high similarity of statoliths from southern Italy (Sea East of Sardinia, Western Ionian Sea, South Adriatic Sea) and lower classification accuracy, which collectively suggested a substantial exchange of individuals belonging to the species *I. coindetii* and the absence of distinct stocks in this part of the Mediterranean Sea. Furthermore, statolith shape from the Balearic Sea differed from all other areas, except the Southern Adriatic Sea, while the Celtic Sea and North Sea did not differ from the Sea East of Sardinia. We expected to find different stocks in geographically distant or topographically separated areas, such as the Balearic Sea and the Adriatic Sea (assuming different stocks in these areas). Unlike the Fourier method, which is based on cosine and sine functions, wavelets are well-suited for approximating data with sharp discontinuities (Graps, 1995; Libungan & Pálsson, 2015), and therefore future analysis using wavelets might detect differences between these regions. This shows the limitation of (Fourier) shape analysis and a need of further studies on determinants of statolith shape. However, we assume that the Mediterranean Sea harbours a separate *I. coindetii* stock in the Balearic Sea area, probably related to geomorphology and habitat characteristics (Quetglas et al., 2012), which would benefit from further research.

In *L. forbesii*, we found that statolith shape differed between the Balearic Sea and Adriatic Sea, whereas microsatellite analysis only revealed small differences between individuals from these two areas (Göpel et al., 2022). In general, due to a high rate of correct classification and differences in statolith shape of *L. forbesii* among most areas, we conclude that these regions harboured separate stocks of this species, at least at the times of year sampled. *L. forbesii* has varying spawning seasons within the North East Atlantic, encompassing Scottish waters, Celtic Sea, English Channel, Faroe Bank and North Sea (Gaard, 1987; Holme, 1974; Laptikhovsky et al., 2022; Oesterwind et al., 2022; Pierce et al., 1994, 2005). However, we found relatively high misclassification of *L. forbesii* samples from the Celtic Sea, and that statolith shape only failed to differ significantly between samples from the Celtic Sea and the North Sea, which suggests connectivity between the North Sea and Celtic Sea, a confirmed spawning area for *L. forbesii* (Laptikhovsky et al., 2022) connected by migration (Holme, 1974). Juvenile *L. forbesii*, hatched near the western end of the English Channel, migrate eastward to foraging areas in the eastern Channel and southern North Sea, and migrate back to the Celtic spawning areas in autumn (Holme, 1974). The timing of eastward migration within the English Channel likely depends on water temperature and can vary up to 150 days (Sims et al., 2001). Consequently, we conclude that statolith shape develops during foraging in the North Sea. Alternatively, lower classification accuracy in the Celtic Sea in our study may have been caused by small sample sizes from this area. In addition to the exchange between

TABLE 3 Classification matrix for *Illex coindetii* and *Loligo forbesii* from the Balearic Sea, Celtic Sea, North Sea (Q1 & Q3 combined), 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 Northern Mediterranean Sea during 2021–2022.

		Predicted area							
Illex coindetii		**Balearic Sea**	**Celtic Sea**	**North Sea**	**Sea E. of Sardinia**	**Sea W. of Sardinia**	**S. Adriatic Sea**	**W. Ionian Sea**	**Classification success rate (%)**
Observed area	Balearic Sea	**7**	2	0	1	0	1	2	53.85
	Celtic Sea	0	**34**	5	1	1	0	1	80.95
	North Sea	0	2	**44**	0	0	2	2	88.00
	S. E. o. Sardinia	0	1	2	**4**	1	0	4	33.33
	S. W. o. Sardinia	2	6	1	0	**13**	0	1	56.52
	S. Adriatic Sea	1	3	0	0	2	**18**	1	72.00
	W. Ionian Sea	0	3	1	0	0	6	**12**	54.55

		Predicted area					
Loligo forbesii		**Balearic Sea**	**Celtic Sea**	**North Sea**	**Sea W. of Scotland**	**S. Adriatic Sea**	**Classification success rate (%)**
Observed area	Balearic Sea	**29**	0	0	1	3	87.88
	Celtic Sea	5	**11**	8	0	1	44.00
	North Sea	1	7	**112**	6	2	87.50
	S. W. o. Scotland	1	3	3	**40**	2	81.63
	S. Adriatic Sea	0	0	2	0	**17**	89.47

Note: Predicted versus observed area classes in individual numbers and correct classification are also provided as percentage. Correct classified samples are shown in bold.

North Sea/Celtic Sea, immigration from northern and western Scottish waters into the North Sea cannot be excluded, as indicated by migration patterns (Viana et al., 2009) and temporal patterns of egg mass, paralarvae, and mature female movements (Laptikhovsky et al., 2022). However, *L. forbesii* spawning also occurs in warmer months in the northern North Sea, so a "native" *L. forbesii* stock also occurs in the area (Laptikhovsky et al., 2022).

The occurrence of different *L. forbesii* stocks within the North Sea is also supported by different size classes and breeding populations. Pierce et al. (2005) described two different breeding populations in the North Sea, while Kristensen (1959) identified two size groups and speculated about disparate spawning areas – one in the English Channel and another in the North. However, Laptikhovsky et al. (2022) were not able to identify any evidence of spawning activity of *L. forbesii* in the English Channel so that it seems that Kristensen's (1959) former assumed southern spawning area is the Celtic Sea nowadays. Again, the combination of significant differences between the statolith shape of Q1 and Q3 North Sea individuals and the occurrence of different size classes infers that the North Sea harbours at least two temporally separated stocks of *L. forbesii*, namely individuals hatched in the Celtic Sea and North Sea spawners and very likely Scottish individuals (but the latter were not identified in this study). Furthermore, the slightly higher misclassification within the North Sea in Q1 (Tables S9 and S10) indicates that the stock mixture in Q1 is higher compared to Q3. It is not yet possible to quantify the mix of individuals spawning in the (northern) North Sea and those of Celtic and (presumably) Scottish west/north coast origin which use the North Sea as a foraging area.

Although *L. forbesii*, like *I. coindetii*, differed in statolith shape between sampling periods in the North Sea, *L. forbesii* size distribution and potential immigration from Scottish and Celtic waters clearly demonstrates that shape analysis itself provides only coarse stock identification that is not singularly interpretable without a multi-method approach (Sheerin et al., 2022). Rather, we propose that a combination of shape analysis and biological data (e.g., maturity, size and age) is sufficient for stock discrimination. The many factors that influence statolith shape are not completely understood or identified, which complicates interpretation of the results of shape analysis (Arkhipkin, 2005; Sheerin et al., 2022). For instance, some squid species are sexually dimorphic, including *I. coindetii* and *L. forbesii* (Jereb & Roper, 2010). Furthermore, some squids migrate separately in sex-specific schools (Kubodera et al., 1983; Sauer et al., 1992). Neither species are known to migrate separately by sex like other species (e.g., *Todarodes sagittatus*, Jereb et al., 2015; *Doryteuthis gahi*, Arkhipkin & Middleton, 2002), but sexually mature female *I. coindetii* were significantly larger than males, whereas male and female length in *L. forbesii* were similar in our study. Because of these biological differences, we tested for sex-specific differences in statolith shape (Tables S2 and S3). However, results indicated that statolith shape did not differ significantly between males and females.

We did find that statolith shape of *L. forbesii* differed with maturity stage (size or age) in Balearic and Scottish waters, which was consistent with other research showing maturity stage (a proxy for age or size) of squid influencing statolith shape (Wang et al., 2021). Several factors may contribute to shape differences within a species (Arkhipkin & Bizikov, 2000). For example, we found that statoliths of earlier maturity stages (young small squid) differed in shape from later maturity stages (older larger squid), because statoliths from squid of earlier maturity stages were more similar than statoliths from squid of later maturity stages (Tables S6 and S7 and Figure S1). Potentially, statolith shape characteristics need time to develop (Sheerin et al., 2022). Furthermore, diet of *L. forbesii* from the Balearic Sea varied with body size and season, with larger squid migrating into offshore regions, potentially indicating that statolith shape differences between maturity stages can be affected by habitat type or different prey species (Valls et al., 2015). However, even if these differences were less pronounced than shape variations among regions, we recommend to compare only similar life stages for future stock identification by statolith shape analysis.

5 | CONCLUSION

Our findings indicate that statolith shape analysis is useful for stock discrimination on a large geographical scale. While extending the applicability of this method to stock discrimination of ommastrephid squids (*I. coindetii*) with less differentiated statolith forms, we also showed the limitation of this method and recommend combining statolith shape analysis with biological or genetic analysis for further stock discrimination. We found the seasonal occurrence of at least two different stocks of *L. forbesii* in the North Sea, i.e., Celtic Sea and North Sea spawners, and likely also some immigration from Scottish waters. Thus, our results confirm the presence of multiple stocks in the North Sea, which was previously inferred by the presence of different size classes (Gaard, 1987; Holme, 1974; Laptikhovsky et al., 2022; Oesterwind et al., 2022; Pierce et al., 1994, 2005). These results illustrate the advantage of including length distribution in fisheries management. Mixing of stocks from other areas through immigration and emigration (Celtic Sea and presumably Scottish waters) should be considered in sustainable fisheries management, after further investigation. A multi-method approach can be useful for cephalopod stock separation due to the extreme environmental responsiveness in life history traits within this taxon (Sheerin et al., 2022). An improved knowledge of the factors that influence statolith shape would improve our understanding of migration of stocks and thus connectivity of stocks from different areas.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest.

DATA AVAILABILITY STATEMENT

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

ETHICS STATEMENT

There is no approval necessary.

ORCID

Pierluigi Carbonara https://orcid.org/0000-0002-2529-2535
Daniel Oesterwind https://orcid.org/0000-0002-1093-4283

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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