ICES Journal of Marine Science, 2022, **0**, 1–13
DOI: 10.1093/icesjms/fsac128
Original Article

Spatial and temporal variability of spawning and nursery grounds of *Loligo forbesii* and *Loligo vulgaris* squids in ecoregions of Celtic Seas and Greater North Sea

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The inshore commercial squids, *Loligo vulgaris* and *L. forbesii*, co-occur in the ecoregions of Celtic Seas and Greater North Sea but the spatio-temporal structure of their spawning ranges is poorly understood. To help solve the problem, data sets collected during the last 30 years by British, German, French, and Irish scientists, as well as observations from multinational Citizen Science, were combined. Spawning grounds of *L. forbesii* were found to form an external semi-circle around the spawning grounds of *L. vulgaris*, with the latter being centred on the English Channel and southernmost North Sea. The nursery grounds of both species appear to coincide with the respective spawning grounds, though *L. forbesii* makes much wider use of the North Sea. Seasonally, the position of the spawning grounds of both species is driven by the local temperature regime, although this is possibly subject to interannual variability. Spawning of both species begins around November and gradually progresses eastward following favourable currents and increasing water temperatures. Spawning in both species is mostly over by July, though some egg masses persist until August–November. Nursery grounds follow the same seasonal shift from west to east, at least in *L. forbesii*.

Keywords: English Channel, life cycle, *Loligo forbesii*, *Loligo vulgaris*, North Sea, reproduction, spawning.

Introduction

Veined squid *Loligo forbesii* and European squid *L. vulgaris* are the two main commercial squid species co-occurring on the northern shelf of the European continent, with very similar ranges from Northwest Africa to north European waters and the Mediterranean. The range of *L. vulgaris* extends poleward to north of Ireland, north of Scotland, the Kattegat, and possibly southern Norway. *Loligo forbesii* extends slightly farther north, to the Orkney Is. and to central Norway (Jereb *et al.*, 2015; present study). *Loligo forbesii* is thought to spawn in slightly deeper waters, usually 10–150 m occasionally at 300–500 m, and even as deep as ~700 m in the warmest part of its range, such as the very steep shelf slopes of the east Aegean Sea (Salman and Laptikhovsky, 2002). *Loligo vulgaris* lay eggs at a depth of 2–120 m, and mostly in waters shallower than 50 m (Jereb *et al.*, 2015). However, even if some differences in spawning grounds are known, it is assumed that there are substantial spatial and temporal overlaps in the reproductive ranges of both species (Martins *et al.*, 1997; Oesterwind *et al.*, 2010).

The biology of these squids was first studied by Aristotle, with the first research on egg masses in the eighteenth century by Iohann Bohadsch (1761) and, since then, the reproduction of these squids has been given much attention (e.g. Faussek, 1901; Lo Bianco, 1909; Grimpe, 1925; Naef, 1928; Jecklin, 1934; Tinbergen and Verwey, 1945; Mangold-Wirz, 1963) and numerous diverse publications from the last hundred years were thoroughly and exhaustively summarized in an ICES Cooperative Research Report (Jereb *et al.*, 2015). As a result, these two species might be expected to be among the most studied squids in the world, with respect to their reproductive biology. However, we still have little idea of the seasonal distribution of spawning and nursery grounds within the oceanic water circulation systems that these species inhabit.

Individual aspects of reproduction of these species (fecundity, fertilization, egg mass morphology, and egg development) are well known, along with population aspects (seasonality of spawning, growth and maturation rates, size at maturity and its variability) because these have been the subject of numerous past studies (e.g. Pierce *et al.*, 1994; Collins *et al.*, 1995;

Received: March 26, 2022. **Revised:** June 13, 2022. **Accepted:** June 15, 2022

Moreno *et al*., 2002; Oesterwind *et al*., 2010). Nevertheless, despite these advances, spatial aspects of reproduction within the distribution ranges of *L. forbesii* and *L. vulgaris* remain largely a mystery. This partly arises because neither species is reported separately in the landings of longfin squid in north European waters. In addition, during past research surveys, adult squids were often measured but sex and maturity were not assigned, hence there is insufficient information on the timing and location of spawning in these squids. Both species are known to reproduce during many months of the year, but it is unlikely that different squids lay eggs at the same location in different seasons (though this is not impossible), meaning that the timing of egg laying appears to be highly variable between areas. Unambiguously distinguishing between egg masses of both loliginids in the field without expensive genetic work has just been solved (Laptikhovsky *et al*., 2021), but this requires egg size to be measured and approximate stage of embryonic development to be estimated, and so it still requires collection of a few egg strings. However, because of this long-standing difficulty, the spatial distribution of egg masses and its seasonal variability has not been systematically investigated. Finally, little information is available on the spatiotemporal distribution of early life stages (nursery grounds), a time-period during which the recruitment strength is "shaped", due to the fact that, until now, juvenile squids have usually been assigned as *Loligo* spp. in surveys.

This study aims to cover the "spatial and seasonal gap" in our knowledge of reproduction in *L. vulgaris* and *L. forbesii*, specifically, to delimit reproductive ranges (spawning grounds and nursery areas) of these two species in the Celtic Sea, Irish Sea, and Greater North Sea. We carry this out based on historical samples and new data, including Citizen Science observations.

Material and methods

To achieve our aim, we explored all available materials collected by French, German, Irish, and UK scientists using diverse approaches and protocols during the last ~30 years, from 1990 to 2021.

During research surveys and sampling of landings, depending on the data collection protocol, squids might be measured to either within 1 mm, or to the nearest 5 mm below, whereby a squid of 27 mm DML would be allocated to the 25-mm-size class that contains squids from 25 to 29 mm DML. Because of this, all squid length data, regardless of how individuals were measured, were aggregated by 5-mm-size classes, and the size class of 30 mm DML encompassed all squids of 30–34 mm DML. When biological analysis was performed, maturity was assigned using either the ICES WGCEPH maturity scale (ICES, 2010) or modified Lipiński's (1979) maturity scale (Lipiński and Underhill, 1995). For the purposes of this study and to avoid confusing the different stages, all females containing some ovulated ripe eggs in the oviducts were considered mature.

Presence / absence of different life stages related to spawning and nursery grounds (i.e. egg masses, paralarvae, juveniles, and mature females) in *Loligo* spp. were established on the basis of 13 037 separate fishing hauls carried out on research vessels from England, France, Germany, Ireland, and Scotland. As there was a variety of fishing gear deployed, we used these data only to confirm the presence of a particular life stage of either species in each area. These hauls resulted in captures of 6 008 paralarvae up to 20 mm DML (all assumed to be identified to genus level), 72 218 juveniles with a reported DML between 25 mm and 60 mm DML (3 419 *L. forbesii*, 28 *L. vulgaris*, the rest being *Loligo* spp.) and 560 mature females (497 *L. forbesii* and 63 *L. vulgaris*).

Presence / absence of mature females in commercial landings was established from monthly samples taken at Aberdeen, the Minch, Moray Firth, Fraserburgh, Shetland Islands, and Rockall Bank (Scotland) in 1990–2001 and 2006–2008 (*L. forbesii* $n = 35\,234$ and *L. vulgaris* $n = 10$), Kiel (Germany) in 1992 (*L. forbesii* $n = 6$ and *L. vulgaris* $n = 47$), Isle of Man in 1991 (*L. forbesii* $n = 24$), Cork, Dingle, Dunmore East, Killibegs, Kilmore Quay, Schull, Youghal (Ireland) in 1991–1993 (*L. forbesii* $n = 2\,609$), Port-en-Bessin (France) in 1993–1998 (*L. forbesii* $n = 1\,339$ and *L. vulgaris* $n = 1\,589$), Faroes Is. (Denmark) in 1991 (*L. forbesii* $n = 59$), Plymouth, Looe, and Brixham (south England) in 1991–2017 (*L. forbesii* $n = 239$ and *L. vulgaris* $n = 221$), Bangor (Wales) in 1994 (*L. forbesii* $n = 343$). This information (*L. forbesii* $n = 39\,853$ and *L. vulgaris* $n = 1\,867$) included 4 609 mature female *L. forbesii* and 94 mature female *L. vulgaris*. We also used information (e.g. ID photos of internal organs) provided upon request from recreational Lithuanian squid fishermen from Norway "Kalmarų žūklė Norvegijoje" (https://www.facebook.com/groups/1135839429939981/) and recreational squid fishers from the United Kingdom "Squid fishing UK" (https://www.facebook.com/groups/774425619306338). Presence of mature females of a particular species was used for tentative allocation of unidentified egg masses to one of these two squids rather than for mapping spawning grounds because the distribution of adult females might be much wider than the area where they actually lay eggs.

To map the position of spawning grounds, we used data on occurrence of egg masses, as observed by recreational divers and reported online. They were extracted from the Facebook pages of UK Cephalopod Reports (https://www.facebook.com/groups/1772714999 700580/), Blekksprutobservasjoner i Norge (https://www.facebook.com/groups/669716393533330), Inktvis waarnemingen Nederland/België (https://www.facebook.com/groups/1915579675410208) and Tintenfisch-Sichtungen Deutschland (https://www.facebook.com/groups/1011071792400550). All these groups are parts of the Cephalopod Citizen Science Project. More observations were found on the French web page Base pour l'inventaire des observations subaquatiques (https://bioobs.fr/les-especes/especes-recherchees/), and international web pages iSpotNature (https://www.ispotnature.org/communities/uk-and-ireland) and Beach Explorer (https://www.beachexplorer.org/en/). With respect to the latter two web pages, as egg masses are negatively buoyant, we assumed that any washed onshore were laid close to where they were found, perhaps not farther than a few dozen kilometres. Citizen science monitoring of cephalopod presence using these methods occurred all year round. Despite some seasonality in this activity, caused by day length, weather and water temperature, no important gaps appeared, as exemplified by observations in winter months by the UK Cephalopod Reports Facebook group (Table 1).

In addition, information on 176 egg masses of *Loligo* spp. observed in January–September 1995–2020 was downloaded from the Seasearch database (Seasearch, 2021a–f). Only observations identified as *Loligo* were taken into consideration, while "Loliginidae" were ignored as likely also containing *Alloteuthis*.

Table 1 Monthly number of Facebook posts on cephalopods observed in the UK waters/shores (all species and life stages combined) by the UK Cephalopod Report during July 2019 to October 2021.

Month	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
Number of reports	103	63	37	43	27	39	35	39	77	80	57	123

Other posts on the web page were ignored.

In total, 378 egg masses and groups of egg masses were photographed/reported by the public and shared to Citizen Science projects and Seasearch (2021a–f), four of which had large adult *L. vulgaris* inside the frame and one of which was with an adult *L. forbesii*. To this online information were added data on egg masses published during earlier studies, $n = 57$ including seven records from 1987–1989 (Lum Kong *et al.*, 1992; Collins *et al.*, 1995; Martins, 1997; Craig, 2001; Emery *et al.*, 2001; Lordan and Casey, 1999; Laptikhovsky *et al.*, 2021).

While summarizing the data, we used the following approach:

(1) *Loligo* egg masses that were not studied by professional scientists were not allocated to a particular species; they were combined into *Loligo* spp., apart from those that were photographed with identifiable adult spawners.
(2) Paralarval *Loligo* are very difficult to identify so all paralarvae were combined into *Loligo* spp. even if these had tentatively been identified in the database.
(3) Early stages of squids identified as "Loliginidae" were excluded as likely containing *Alloteuthis* together with *Loligo*.
(4) The juvenile stage included squids between 25 and 60 mm DML, in order to exclude all squids which might be close to maturity.
(5) Females were considered mature if they had reached at least stage 3a of the ICES scale (ICES, 2010), which corresponds to an ovary containing a high proportion of large turgid amber-coloured oocytes (≥2 mm), with plenty of oocytes in the oviducts. Females at maturity stage 3b were also included. These stages correspond to stages 4 and 5 on Lipinski's scale.
(6) The inshore water temperature in the areas of interest (North Sea, English Channel, Irish Sea, and north of Scotland—https://en.climate-data.org/) is highest in July–October with slight regional variations and this period was defined as oceanographic summer. The water temperature is lowest in January–April, which was defined as oceanographic winter. May–June and November–December represent oceanographic spring and autumn respectively.
(7) Areas of paralarval occurrence were considered to be early nursery grounds and areas with juveniles up to 60 mm DML were considered late nursery grounds.
(8) Seasonal distribution of mature females was used as a proxy for tentative allocation of unidentified egg masses to each species but was not used as a proxy for spawning grounds if no egg masses were found, as females might migrate elsewhere to lay eggs.

All datasets were plotted seasonally, with oceanographic summer and winter split into two bimonthly periods. Seasonal spawning grounds were defined based on occurrence of egg masses. Regarding identification, we assumed the egg masses had been laid by mature females of whichever species was captured nearby in the same or previous month. The "average" distribution of nursery grounds was defined from captures of paralarvae and early juveniles, and the species identification was inferred, where possible, from the nearest proximity of identified egg masses.

Monthly mean seabed temperature data from 2012 to 2020 were downloaded from Copernicus Marine Service Information (CMEMS) (https://marine.copernicus.eu/access-data). Data were imported into R (R Core Team, 2021) and converted into raster files (Hijmans, 2022). Data were subsetted by month and average values of months across all years were combined and exported into separate raster files. Raster files were imported into ArcGIS (ESRI, 2016) and converted into images for the different months.

Results

Mature squid

Loligo forbesii

In January–February, mature female *L. forbesii* were distributed in the northern and central North Sea (where some mature *L. vulgaris* also occurred), west and south of Ireland down to Cornwall, as well as on the Rockall Bank. In these months, mature females that were "full of eggs" also appeared in catches of recreational fishermen from western and central Norway [Tomas Nenius, Donatas Eicas (Kalmarų žūklė Norvegijoje) pers. comm.]. During this period, mature females of *L. forbesii* were landed in Scotland, south Ireland, in the English Channel (Figure 1). Mature females were recorded in landings from the different areas east, north and west of Scotland (e.g. Aberdeen Bay, Sula Sgeir, Flannan Isles, etc.). Irish landings came from west of Ireland, the Celtic Sea, and Irish Sea. The source of landings in the English Channel (Port-au-Bessin) is not clear, but these are not thought to have come from remote waters.

Later, in March–April, mature females, as demonstrated by survey data, were recorded mostly west and north of Ireland, around Scotland and at Rockall. They were occasionally present in the Celtic Sea and in the westernmost English Channel and north Cornwall coast. Recreational divers and fishers of Norway reported the presence of large (divers) and mature (fishers) squid of this species in March–May. Mature females were recorded among the landings from surrounding waters in Scotland, and from commercial catches north, west and south of Ireland, as well as in the English Channel.

In May and June, a few mature females of *L. forbesii* were reported from research surveys in the north of Ireland and around Scotland. Mature females were also landed in France and Scotland, with Scottish landings coming from the north and west of Scotland.

In July–August, despite extensive sampling, few mature female *L. forbesii* were reported from research surveys; all occurrences were in Scottish waters or, more rarely, in the

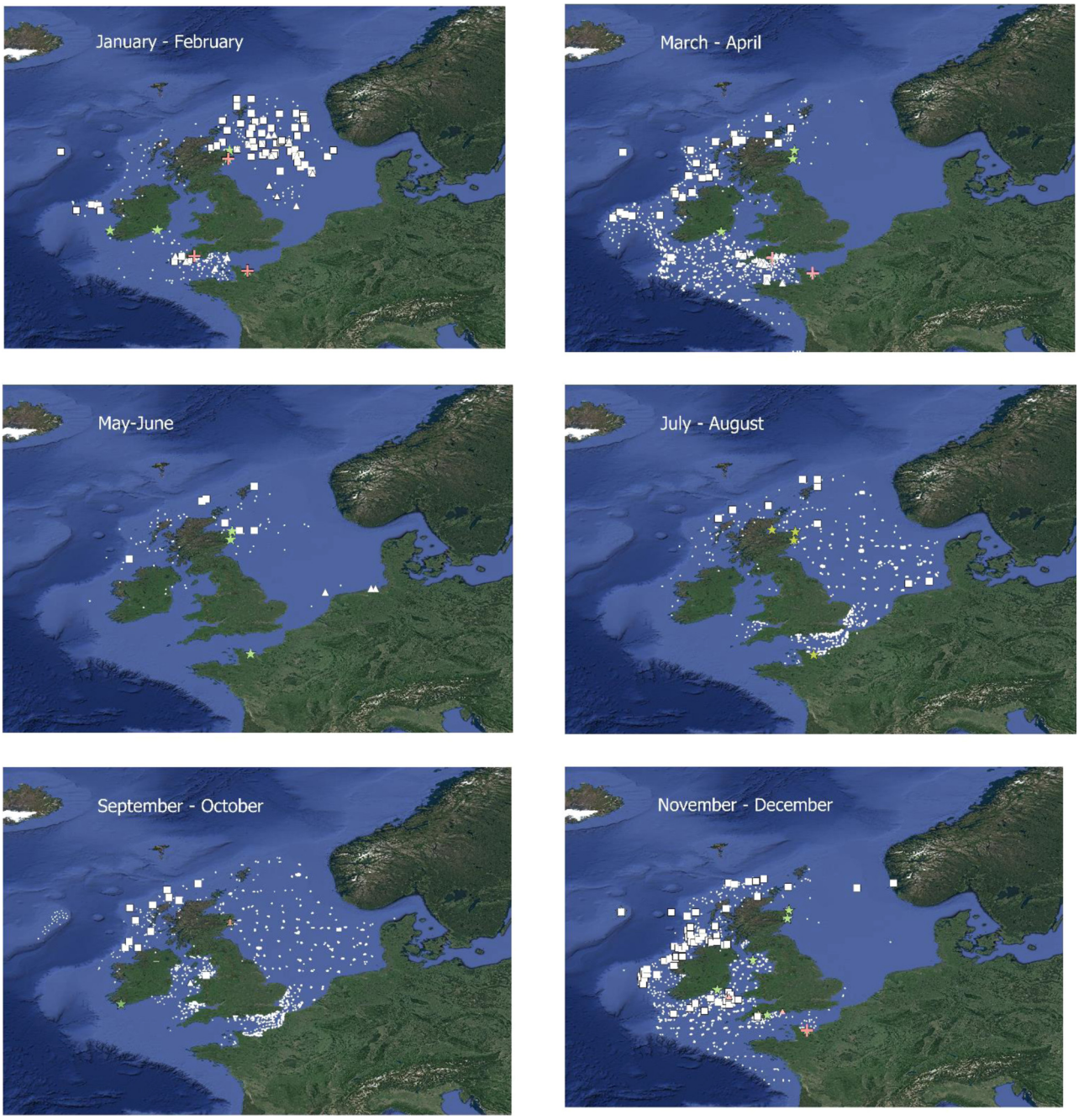

Figure 1. Distribution of mature females. Squares—*L. forbesii*, triangles—*L. vulgaris*, stars—landings of mature female *L. forbesii*, crosses—landings of mature female *L. vulgaris*, and dots—position of studied hauls.

southern North Sea. They also occasionally occurred in the landings in Scotland (e.g. Aberdeen Bay, North Rona, and Solan Bank) and in the English Channel (Port-en-Bessin).

Later in the oceanographic summer, in September–October, mature *L. forbesii* females were found in research surveys north of Ireland and Scotland, and were also landed in local ports from west of Ireland, Rockall Bank (although they were absent at this time during surveys), north, east, and west of Scotland. Norwegian recreational fishers reported that October was when *L. forbesii* began to appear in inshore waters but photos of their internal organs confirmed that squids captured there in October were immature. There was a single occurrence of a mature *L. forbesii* female in the eastern Irish Sea at this time.

Records of mature female *L. forbesii* increased in November–December, occurring all around Ireland and the north of Scotland, at Rockall, and they were also documented by recreational fishers on the Norwegian coast. They were landed in Scotland, Isle of Man, Ireland, England (Plymouth and Brixham), and France (Port-en-Bessin), and were caught in waters all around Scotland, the Irish Sea, the west of Ireland, the Celtic Sea, and the western English Channel.

Loligo vulgaris

Mature females of *L. vulgaris* were present over a much less extensive part of the study area than were *L. forbesii*, and these were recorded in a much lower number of samples, being

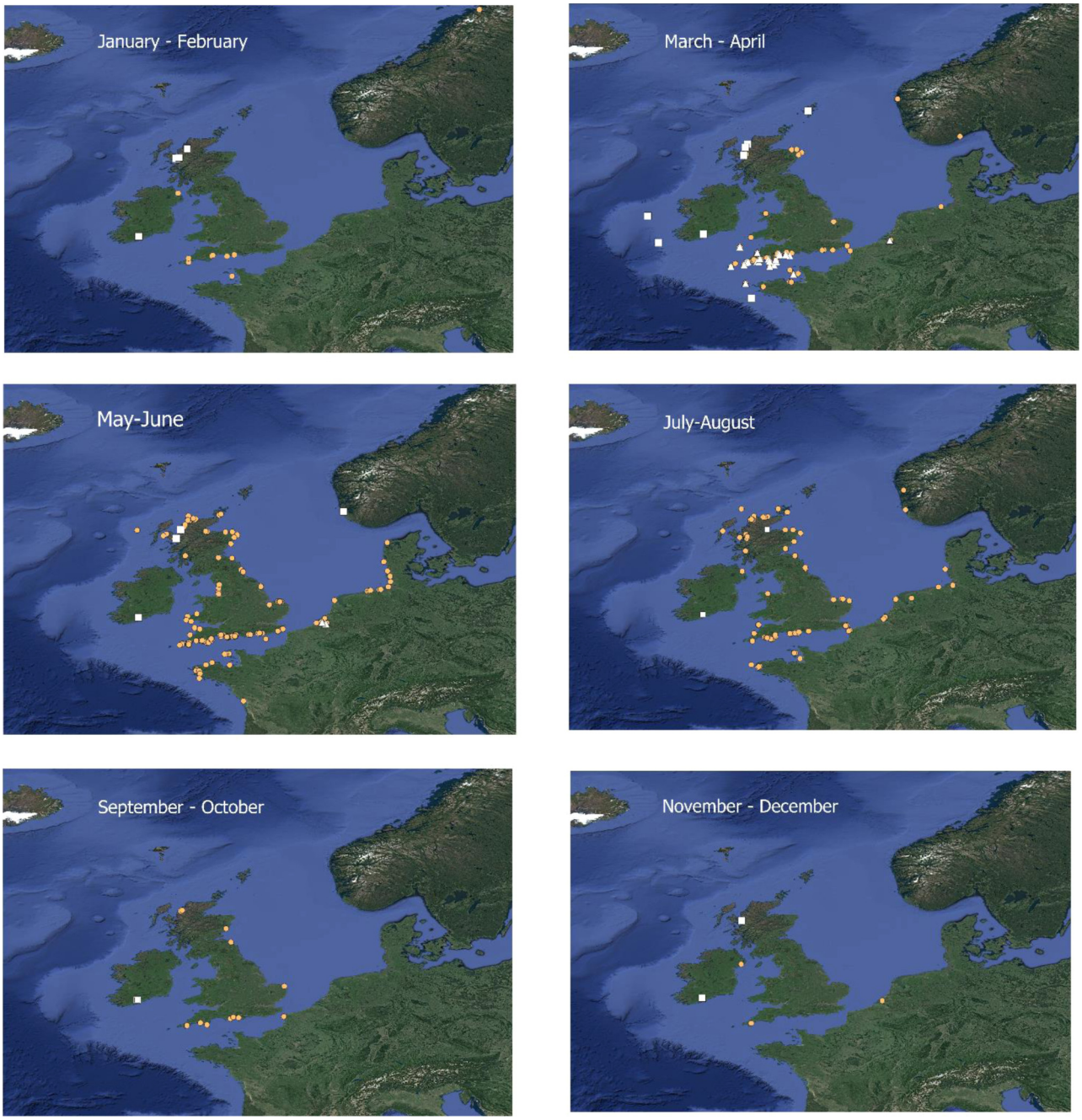

Figure 2. Distribution of egg masses. Circles—*Loligo* spp., squares—*L. forbesii*, and triangles—*L. vulgaris*.

restricted to the Irish Sea (few observations), English Channel, and central and southern North Sea.

In January–February, mature female *L. vulgaris* occurred mostly in the western Channel, where they were landed by commercial and recreational fishers, with further observations made on research surveys at several stations in the central and northern North Sea, and with small numbers observed in the landings in eastern Scotland. In March–April, surveys in the western English Channel recorded mature females at many stations and landings also occurred at ports on both sides of the English Channel.

Data for May–June were not abundant; mature females were captured in a few research samples coming from the southern North Sea. Simultaneously, during this period (30 April–2 June), large squid of this species were photographed by recreational divers, together with egg masses off the Netherlands (Eastern Scheldt and an unspecified location). Records of these supposedly mature squids are not mapped on Figure 1 as they were not dissected for a maturity estimate, but the respective egg masses were included in Figure 2.

In July–October, despite extensive sampling, mature female *L. vulgaris* were seen only at a single station in the Irish Sea, plus there was only a single female found in the landings from the Aberdeen area in October. They re-appeared at the end of November when individuals of this species began to be landed at Port-en-Bessin (English Channel) and captured by

recreational fishers in the western English Channel (Weymouth, UK), as well as occasionally farther west, in the Celtic Sea.

Egg masses

In the beginning of oceanographic winter (January–February), scarce *Loligo* egg masses were observed from so-called "western waters" (from west of Scotland to the western English Channel) and central Norway, with those seen in shallow waters along Scottish and Irish shores being identified as *L. forbesii*. The English Channel egg masses were not identified to species. Later in this season (March–April), spawning grounds extended in shallow waters along all shores of the North Sea, with both species having distinctive spawning areas. Egg masses were distributed along the shelf from deeper waters off Brittany to the west of Ireland and then from Scotland through Orkney Is. to Norway (Figure 2). All identified eggs in this area belonged to *L. forbesii*. Unidentified Norwegian egg masses were tentatively assigned to *L. forbesii* as very large squid of this species, some of them mature, were reported there between November and May, although they were not photographed at the moment of egg laying. Meanwhile, *L. vulgaris* was never reported close to central Norway. In the southwestern part of this area, egg masses of *L. forbesii* tended to occur in relatively deep waters, closer to the shelf edge. Occurrence of the egg masses in the south was centred in shallow waters of the western English Channel expanding into the Celtic Sea and occasionally along southern shores of the North Sea from Belgium to Germany and northwards in the North Sea as far as the coast of Norfolk. All identified egg masses in the Channel belonged to *L. vulgaris*.

In spring (May–June), egg masses of *L. forbesii* were observed around Scotland and Ireland and freshly laid eggs were filmed together with large individuals of this species off Norway (Figure 2). In the south of the studied area, the spawning grounds extended along European shores all the way from Brittany and Cornwall to Denmark, and some of these egg masses were identified as belonging to *L. vulgaris*. Unidentified egg masses were found all along the east coast of Britain, thus connecting the northern spawning grounds (of *L. forbesii*) with the southern spawning grounds (*L. vulgaris*).

The distribution of egg masses in early summer (July–August) was similar to that in May–June, although there was some degree of a gap between Durham and Lincolnshire on the east coast of England, where egg masses had been more in evidence during the previous two months. Some egg masses laid around Scotland and Ireland were identified as belonging to *L. forbesii*. In Germany and Norway, the last egg masses of the year were seen in August. The Norwegian egg mass was seemingly freshly-laid, while the observation made off Germany was of an egg mass, which contained well-developed embryos.

By the end of the summer (September–October), the occurrence of egg masses strongly declined everywhere, some *L. forbesii* masses were identified on the south coast of Ireland. *Loligo* egg masses were also recorded on the south and east coast of Britain and in north and east Scotland, with a single finding in northern France. Egg masses were rarely seen in November–December, apart from on the west coast of Scotland, Celtic Sea (both *L. forbesii*), Irish Sea, and south Cornwall. The only *Loligo* egg mass recorded during this period in the southernmost North Sea, off the Netherlands (Grevelingenmeer), was freshly laid.

Juveniles and paralarvae

In January–February, paralarvae and juvenile squids occurred at many stations north of Scotland and Ireland and in the central-northern North Sea, and all those identified were *L. forbesii* (Figure 3). There was no visible difference between the spatial distribution of paralarvae (up to 25 mm DML) and juveniles (25–65 mm DML), i.e. between early and late nursery grounds but, interestingly, many of the observations were made quite a distance offshore. Larvae and juveniles were mostly absent in the western English Channel. In March–April, early stages were farther inshore and occurred in two distinctive clusters; one was north of Ireland and north of Scotland, including the Shetland Islands. Another was in the southern Celtic Sea and westernmost English Channel, with juvenile *L. forbesii* also captured at the shelf edge south of Ireland. By May–June, the zone of distribution of juveniles moved eastward and clockwise around northern Scotland and into the northern North Sea (no paralarvae were found at this time); however, sampling intensity was also relatively low at this time of the year.

In July–August, both juvenile squid and paralarvae occurred in the North Sea and English Channel but were absent in the west and north, apart from at Rockall Bank, where both of them were recorded. Paralarvae were not discovered in the English Channel: instead juvenile populations of both species were sampled here at coastal stations. Meanwhile, the entire North Sea was populated by juvenile *L. forbesii*, whereas *L. vulgaris* were not identified there. In September–October, unidentified juveniles were not commonly observed in the study area, apart from on the north coast of Scotland and at Rockall Bank, where paralarvae, unidentified juveniles and juvenile *L. forbesii* were observed.

Paralarvae were more widespread, occurring in the latter locations, plus the Irish Sea, Bristol Channel, and south coast of Britain. *Loligo forbesii* juveniles occurred west and north of Britain, from near the Bristol Channel to the north of Scotland (one station) and at many stations on Rockall Bank. Juvenile *L. vulgaris* were found from the Bristol Channel to the east of the English Channel. Juveniles of both species were mostly found at coastal stations at this time of year. In November–December, paralarvae and juvenile *L. forbesii* were extremely abundant around all coasts of Ireland and north of Scotland. Paralarvae tended to be more distributed to the north of this range and juvenile squid to the south of it. An exception was the English Channel, where hardly any juvenile squid were found, and no paralarvae were seen at this time. Early life stages were also absent from the few stations sampled in the northern North Sea in November–December.

Discussion

As squid are highly mobile animals and Loliginidae are known to migrate from offshore foraging grounds to inshore spawning habitats (e.g. Holme, 1974; Sauer and Smale, 1993; Sims *et al.*, 2001; Arkhipkin *et al.*, 2004; Shashar and Hanlon, 2013), the location of spawning areas might be better indicated from the occurrence of egg masses rather than from the distribution of mature females. However, egg masses are difficult to

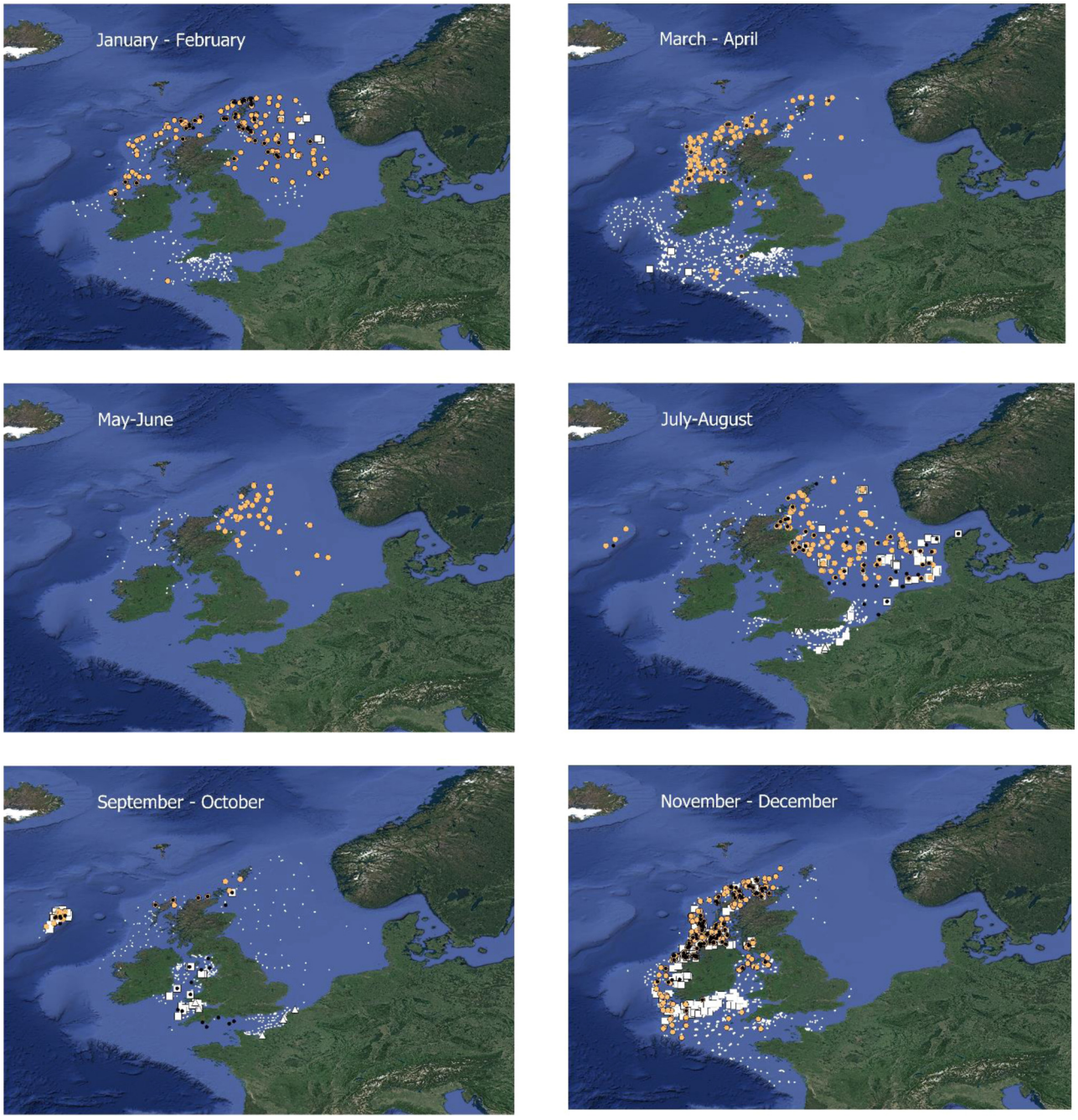

Figure 3. Distribution of paralarvae and juveniles. Black dots—unidentified paralarvae, circles—unidentified juveniles, squares—juvenile *L. forbesii*, triangles—juvenile *L. vulgaris*, and dots—position of studied hauls.

identify to species level from underwater observations, so in the interpretation of our results, we still have to rely on the presence of mature squid of a particular species at or close to the spawning grounds at the relevant time of year. The data presented in this study demonstrate that *L. forbesii* dominates numerically and also predominates spatially in the studied area, reproducing in deeper waters from the outer shelf edge of the Celtic Sea to the west of Ireland, on Rockall Bank, the waters around Scotland and east to the central North Sea and coast of Norway. Such a predominance is consistent with an observed shift northward of both the *L. forbesii* species range and centre of abundance in recent decades (Chen *et al.*, 2006; Oesterwind *et al.*, 2022).

Comparative analysis of data on the distribution of egg masses, mature females, and juveniles allowed delineation of two major reproductive areas (i.e. spawning and nursery grounds): northern and southern grounds (Figure 4).

Northern spawning grounds occupy the waters around Ireland, north England, Scotland, and western Norway and are used exclusively by *L. forbesii* as all egg masses identified there belong to this species. The reproductive area of *L. forbesii* also extends farther south, in the deeper waters of the Celtic Sea and the outer shelf edge of the Bay of Biscay. Seasonal variability in the distribution of egg masses and mature females allows us to assume that spawning activity expands eastward into the North Sea from November–December onwards, as

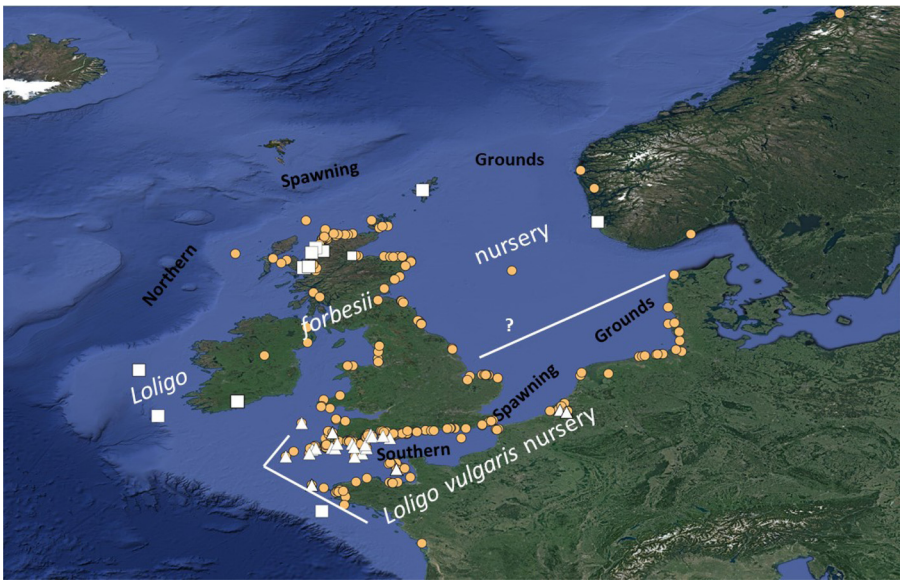

Figure 4. Structure of reproductive area of *Loligo* spp. in north European waters (symbols as in Figure 2). Position of spawning and nursery grounds. Symbols as in Figure 1.

well as southwards and westwards around Ireland from this time of year. Mature females and egg masses were present in most months of the year along the coast of Scotland, while juveniles (< 60 mm ML) were found among the discards of fishing vessels off the Moray Firth in July–September, which were probably descendants of the main winter spawning period in this part of the range (Hastie *et al.*, 2009).

Holme (1974) hypothesized that juvenile *L. forbesii*, hatched from eggs laid in the western English Channel in December–January, appear off Plymouth around May, and gradually migrate eastward foraging in summer in the eastern Channel and southernmost North Sea, off the Netherlands. Squid return to the western approaches in autumn with females becoming mature in November and spawning in December–January. Peak abundance of *L. forbesii* at Plymouth during this return migration occurs earlier in warmer years, varying from August to December (Sims *et al.*, 2001). Our data generally do not contradict this scheme and do not show any consistent presence of mature female *L. forbesii* in the English Channel and southern North Sea between July and October. Some scarce mature females captured off German shores in summer might be related to the spawning grounds off Scotland and southern Norway, though alternatively, these might be some early maturing squids from the migration through the English Channel. However, due to the absence of unambiguous egg masses of this species in the English Channel (Laptikhovsky *et al.*, 2021), we suppose that spawning in *L. forbesii* takes place in deeper waters of the outer shelf and upper continental slope of the Celtic Sea, rather than in the Channel itself. A migratory life style in *L. forbesii* means that isolated breeding groups are absent, apart from at the Azores and Faroe Is. (Brierley *et al.*, 1995; Shaw *et al.*, 1999; Göpel *et al.*, 2022) and Rockall Bank; the latter shows significant genetic differences only sometimes, but ecological stocks have been described in this species based on statolith shape analyses (Sheerin *et al.*, 2022). This means that regional groups are identifiable and these become established over the same timeframe as the statolith shape development (Sheerin *et al.*, 2022).

The eggs of *L. forbesii* develop normally at temperatures as low at 8°C, although egg development would take as long as 140 days in such conditions (Gowland *et al.*, 2002). This means that the climate of waters off the west of Ireland are within the range to permit year-round reproduction. In Norwegian waters, where egg masses occur from January to August, temperatures seem to be too low for normal development between January and April, when pre-spawning mature females are also captured there in numbers by fishermen. It is possible that eggs of *L. forbesii* might simply pause their development at temperatures between 6°C and 8°C as no development apparently occurs at 6°C (Craig, 2001). Such a pause might also explain all year-round occurrence of egg masses around Scotland, where winter temperatures are too low for development (Figure 6). The differences in temperature regime might also explain a visible shift of spawning peak eastward, due to western waters being warmer than in the east in the oceanographic winter season (i.e. January–February, Figures 1 and 2).

Overall, the spawning and nursery grounds of *L. forbesii* are likely defined by the Shelf Edge Current, travelling along the shelf edge from Brittany to the north of Scotland and on towards the North Sea via Atlantic Water currents (Figure 5).

Irish Coastal Currents and the complicated pattern of water circulation in the northern and central North Sea (the Fair Isle Current, Scottish Coastal water, Central North Sea Water, and Norwegian Coastal Current) provide numerous stable gyres (Paramor *et al.*, 2009) supporting retention of early stages across the nursery grounds. The Shelf Edge Current provides an uninterrupted link between spawning grounds in western France, the British Isles and north to Scotland. Such a current-defined range structure is known for other loliginid squid, including *Doryteuthis gahi* (Arkhipkin *et al.*, 2006).

Southern spawning grounds extend from the eastern shallow part of the Celtic Sea and Bristol Channel to waters off the Netherlands and Germany. These spawning grounds are mainly used by *L. vulgaris*, though reproduction of *L. forbesii* is also possible there, e.g. in the westernmost Channel and off

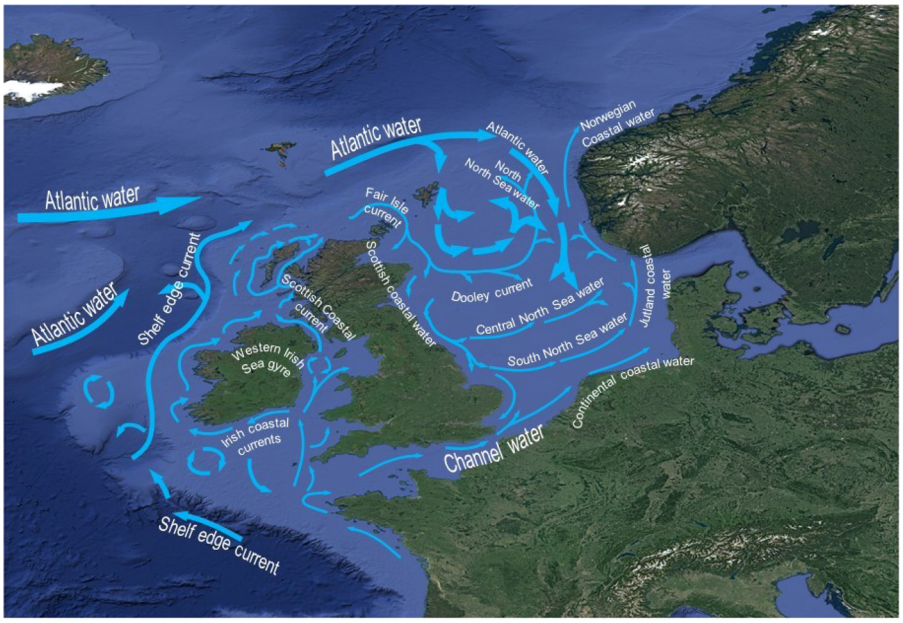

Figure 5. Oceanographic structure of shelf waters on the north European shelf. Scheme of subsurface water circulation.

German shores. In particular, eggs of *L. forbesii* were found at Helgoland in July 1921 (Grimpe, 1925) and a more recent observation of an unidentified egg mass off Germany in August 2009 was also close to the spawning grounds of *L. forbesii* in southern Norway. Hence, there is no visually distinguishable gap between the northern spawning grounds (*L. forbesii*) and southern grounds (mostly or entirely *L. vulgaris*).

Mature squid captured by recreational and commercial fishers in the Western Channel during November–December were all *L. vulgaris*, maturing in October and mature by January. This is supported by numerous photographs posted on Facebook by recreational squid fishers, none of which included *L. forbesii*. However, mature females of *L. forbesii* were fished at this location in March, when no egg masses of this species were identified. There might be a gradual seasonal shift of spawning eastwards, as occurs in the northern grounds off Ireland and Scotland. It is also possible that the spawning grounds of *L. forbesii* extended farther south into the English Channel in the past, but retreated northward with warming sea temperatures in recent decades. However, the Channel is still used as foraging grounds by pre-spawning females of *L. forbesii*, and this area is possibly also used as a migration route into the southernmost North Sea.

Loligo vulgaris is known to spawn in the English Channel between November and April, peaking in February (Moreno *et al.*, 2015), which is consistent with our data. Some egg masses likely belonging to this species are already seen by divers in December–January, but the strong increase in their records occurs later, in March–April, supporting the idea that peak spawning takes place around February–March. After this coldest period of the year, the spawning of *L. vulgaris* extends farther east up the coast of the Netherlands as well as northwest, into the Bristol Channel. In May–June, the southern zone of distribution of mature females reaches Germany (at least they were recorded there in 1992–1993), but only eggs observed off the Netherlands could reliably be identified as *L. vulgaris*. Spring-summer spawning (from May to July–August, peaking in May) in the southern North Sea, up to the Danish coast, was described in the mid 20th century (Grimpe, 1925; Tinbergen and Verwey, 1945) but recent research surveys of Cefas (2014–2021) failed to find mature female *L. vulgaris* there in July–August. In recent years, the unidentified egg masses observed in summer off the German coast might be an "extension" of this spawning, as egg development in *L. vulgaris* takes between 26 and 45 days at 12–22°C (Mangold-Wirz, 1963), but, these also might belong to *L. forbesii* or to a mixture of both species.

The nursery grounds of *L. vulgaris* generally coincide with the spawning grounds, at least we found no evidence of early juvenile presence outside the area of observed egg masses. This area is shaped by an eastward flow of the warm Channel Water originating in the Bay of Biscay and gradually extending into the Continental Coastal Water in the southern North Sea (Figure 5). This flow is limited from the north, first by the shores of south England, then by the cold flow of the South North Sea Water (Figure 6). The spawning area also expands into the Bristol Channel along the eastern flow of the anticyclonic circulation in the Celtic Sea (Paramor *et al.*, 2009; Figure 5).

A gradual extension of the *L. vulgaris* spawning grounds from the western Channel in March–April to at least as far as the Dutch, and likely German shores, in May–June or even later, generally occurs following the already-mentioned longitudinal currents flowing from the Celtic Sea through the English Channel and along the European mainland coast up to Jutland.

Distinct seasonal temperature changes are observed in the English Channel and North Sea. Along the line connecting the westernmost English Channel and the southeastern North Sea, winters become progressively colder and summers warmer, with peaks of both low and high temperatures occurring earlier in the season (Figure 6). Notably, for 6 months of the year (from May–October) there is a strong gradient in warmer and cooler areas in the North Sea, which is similar to the delineation of the "northern" and "southern" grounds in Figure 4.

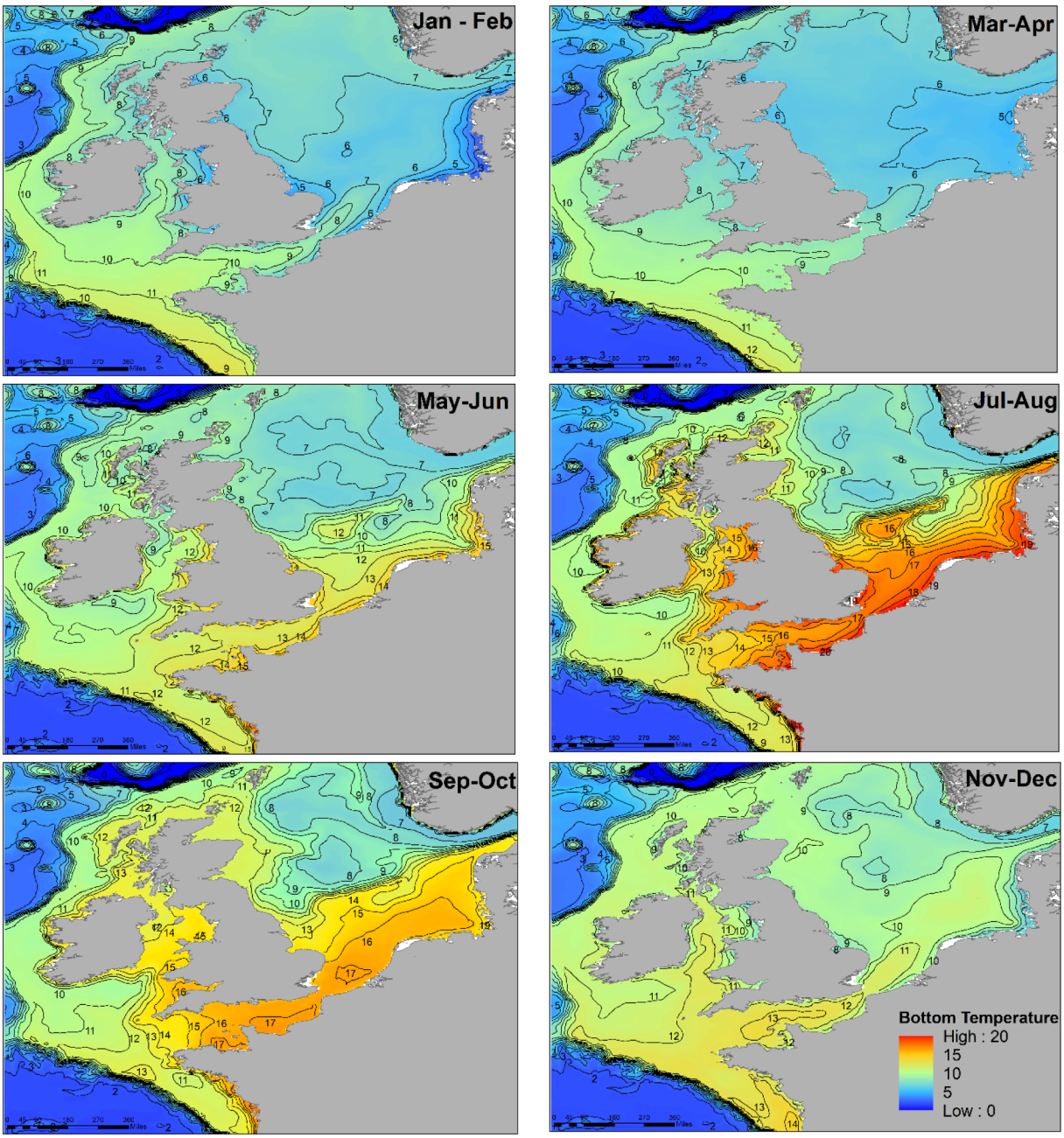

Figure 6. Seasonal changes in bottom temperatures.

As normal embryonic development of *L. vulgaris* takes place at 12–24°C and the eggs do not develop and die at 10°C (Villanueva *et al.*, 2003; Sen, 2005), it can be deduced that only the environment of the western English Channel is suitable for reproduction all year round. Temperatures in the central and eastern English Channel, as well as in the southern North Sea (from Den Helder to Bremerhaven), descend to a mean of ~10°C in January–April. Therefore, spawning might only start in this area in late April–May, depending on the year, and favourable temperatures only remain in the North Sea until October–November. This difference between west and east Channels might explain the situation of the two observed spawning peaks in *L. vulgaris*. The freshly laid egg mass found at Grevelingenmeer Netherlands in November 2020 probably was not the beginning of a new spawning season (2020–2021), but the very end of the previous one (2019–2020).

It should be kept in mind that this northernmost population of *L. vulgaris* might potentially have slightly higher tolerance of cold temperatures, with eggs able to survive at 10°C (or even below this temperature), at least for some weeks, as happens in the common cuttlefish, *Sepia officinalis*, living in the same waters and generally having almost the same distribution as *L. vulgaris* in the Atlantic and Mediterranean. Development of cuttlefish eggs ceases at temperatures below 9°C, but when the temperature increases, embryogenesis restarts (Bloor *et al.*, 2013). Therefore, we may not exclude a hypothesis that *L. vulgaris* reproduces in the English Channel all year round with its eggs pausing development during a few weeks when water temperatures are too low. Farther east, only

spring-summer spawning is possible as winters are longer and colder. We suggest that this pattern of longitudinal changes in water temperature shapes the particular style of spawning seasonality in this northernmost population of *L. vulgaris*, with a seasonal shift of the main spawning peak from west to east.

Despite the fact that the ranges of both *Loligo* species nearly coincide, their reproductive areas were found to be mainly separate, with some overlap seen only in the Celtic Sea/Bristol Channel and possibly Irish Sea, and along German shores. The spawning grounds of *L. forbesii* generally forms an external semi-circle around the spawning grounds of *L. vulgaris*, with the latter centred on the English Channel and southernmost North Sea. The nursery grounds of both species appear to coincide with the respective spawning grounds, though *L. forbesii* makes much wider use of the North Sea penetrating south to shores of Germany and Netherlands—a zone of reproduction of *L. vulgaris*. Seasonally, spawning grounds and nursery grounds of both species mirror each other gradually shifting eastward. Reproduction begins around November and gradually progresses eastward following favourable currents and increasing water temperatures. Spawning in both species is mostly over by July though some egg masses persist until August–November.

The two *Loligo* species considered in this study are closely related. Phylogenetic analyses of mitochondrial DNA (Anderson, 2000; Göpel *et al.*, 2022) and nuclear and mitochondrial DNA combined (de Luna Sales *et al.*, 2013) identify *L. forbesii* as the sister species to *L. vulgaris*–*L. reynaudii* pair. Presumably both these species of *Loligo* evolved from the same ancestor and were adapted to very similar life styles, though at slightly different temperatures, and this may explain how they entered the North Sea after it became habitable with the retreat of the ice sheet ~14,500 years ago (Clark *et al.*, 2009). Thereafter, *L. forbesii* followed the deeper path of the colder Shelf Edge Current (or its oceanographic predecessor), and *L. vulgaris* followed the shallower path of Channel Water (or some similar prehistorical eastbound flow between modern England and France).

The difference in reproductive areas of both species shown in the present study requires closer attention to be paid to their regional exploitation rates, and should be taken into account in any elaboration of management measures to support their sustainable use in years to come.

Several past studies point to variation in aspects of the reproductive cycle over longer time scales, e.g. in phenology and spatial aspects of the distribution (Boyle *et al.*, 1995; Collins *et al.*, 1997; Pierce *et al.*, 2005), including the possible existence of defined seasonal cohorts (Holme, 1974). Hence, results of the present study should be considered as providing a "multi-annual average" representation of the spawning patterns of these species. Interpretation of our results might depend on how the data were collected spatially and temporally, with cold and warm years potentially giving rise to additional important differences that remain to be described in the future.

Data availability statement

Data cannot be shared for privacy reasons of individuals who participated in the study, but will be shared on reasonable request to the corresponding author subject to agreement with all participants.

Author contributions

VL, DO, AMP, GC, and GJP conceived the ideas and designed the approach and methodology. All co-authors participated in biological data collection and analysis, EML led in oceanographic contribution. The draft manuscript was produced by VL, edited by DO, AMP, and GJP, improved by other authors, and submitted with the approval of all the authors. Figures were produced by VL, AMP, and EML.

Funding

Irish data observations were supported by funding from the Cephs & Chefs project of the European Regional Development Fund through the Interreg Atlantic Area Programme grant number EAPA 282/2016.

Conflict of interest statement

The authors have no competing interests to declare.

Acknowledgements

The work was initiated and supported by ICES Working Group on Cephalopod Fisheries and Life History (WGCEPH). The authors sincerely thanks Dr Angus Jackson (Marine Conservation Society) and Dawn Watson (Seasearch East) for helping them to obtain abundant materials on distribution of egg masses collected by Seasearch (https://www.seasearch.org.uk/). The authors wish to thank the Irish Marine Institute staff and crew of the RV "*Celtic Explorer*", as well as cruise leaders, participating staff and Ingo Wilhelms from the Thünen Institute, and scientific staff and crew of RV "*Cefas Endeavour*" for collection of squid samples, Dr Gary Burt (Cefas) for help with data management. Further, the authors want to thank all recreational fishermen and divers who have provided records to the Cephalopod Citizen Science Project, and Dr Marta Söffker (Cefas) and two anonymous reviewers for valuable comments.

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Handling Editor: Alexander Arkhipkin