



Climate change-related changes in cephalopod biodiversity on the North East Atlantic Shelf

Daniel Oesterwind¹ · Christopher J. Barrett² · Anne F. Sell³ ·
Ismael Núñez-Riboni³ · Matthias Kloppmann³ · Uwe Piatkowski⁴ ·
Kai Wieland⁵ · Vladimir Laptikhovskiy²

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Abstract

Global studies imply that cephalopods have benefited from climate change. However, in most areas, species-specific long-term cephalopod data sets do not exist to support this implication and to analyse the response of cephalopods to environmental changes. Our results illustrate that historical studies, in combination with recent data sets, can fill this gap, enabling descriptions of ecological changes over a long time. We show substantial changes in the cephalopod biodiversity of the North Sea at species level over the past 100 years. Some species, which seemed to migrate into the North Sea only for spawning or foraging in the nineteenth century, occur permanently in the North Sea nowadays. This applies, for example, to the loliginids *Loligo forbesii* and *Alloteuthis subulata*. The ommatrephids *Todaropsis eblanae* and *Illex coindetii*, now constantly present as well, had been described only as accidental migrants 100 years ago.

Keywords Cephalopod community · Biodiversity · Distribution · Environmental changes · Expansion · Life cycle

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✉ Daniel Oesterwind
daniel.oesterwind@thuenen.de

¹ Thünen Institute of Baltic Sea Fisheries, Rostock, Germany

² Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft, UK

³ Thünen Institute of Sea Fisheries, Bremerhaven, Germany

⁴ GEOMAR, Helmholtz-Zentrum Für Ozeanforschung Kiel, Kiel, Germany

⁵ National Institute of Aquatic Resources, Technical University of Denmark, Hirtshals, Denmark

Introduction

Climate change led, and will lead, to changes in floral and faunal communities. Rising ocean temperatures are associated with changes in thermal stratification, ocean circulation, oxygen and carbon concentration and an increasing climatic variability with extreme events. Locally, these changes can impact biodiversity directly or indirectly, when environmental conditions exceed individual species' physiological tolerances or when the functionality of habitats and availability of nutrients change (Worm and Lotze 2016). Broader, biological communities and interactions within them can change and some species replace others, so that 'winners and losers' exist. However, impacts of climate change on marine biodiversity will be greatest when key ecological species are affected because those effects might indirectly impact broader associated communities (e.g. through the food web) (Wernberg et al. 2014).

To observe biodiversity responses to climate change, different time periods need comparing. The wider the time period, the more likely it is to observe the changes and adaptations of biodiversity even if ecosystem adaptation is slow. This means that for slow processes like the increasing global warming, larger timescales, namely climate scales, must be compared. Where climate scale is the range of time periods and spatial lengths for which climate-related changes are relevant, i.e., periods of time longer than various decades and lengths larger than some hundreds of kilometres. For fast and heavy impacting events like eruptions and oil spills, or when key species are affected, shorter time scales might be sufficient. Consequently, to observe climate change-induced changes, long-term datasets and knowledge of the biology of the species and communities as well as the habitat are essential. In many cases, this knowledge and especially long-term datasets are missing and changes in data-poor communities and areas are therefore impossible to capture. Where long time series on species level are unavailable, historical studies become important for evaluation of changes over time. In our case study we focus on the North Sea, a marginal sea to the North East Atlantic, which is one of the longest and mostly intensely studied fishing areas worldwide.

In addition to environmental data, huge amounts of historical fishing and fisheries research data are available for the North Sea and enable identification of ecosystem changes as a response to the environmental variability (Desmit et al. 2020; Heath 2005; Jennings et al. 2002). Climate change has caused a range of unidirectional shifts in distribution and life styles of North Sea species and an increase in species richness of marine fishes (Hidink and ter Hofstede 2008). Within recent years, several examples of life cycle, phenology (e.g. Greve et al. 2005), distribution and migration shifts (e.g. Perry 2005; Engelhard et al. 2014; Núñez-Riboni et al. 2019), as well as the occurrence of new species (e.g. Beare et al. 2004) have been documented, illustrating a dynamic ecoregion.

Many studies concentrate on changes in fish communities, as well as abundance and distribution of different single species, but other taxonomic groups and communities are also scrutinised from zooplankton (e.g. Reid et al. 2003) to seabirds and marine mammals (Wolff 2000). However, little is known about cephalopod community shifts in the North Sea. Due to their short life cycles, cephalopods can quickly adapt to environmental changes, conquering newly developing ecological niches and might, therefore, benefit from climate changes (Sims et al. 2001).

A few studies on the ecology and distribution of different North Sea cephalopods exist (e.g. Lordan et al. 2001b; Zumholz and Piatkowski 2005) though most were performed in a framework of short projects where species were reliably identified, but time series are

insufficient for longer observations. Furthermore, most studies are based on bycatch data from the commercial fishery or standardized fishery research cruises. While such data are insufficient to determine absolute abundance of cephalopods, they allow comparisons of distribution, relative abundance, size, age, sex and maturity of different cephalopod species and individuals as well as between years and seasons. Therefore, such data can provide useful snapshots of cephalopod biology (e.g. Lordan et al. 2001b; Oesterwind et al. 2010) and some indicate already changes in species biology, distribution and abundance of North Sea cephalopods (e.g. Pierce et al. 2005; Oesterwind et al. 2020).

Only one recent study focuses on long term changes of North Sea cephalopods on a higher taxonomic level (van der Kooij et al. 2016). That study reveals that North Sea squids benefited from climate change within the last 35 years, but due to the lack of species-specific information, changes and adaptation on the species level are uncertain.

Historical information on the North Sea cephalopod fauna was published by Grimpe (1925), who provided a baseline and allows a comparison between the former status (~ 100 years ago), and the current status of the North Sea cephalopod species.

To describe potential changes in the cephalopod community, we reviewed and analysed recent publications and datasets (2000–2020) of North Sea cephalopods and compared this information with Grimpe's aforementioned review, as well as with publications of the late nineteenth century. We included all taxonomic groups except Sepioloidae, which are difficult to identify to species level. Furthermore, we describe the oceanographic changes in the North Sea and discuss their potential impacts on cephalopods.

Material and methods

Data and analysis

Our case study focuses on the greater North Sea including the English Channel, Skagerrak and Kattegat (ICES 2018), but information about the adjacent waters are discussed to complete the picture. To understand cephalopod occurrence, commercial catch data were downloaded from ICES and filtered for North Sea cephalopod catches and 'other catches' (ICES 2020c, d) and plotted in SigmaPlot 13.0.

The publicly available 'Exchange' dataset of the ICES coordinated North Sea International Bottom Trawl Survey (ICES-NS-IBTS) and ICES coordinated Beam Trawl Survey (ICES-BTS) provided by ICES Data Centre (ICES 2020a, b) were downloaded from <https://datras.ices.dk> (for further survey information see ICES 2009, 2015). To document species presence, we analysed the last 20 years of both datasets, reviewed current literature, considered personal observations, and listed all documented cephalopod species.

To analyse the current distribution of the different species, we filtered the years 2016–2020 of both data sets and classified the original taxonomic entries (in brackets) into the following taxa: *Alloteuthis subulata* (*Alloteuthis*; *Alloteuthis subulata*), *Loligo forbesii* (*Loligo forbesii*, *Loligo forbesi*), *Loligo vulgaris* (*Loligo vulgaris*), *Illex coindetii* (*Illex*, *Illex coindetii*, *Illex illecebrosus*), *Todaropsis eblanae* (*Todaropsis*, *Todaropsis eblanae*) and *Todarodes sagittatus* (*Todarodes*, *Todarodes sagittatus*). Regularly reported octopus *Eledone cirrhosa* and cuttlefishes *Sepia* spp. were excluded from quantitative analysis, but a comparison based on a literature review had been performed for Octopoda, Sepiida and various Oegopsida. Taxonomic classification at genus or family level were excluded when different species might occur. Regarding

Illex, only *I. coindetii* is present in the North Sea (Oesterwind et al. 2020), while the genus *Alloteuthis* is more complex (see section '*Alloteuthis subulata*' and '*Alloteuthis media*'). Both datasets were combined and presence and absence for each species were plotted in ArcMap 10.6. The historical distribution is based on the maps provided by Grimpe (1925) and were digitalized with ArcMap 10.6 and image editing programs, and shows only stations with presence of the species.

To illustrate species distribution shifts and to describe changes in species biology we first calculated the relative frequency distribution (RFD), for species with the most commercial interest; we counted all presence observations for each species separately in the entire study area in each of both maps, then divided the North Sea into a geographical grid with cells of 5° longitude and 5° latitude before calculating the species-specific proportion of presence observations for each of the grid cells (the share of presence per cell in the total of all observations for the respective species). We then calculated the differences between the historical RFD and present RFD for each species and specific grid cell by subtracting the percentages of historical map from the present map. Second, we compared historical biological information of selected cephalopods, mainly based on Grimpe (1925) and other studies from this period, with recent studies.

We then describe the changes in the environmental conditions of our study area. We focus on temperature and salinity because even though the North Sea is one of the best sampled regions of the world oceans, few environmental variables (except temperature) were measured at the beginning of the twentieth century to explain the observed changes in cephalopod biodiversity and distribution. Salinity observations before 1960 were sparse (Huthnance et al. 2016) although individual values are available from the 1940s onwards. Observations of other environmental variables (currents, oxygen and pH) are more recent. The only available variable measured since the end of the nineteenth century in the North Sea is Sea Surface Temperature (SST) (Huthnance et al. 2016), while Sea Bottom Temperature (SBT) data were available since the early 1950s. Both are a good proxy to explain the changes in the cephalopod biodiversity because several studies illustrate a strong relation between occurrence and abundance of cephalopod and SST and SBT (e.g. Pierce et al. 1998; Bellido et al. 2001). Additionally, it is plausible that other environmental variables present similar spatiotemporal changes to temperature at climate scale; oxygen content, for instance, is related to temperature over its solubility (Stramma et al. 2012). SST from the Met Office Hadley Centre (Hadley 2020) for the period January 1870 to December 2019 were extracted and annually averaged for the North Sea region (from 5 °W to 10 °E and 49 to 62 °N). Spatially resolved SBT and SBS were obtained for 1950 to 2017 from a new run of the Adjusted Hydrography Optimal Interpolation (AHOI; Núñez-Riboni and Akimova 2015).

Results

Cephalopod landings

Total reported landings of exploited marine species from the North Sea other than cephalopods showed a steady decrease since the early 1990s, stabilizing since around 2010. In contrast, cephalopod landings show stronger interannual variability, but increased conspicuously over the recent decades (Fig. 1).

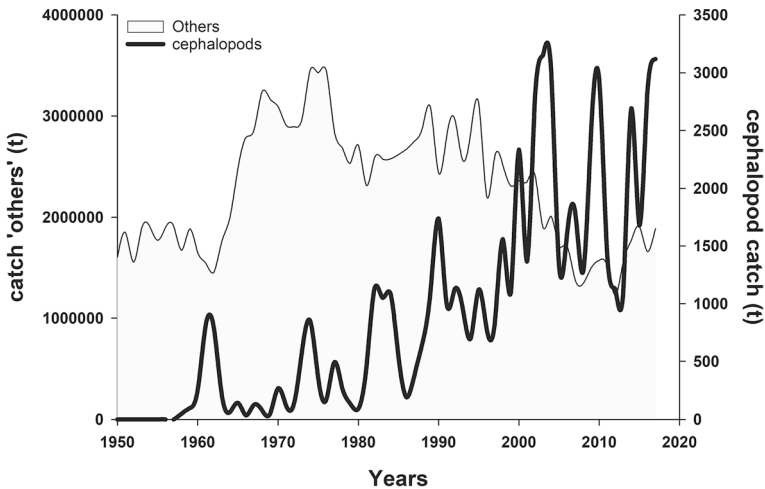


Fig. 1 Cephalopod catches from the North Sea (black line) and North Sea catches of other marine species (grey; predominantly fish and crustaceans) in comparison. (Downloaded from <https://www.ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx>)

Cephalopod biodiversity

In the early twentieth century, Grimpe (1925) identified 18 cephalopod species in the North Sea and reported 5–7 species, whose occurrences were documented through other, reliable sources, therefore totalling ~24 North Sea cephalopod species (Table 1). He classified those species by their occurrence as permanent resident North Sea inhabitants: *Eledone cirrhosa*, *Sepietta oweniana*, *Sepiola atlantica*, *Adinaefiola pfefferi*, *Rossia glaucopsis*, species with high probability to be present permanently: *Rossia macrosoma*; and species with seasonal occurrence: *Sepia officinalis*, *Octopus vulgaris*, *Loligo forbesii*, *Loligo vulgaris*, *Alloteuthis subulata*, and *Todarodes sagittatus*. All other species were considered vagrant in the North Sea (Grimpe 1925).

Whilst total number of species has not changed substantially over the last 100 years (Table 1), their occurrence has. Seven species being reported by Grimpe as seasonal immigrants, vagrant or absent, are now likely permanent year-round residents in the North Sea: *A. subulata*, *I. coindetii*, *L. forbesii*, *Sepiola tridens*, *R. macrosoma*, *T. eblanae* and most likely *L. vulgaris*. *T. sagittatus* and *S. officinalis* still occur seasonally but nowadays their occurrence is regular, whereas the status of *Alloteuthis media* is unclear.

Newcomers include *S. tridens* which has been identified with modern genetic techniques (de Heij and Goud 2010), *Gonatus* sp. as an accidental immigrant and *Rondeletiola minor* with unknown status, whereas *Architeuthis dux*, *Ommastrephes caroli*, *Stenoteuthis pteropus* and most likely *O. vulgaris* (see section ‘Octopoda’) currently appear to be absent and have not been reliably recorded within the last 20 years.

Our data illustrate spatiotemporal changes of many cephalopod species. Some, which used to migrate into the North Sea only for spawning or foraging in the nineteenth century, occur permanently in the area nowadays. Further changes include spawning periods, distribution and migration patterns which are described in the following sections.

Table 1 Historical and recent documented cephalopod species in the North Sea (including Skagerrak and Kattegat) ordered by family and names; historical documentation mainly based on Grimpe (1925) indicated by 'H'; recent documentation by various sources indicated by 'R'

Current species name	North Sea presence
Sepiidae	
<i>Sepia elegans</i>	H, R ^{1,2,5,6}
<i>Sepia officinalis</i>	H, R ^{1,2,3,6}
<i>Sepia orbignyana</i>	H, R ^{2,6}
Sepiolidae	
<i>Adinaefiola pfefferi</i>	H, R ^{2,4,5,6}
<i>Sepietta neglecta</i>	H, R ^{2,4,5,6}
<i>Sepietta oweniana</i>	H, R ^{1,2,4,5,6}
<i>Sepioli atlantica</i>	H, R ^{1,2,3,4,5,6}
<i>Sepioli tridens</i>	R ^{2,4,5,6}
<i>Rondeletiola minor</i>	R ^{2,6}
<i>Rossia glaucopsis</i>	H
<i>Rossia macrosoma</i>	H, R ^{1,2,5,6}
<i>Rossia palpebrosa</i>	R ^{2,6}
Loliginidae	
<i>Alloteuthis media</i>	H, R ⁰
<i>Alloteuthis subulata</i>	H, R ^{1,2,3,6}
<i>Loligo forbesii</i>	H, R ^{1,2,3,5,6}
<i>Loligo vulgaris</i>	H, R ^{1,2,3,5,6}
Architeuthidae	
<i>Architeuthis dux</i>	H
<i>Architeuthis</i> sp.	H
Brachioteuthidae	
<i>Brachioteuthis riisei</i>	H, R ²
Gonatidae	
<i>Gonatus</i> sp.	R ²
Ommastrephidae	
<i>Illex coindetii</i>	H, R ^{1,2,5,6}
<i>Ommastrephes caroli</i>	H ⁷
<i>Todarodes sagittatus</i>	H, R ^{1,2,5,6}
<i>Todaropsis eblanae</i>	H, R ^{1,2,3,5,6}
<i>Sthenoteuthis pteropus</i>	H
Onychoteuthidae	
<i>Onychoteuthis banksii</i>	H, R ^{3,6}
Bathypolypodidae	
<i>Bathypolypus</i> sp.	H, R ^{2,6}
Eledonidae	
<i>Eledone cirrhosa</i>	H, R ^{1,2,3,5,6}
Octopodidae	
<i>Octopus vulgaris</i>	H, R ²

⁰pers. obs. Laptikhovsky, ¹Oesterwind et al. (2010), ²ICES (2020a, b), ³de Heij and Baayen (2005), ⁴Groenenberg et al. (2009), ⁵Gebhardt and Kneibelsberger (2015), ⁶Goude et al. (2019), ⁷recorded in 1933 by Hertling (1938)

Cephalopods which have become permanent residents in the North Sea

Alloteuthis subulata

In the nineteenth century *A. subulata* was seasonally present and the most common cephalopod in the North Sea (Grimpe 1925), occurring mainly in the south-eastern part of the North Sea from the English Channel to the Danish west coast and Skagerrak and Kattegat. It was rare off the south-eastern coast of England, but occurred near the Shetland and Orkney Islands, along a section in direction to the Great Fisher Bank, as well as in the Moray Firth (Fig. 2).

Though controversy exists about the status of *A. subulata* and *A. media*, due to frequent misidentification (Sheerin et al. 2021; see section '*Alloteuthis media*'), it can be assumed that, regardless, *A. subulata* is the most common cephalopod in the North Sea (Oesterwind et al. 2010), and that its distribution has expanded substantially (Fig. 2). Recent studies confirm that *A. subulata* is omnipresent throughout the entire North Sea (De Heij and Baayen 1999, 2005; Oesterwind et al. 2010) and the RFD quantifies a westward distribution shift (Table 2). *A. subulata* is also regularly present in the Kattegat and sporadically in the western Baltic Sea (Hornborg 2005; Herrmann and Piatkowski 2001; Oesterwind pers. obs.).

In the last century, *A. subulata* seemed to be absent in the North Sea from November until February. Grimpe (1925) assumed that *A. subulata* winters in western waters off Ireland, Hebrides and Shetlands, as it was already known that the species winters in the deeper northern, western and southwestern oceanic waters off Ireland. A spring and autumn form of the species was described (Grimpe 1925). The spring form started its migration into the North Sea in March from western deeper waters, and large but immature individuals of *A. subulata* appeared in the north. Mature individuals arrived in the central North Sea

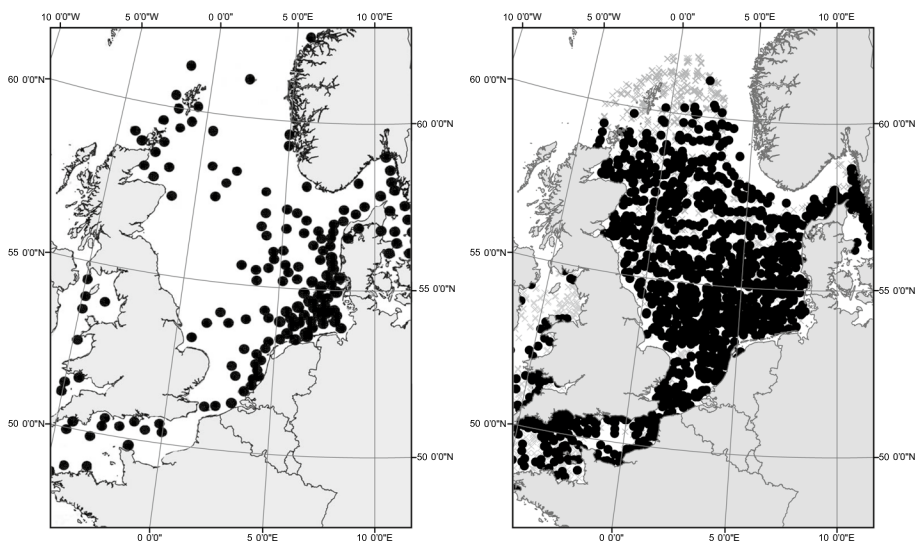


Fig. 2 Distribution of *Alloteuthis subulata*. Left map: past presence distribution based on Grimpe (1925), right map: recent presence/absence distribution based on ICES DATRAS dataset (2016–2020 combined). Black dots: stations with *A. subulata*, grey crosses: zero catches

Table 2 Comparison of historical and recent relative frequency distribution (RFD) of *A. subulata* within the last ~ 100 years. Numbers indicate changes in %. Positive numbers (dark grey cells) indicate an increase in RFD, zero (light grey cells) indicate no changes, negative numbers (white cells) indicate a decrease in RFD. Black cells represent mainland

		Longitude			
		- 5°-< 0°	0°-< 5°	5°-< 10°	10°-< 15°
Latitude	60°-< 65°	- 2	0	- 1	
	55°-< 60°	5	12	- 10	- 2
	50°-< 55°	- 2	15	- 14	0
	45°-< 50°	- 1	0		

and along the Norwegian trench in April, then in May in the Kattegat and German Bight, where the main spawning activity took place between mid-June and mid-July before adults died. First paralarvae occurred during the end of July and beginning of August. Within the first weeks, ventral mantle length (VML) reached 6–14 mm and increased to ~25 mm in August. Those hatchlings left the German Bight in October but had been observed in the central North Sea and at the Belgian and Dutch Coast afterwards so that Grimpe (1925) assumed a northern and southern emigration route. In November the species was absent until the following March. In some years, mature individuals (autumn spawners) became present in September. Grimpe (1925) speculated that the small individuals of the autumn cohort left the North Sea in October together with the individuals from the spring cohort.

Presently, mainly immature and maturing individuals are present in large numbers in the central and northern North Sea in winter, while in summer, mainly mature and larger individuals are fished in the southeastern coastal waters (Oesterwind et al. 2010). Spawning occurs until June–July, with hatchlings appearing in plankton samples towards the end of July (Yau 1994). From spawning grounds, the juveniles appear to conduct a temperature-driven migration to feeding grounds in the deeper and relatively warmer waters of the central and northern North Sea in winter (Oesterwind et al. 2010).

Grimpe (1925) recognized different size classes, which Oesterwind et al. (2010) recently confirmed and linked to temperature. No evidence exists whether the average length of *A. subulata* has increased over the past 100 years. Lönnberg (1891, as citet in Grimpe 1925) considered *A. subulata* and *A. media* to be synonymous and indicated the maximum size of 130 mm while Grimpe (1925) documented a VML of > 140 mm. Oesterwind et al. (2010) described a maximum dorsal mantle length (DML) of 160 mm; similar to De Heij and Baayen (1999).

Loligo forbesii

Historically, *L. forbesii* was only seasonally present in the North Sea. Reliable records were known for most coastal areas including Skagerrak, Kattegat and the western Baltic (Fig. 3). Its presence started with some single individuals at the beginning of July while the majority began to occur in September catches with some annual variation. Immigrating schools contained maturing individuals, leading Grimpe (1925) to assume that some individuals leave the North Sea in November without spawning, but he was not able to validate his assumption by observations. Nowadays, *L. forbesii* is the second most common cephalopod in the ICES-NS-IBTS (Oesterwind et al. 2010). It is present year-round with a central and

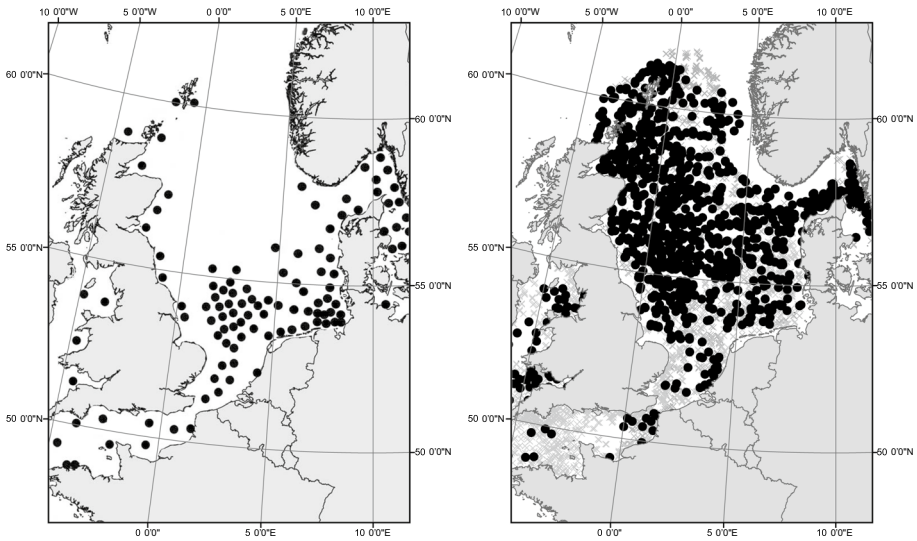


Fig. 3 Distribution of *Loligo forbesii*. Left map: past presence distribution based on Grimpe (1925), right map: recent presence/absence distribution based on ICES DATRAS dataset (2016–2020 combined). Black dots: stations with *L. forbesii*, grey crosses: zero catches

northern distribution in winter and a patchy distribution throughout the entire North Sea in summer with a regular eastern distribution boundary at the Norwegian Trench and highly variable abundances in the Skagerrak and Kattegat (Fig. 3) (De Heij and Baayen 2005; Hornborg 2005; Oosterwind et al. 2010). Its distribution in winter is strongly correlated with SBT, salinity and depth (Pierce et al. 1998; Oosterwind et al. 2010). The RFD quantifies a distribution shift towards northwest (Table 3), where a targeted fishery has developed and major spawning grounds exists (Young et al. 2006).

Spawning time has changed within the last 100 years. Historically, *L. forbesii* was an autumn spawner (formerly known as *L. forbesii moulinsi*, northern type) in the North Sea and egg clusters were present from the end of July until November and small juveniles only in December and January. By then, medium-sized individuals with a VML between 15

Table 3 Comparison of historical and recent relative frequency distribution (RFD) of *L. forbesii* within the last ~ 100 years. Numbers indicate changes in %. Positive numbers (dark grey cells) indicate an increase in RFD, zero (light grey cells) indicate no changes, negative numbers (white cells) indicate a decrease in RFD. Black cells represent mainland

		Longitude			
		- 5° < 0°	0° < 5°	5° < 10°	10° < 15°
Latitude	60° < 65°	4	2	- 1	
	55° < 60°	19	25	0	- 8
	50° < 55°	- 4	- 21	- 11	- 1
	45° < 50°	- 4	- 1		

and 85 mm had never been observed in the North Sea (Grimpe 1925) but are recently present year-round. Nowadays, single mature males occur in the North Sea in summer while mature and larger individuals are typically fished in winter and indicate two spawning seasons with winter breeders dominate summer breeders (Pierce et al. 2005; Oesterwind et al., 2010). Consequently, the main spawning period nowadays lasts from late winter to spring (Boyle and Pierce 1994; Oesterwind et al. 2010).

The maximum measured VML by Grimpe (1925) was 480 mm with a total length (TL) of 840 mm while recently a DML of 584 mm during ICES-NS-IBTS in Q1 2017 had been observed and might indicate an increasing length. However, Grimpe (1925) mentioned also individuals of up to 1 m total length.

Illex coindetii

Within the last century, *I. illecebrosus coindetii* (e.g. Nesis 1987) has been renamed to *I. coindetii*. Grimpe (1925) reported one (considered unreliable) individual for the Firth of Forth, documented by Norman (1890) and was able to analyse one individual; a male of 165 mm DML, stranded at Helgoland after a heavy storm in 1909 (Fig. 4).

While De Heij and Baayen (2005) had no *I. coindetii* in their ICES-NS-IBTS samples between 1996 and 2003 a sparse but regular occurrence in summer and single individuals in winter have been documented in ICES-NS-IBTS between 2007 and 2010 (Oesterwind et al. 2010, 2015) following with a substantial increase in abundance. *I. coindetii* is now the most frequently reported ommastrephid in the ICES-NS-IBTS catches (Oesterwind et al. 2015, 2020), occurring in the central and northern North Sea. The increasing abundance in the North Sea implies a recent eastward expansion into the Kattegat and the Belt Sea (Oesterwind and Schaber 2020; Fig. 4).

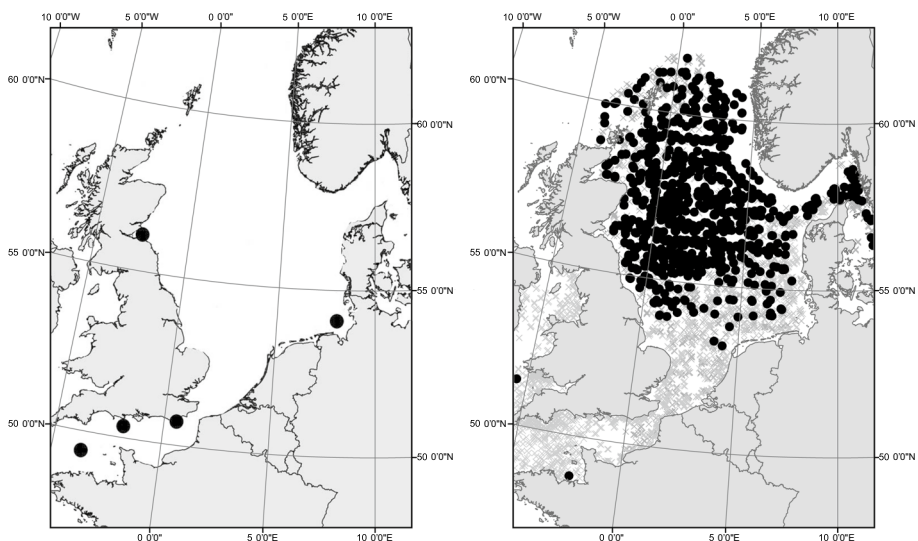


Fig. 4 Distribution of *Illex coindetii*. Left map: past presence distribution based on Grimpe (1925), right map: recent presence/absence distribution based on ICES DATRAS dataset (2016–2020 combined). Black dots: stations with *I. coindetii*, grey crosses: zero catches

In winter, most *I. coindetii* were immature or maturing, while in summer almost exclusively larger individuals were fished; mostly mature and spent (Oesterwind et al. 2020). Furthermore, mated females with spermatangia bundles, were observed in summer and *Illex* eggs were identified in the Greater North Sea and adjacent waters (Barrett et al. 2021; Ringvold et al. 2021). Consequently, it is very likely that the species started to reproduce in the area with a hatching period at least from June to December (Oesterwind et al. 2020; Barrett et al. 2021).

Todaropsis eblanae

Lönnerberg (1891, as cited in Grimpe 1925) does not list *T. eblanae* within the North Sea and within Grimpe's samples, only one individual with a DML of 84 mm was present and has been most likely fished north of the Shetland Islands in a depth of 180 m in March 1911 (Fig. 5). Grimpe (1925) mentioned only two additional reliable records, indicating *T. eblanae* rarity in the North Sea 100 years ago. He further described a small distribution range with high abundances in Irish waters. It seems likely that *T. eblanae* started its expansion into the North Sea from there. It first occurred irregularly with occasional incursions, linked to inflow events of warm, high-salinity Atlantic sea water (Stephen 1944; Rae and Lamont 1963; Hastie et al. 1994), afterwards it has become permanently present in the North Sea, Skagerrak, and Kattegat (Fig. 5; Jaeckel 1958; Hornborg 2005; Zumholz and Piatkowski 2005; ICES 2020a, b) and a summer spawning stock, with an assumed spawning season from summer to autumn has developed (Hastie et al. 1994; Oesterwind et al. 2015; Barrett et al. 2021). Recently, higher catches occur in winter, and north-western of

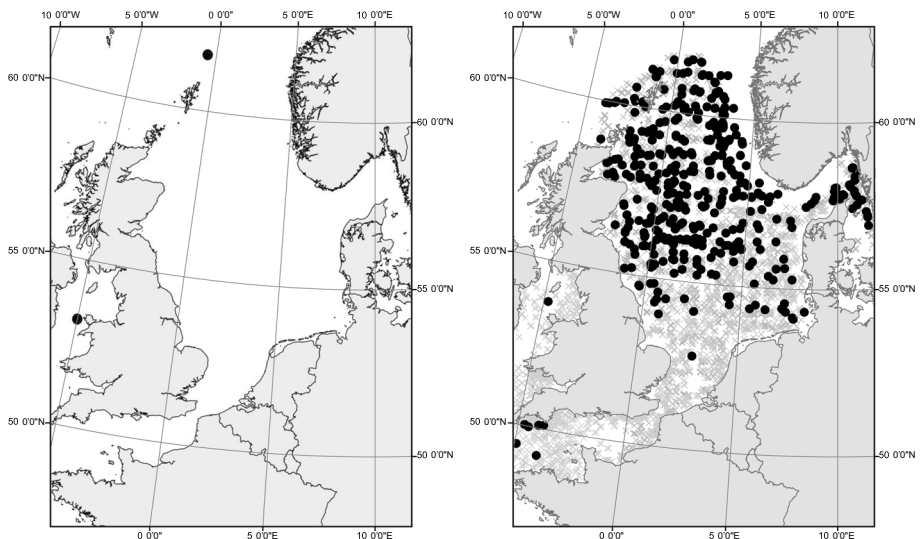


Fig. 5 Distribution of *Todaropsis eblanae*. Left map: past presence distribution based on Grimpe (1925), right map: recent presence/absence distribution based on ICES DATRAS dataset (2016–2020 combined). Black dots: stations with *T. eblanae*, grey crosses: zero catches

the North Sea in depths of 31–170 m (Zumholz and Piatkowski 2005; Oesterwind et al. 2015).

Cephalopods with strong evidence to be permanent in the North Sea

Loligo vulgaris

Historically, *L. vulgaris* was absent only in single years, and always less abundant than *L. forbesii*. It was observed in the North Sea from May until October and was reported mainly from the south-eastern part along the coast from the English Channel to Denmark, and south Sweden, as well as at the Kattegat, Skagerrak and western Baltic (Fig. 6) (Grimpe 1925; Tinbergen and Verwey 1945). Based on its distribution, migration and morphological differences, *L. vulgaris* had been divided into a spring/summer spawning form (*L. vulgaris typica*) which occurred only in the southern North Sea, and an autumn spawning form (*L. vulgaris breviceps*) with its main distribution in the Kattegat and the Danish Sounds (Grimpe 1925).

Grimpe (1925) described that, generally, mature *L. vulgaris* migrated northward along the European coast and arrived French coastal waters in April. Then, the spring form *L. vulgaris typica* migrated through the English Channel into the North Sea and occurred there not earlier than mid-May. Spawning took place in the southern North Sea but eggs had never been found at the English coast, were rare at the French coast, but were abundant off Netherlands in May–August of 1930s (Tinbergen and Verwey 1945). Grimpe (1925) assumed that the autumn spawning form *L. vulgaris breviceps* migrated northwards along the Irish and western Scottish coasts to enter the North Sea for spawning through the Faeroe Channel and along the Norwegian Trench, which, in his opinion, also explained its

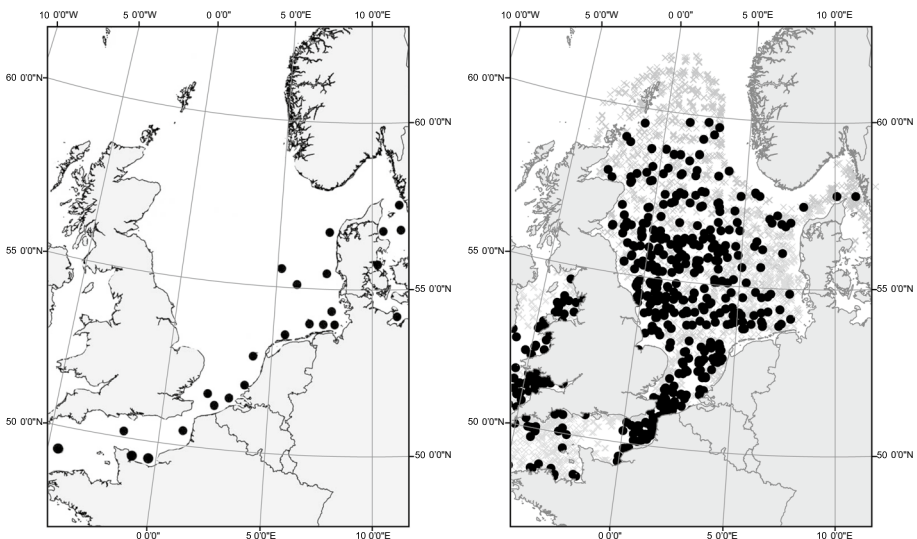


Fig. 6 Distribution of *Loligo vulgaris*. Left map: past presence distribution based on Grimpe (1925), right map: recent presence/absence distribution based on ICES DATRAS dataset (2016–2020 combined). Black dots: stations with *L. vulgaris*, grey crosses: zero catches

main distribution in the Kattegat and Danish Sounds. It arrived in the Kattegat between July and October. He assumed that the longer migration distance was the reason for the later arrival in autumn and that the little morphological differences between both forms are based on the different age. Years later, Tinbergen and Verwey (1945) supported Grimpe’s assumption that *L. vulgaris* enters the North Sea via the Channel, but they were convinced that only one species exists and that the individuals from the Skagerrak and Kattegat originates from the same group and migrate further North along the shoreline.

It is now validated that *L. vulgaris* migrates long distances (up to ~500 km; Jereb et al. 2015), complementing Grimpe (1925), who assumed that hatchlings left the North Sea to migrate southward to the French coast because juveniles had never been observed in the past. Recent data show higher abundance in the western North Sea and particularly around the British Channel (Fig. 6, right panel) and RFD quantifies a western expansion (Tab. 4). In summer, juveniles with low maturity stages are observed while in winter maturing and matured individuals were fished. It seems that the autumn stock (former *L. vulgaris breviceps*, Grimpe 1925) decreased substantially over the last years. Hornborg (2005) describes that the species has not been fished since 1990 in Swedish waters while in 2005 12 specimens were captured. BTS data illustrate a similar decreasing trend in autumn because only a few specimens were caught in the northern part of the North Sea during some years since 1990 (de Heij and Baayen 2005, ICES 2020b). Consequently, there is to our best knowledge no evidence for a second spawning form anymore (de Heij and Baayen 2005; Oesterwind et al. 2010; ICES 2020a).

Cephalopods regularly but seasonal in the North Sea

Todarodes sagittatus

In the past century, *T. sagittatus* was rare in the southern North Sea, and only single individuals had been recorded (Fig. 7; Grimpe 1925). In the northern North Sea, the species regularly immigrated in higher numbers. In some years huge schools of immature squid (~300–400 mm mantle length) were present (Jereb et al. 2015; Zuev and Nesis 1971).

Grimpe (1925) reported a female with a VML of 252 mm and a male with a VML of 425 mm, stranded at Helgoland in 1900 and 1906, respectively. He mentioned different

Table 4 Comparison of historical and recent relative frequency distribution (RFD) of *L. vulgaris* within the last ~100 years. Numbers indicate changes in %. Positive numbers (dark grey cells) indicate an increase in RFD, zero (light grey cells) indicate no changes, negative numbers (white cells) indicate a decrease in RFD. Black cells represent mainland

		Longitude			
		- 5° < 0°	0° < 5°	5° < 10°	10° < 15°
Latitude	60° < 65°	0	0	0	
	55° < 60°	9	22	- 14	- 24
	50° < 55°	14	16	- 17	- 4
	45° < 50°	- 3	1		

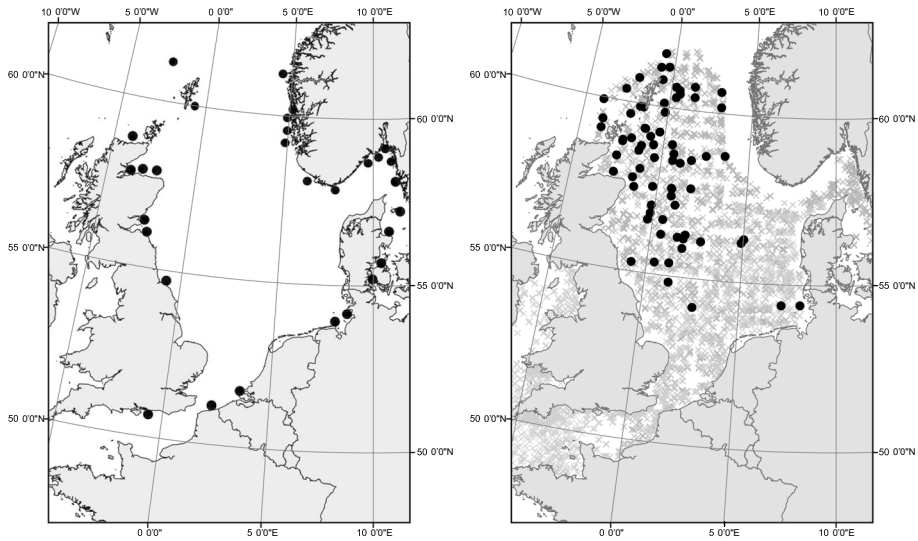


Fig. 7 Distribution of *Todarodes sagittatus*. Left map: past presence distribution based on Grimpe (1925), right map: recent presence/absence distribution based on ICES DATRAS dataset (2016–2020 combined). Black dots: stations with *T. sagittatus*, grey crosses: zero catches

sources which described *T. sagittatus* migrating in large schools close to the Mediterranean and Nordic coasts to follow their prey, rather than for spawning, because the schools consisted of different sizes with only a few matured individuals, and squids consumed plentiful prey which might explain the North Sea occurrence.

More recently, *T. sagittatus* occurred sometimes in the North Sea at the northeast coast of Scotland in February–March (Ritchie 1920) and sometimes further south, off the Yorkshire coast. In March–April two size groups existed; one with a total length between 46 and 51 cm and another between 86 and 118 cm (Stevenson 1935 as cited in Wiborg 1972).

Nowadays, *T. sagittatus* is the least abundant ommastrephid in the ICES-NS-IBTS but juveniles and maturing individuals occur regularly in winter in the northern and central North Sea (Fig. 7; ICES 2020a, b; Oesterwind et al. 2015) and occasionally captured in August - September (CEFAS data). The low abundance is explainable due to its typically neritic and oceanic life (Collins et al. 2001). The North Sea represents a periphery of its foraging range while the species reproduces around Azores and on the western side of Porcupine Bank (Laptikhovsky 2013, Lordan 2001a). It is a slope-oceanic (pseudooceanic) squid, so central and southern North Sea are permanently too shallow (Laptikhovsky 2013). Nevertheless, in some years huge aggregations occurred in the northern area (e.g. Wiborg and Beck 1984; Joy 1990; Boyle et al. 1998; Lordan et al. 2001a, b) and resulted in a substantial commercial fishery in the 1980s in Norway (Sundet 1985) but seems to be absent nowadays.

Cephalopods as irregular guests or with unknown status

Alloteuthis media

Before Grimpe's (1925) publication, no reliable evidence of the presence of *A. media* in the North Sea existed and it was unclear whether its occurrence is due to misidentification. Grimpe (1925) dismissed the use of the relative tail length to distinguish *A. subulata* from *A. media*, instead suggesting the relation between mean arm and mantle length, as published by Naef (1912) to distinguish both species. From 3004 *Alloteuthis* sp. fished in 1919 close to Helgoland, Grimpe (1925) identified four *A. media* individuals, with a VML of 35–67.5 mm. He advocated a separation between *A. subulata* and *A. media* and reveal that *A. subulata* had been the dominant species in northern waters while *A. media* dominates southern waters.

To date, the occurrence of *A. media* in the North Sea is still controversial, due to the difficulties to differentiate *A. subulata* and *A. media* (Anderson et al. 2008). However, Gebhardt and Knebelberger (2015) did not reveal genetical differences between their North Sea samples, consequently assuming that North Sea *Alloteuthis* is represented by a single species. Most recent results from genetic analyses illustrate that around Ireland, *A. media* is the main species present compared to *A. subulata*, and illustrate a high level of misidentification of both species (Sheerin et al. 2021).

Oegopsida

A few historical documentations are available about the existence of the giant squid *Architeuthis dux* (former known as *A. monachus* or *Architeuthis* sp.) in the North Sea and adjacent waters (Grimpe 1925). Between 1556 and 1925, ~10 documented observations exist for the North Sea (including Skagerrak and Kattegat). To our best knowledge, another 23 individuals were recorded after 1925. Notable years are 1949, 1954 and 1982 with two or three reported individuals each (Rae 1950; Stephen 1950; Muus 1959; Knudsen 1957; Brix 1983; Roeleveld 2002; Hoving et al. 2006). The North Sea is too shallow for this deep-water species and the presence of the species is occasional and usually ends up in stranding and death. Also, most individuals reported in the 1930's were dead or in bad condition, so Clarke (1933, 1939) concluded that the individuals drifted into the North Sea. However, the last individual was observed in 1998 near Newburgh in Scotland (Collins 1998).

In the last century, only one single reliable record of *Brachoteuthis riisei* (formerly known as *Tracheloteuthis riisei*) was described by Hoyle (1905). The individual was fished between the Shetlands and Bergen in December 1868 and had a total mantle length of 12 mm. *B. riisei* is a cosmopolitan pelagic oceanic squid that occurs from near the surface to 3000 m depth (Roper and Jereb 2010). It can be assumed that this specimen's existence was accidental. Within the last 20 years, only one evidence of *Brachoteuthis* sp. was documented in 2019 within the ICES-NS-IBTS Quarter 1 in the most Northern area (ICES 2020a), so that the species can still be classified as accidental immigrant.

In former years, *Stenoteuthis caroli* and *Stenoteuthis bartrami* were summarized as *Ommastrephes bartramii* (Dunning 1998) and most recently considered as *Ommastrephes caroli* (Fernández-Álvarez 2020). Grimpe (1925) described the two species separately and mentioned less reliable records per species. However, single individuals were described by different authors for the North Sea (e.g. Robson 1925; Hertling 1938) though the species

was scarce there. Hertling (1938) had indication for a strong oceanic inflow with higher temperatures and salinities before an individual stranded at Juist (German Bight) in winter 1935 and reveal that its occurrence is linked to it. Recently, the species has not been documented (ICES 2020a, b) at all.

Lönnerberg (1891, as cited in Grimpe 1925) mentioned that *Onychoteuthis banksii* had been captured near Gothenburg and along the Swedish coast of the Kattegat and Skagerrak. Grimpe (1925) mentioned a few records of *O. banksii* and assumed that the species enters the North Sea along the Norwegian trench. Within the last years two single *O. banksii* were observed during ICES-NS-IBTS in February 1999. One of those individuals had a DML of 115 mm and was caught in the central North Sea, the other, a female with 170 mm DML, in the entrance of the English Channel (de Heij and Baayen 2005). It seems that the species has never regularly occurred in the North Sea as it requires deep seas for reproduction.

In the last century, three individuals of *Sthenoteuthis pteropus* had been supposedly found in the North Sea; a living individual had washed ashore at North Berwick (West Scotland) (Ritchie 1922). An incomplete specimen with a total length of 132 cm was obtained in 1883 at Scarborough (England), and a perfectly preserved individual with a total length of approximate 191 cm was captured in 1884 (Goodrich 1892). An additional single female was captured in Salcombe (western English Channel) in 1892 (Goodrich 1892). However, the original description of the species by Steenstrup was based on a bad preserved specimen of *Ommastrephes caroli* (former *O. bartramii*) (Zuev et al. 1985) and descriptions of Goodrich (1892) and Lönnerberg (1891, as cited in Grimpe 1925) indicate that it was *O. caroli* that was handled and not *S. pteropus*. The real *S. pteropus* was described by Addison Emery Verrill as congeneric to the giant squid, “*Architeuthis megaptera*” which explains Ritchie’s (1922) “Giant squids on the Scottish coast” publication. *S. pteropus* is widely distributed in warm temperate surface waters of the high seas in the tropical and to some extent subtropical Atlantic where annual surface water temperatures exceed 16 °C. Further north (20–45°N) it is substituted by *Ommastrephes caroli* (Filippova 1974; Zuev et al. 1976, 1985; Laptikhovsky and Nigmatullin 2005). Consequently, there is no reliable evidence that *S. pteropus* has ever been found close to the North Sea.

Sepiidae

Grimpe (1925) was unsure about the occurrence of *Sepia elegans* in the North Sea because the only evidence was of one individual, collected by a fisherman taken from a cod stomach most likely near Northumberland (NE England). All other documentations are based on beached cuttlebones in the southern area. Recently, single individuals are fished in the North Sea (Oesterwind 2011; Goud et al. 2019) and it seems that the species is an accidental migrant there though it is common in the western English Channel, west of 4°W (pers. obs. Laptikhovsky).

Grimpe (1925) described two different groups of *Sepia officinalis*; a summer group *S. officinalis filliuxi* and a winter group *S. officinalis typica*. While the summer group migrated considerable regularly into the southern area for spawning, the winter group visited irregularly the North Sea. In general, he described a southern distribution with a sporadic occurrence around Helgoland or even further North with a spawning period from May to July. Recently *S. officinalis* migrates in spring from the English Channel into the southern coastal North Sea waters for spawning (Goud et al. 2019). Single individuals might migrate further North close to the coast up to Danish waters, into the Skagerrak and

Baltic (Goud et al. 2019) but to our best knowledge, only cuttlebones were reported from Baltic and current datasets indicate a southerly distribution (Hornborg 2005; ICES 2020a, b). Consequently, it seems that only one of Grimpe's described groups exist anymore (if two really ever existed) and that spawning shifted from summer to spring.

It seems most likely that *Sepia obignyana* was absent in the North Sea 100 years ago. No reliable documentation was mentioned by Grimpe (1925); he noted that the species occurs in the English Channel and that it might rarely occur close to the southern entrance to the North Sea, but even cuttlebones were not washed up on the beaches. Currently the species is documented for the southern Channel (ICES 2020b) and some single individuals were documented for the North Sea (ICES 2020a).

Octopoda

There is no evidence of *Bathypolypus* sp. until the beginning of the twentieth century within the North Sea but it was known for the Norwegian Trench and the Faroer Channel (Grimpe 1925). Within the last 20 years, *Bathypolypus* sp. was caught in the Skagerrak but the species was unknown (IBTS 2020a). After Muus (2002) it is most likely *Bathypolypus bairdii* while Goud et al. (2019) assume that it is *Bathypolypus arcticus*.

Historically, *Eledone cirrhosa* and *Octopus vulgaris* occurred in the North Sea and were regularly misidentified (Grimpe 1925). *E. cirrhosa*, was distributed throughout the area and more common than the more southern distributed *O. vulgaris* (Grimpe, 1925). Nowadays, only some single individuals of *O. vulgaris* are documented (ICES 2020a, b) with high probability that those individuals were misidentified *E. cirrhosa*. Goud et al. (2019) describe that it seems that *O. vulgaris* has disappeared from the Dutch continental shelf, where it is likely that a population existed until the 1940ies. It seems likely happening simultaneously with its disappearance from southern waters of the UK after the extremely severe winter of 1962/1963 with many dead thermophile organisms (Crisp, 1964). Since, there were reports of its presence in the western Channel off Dorset and

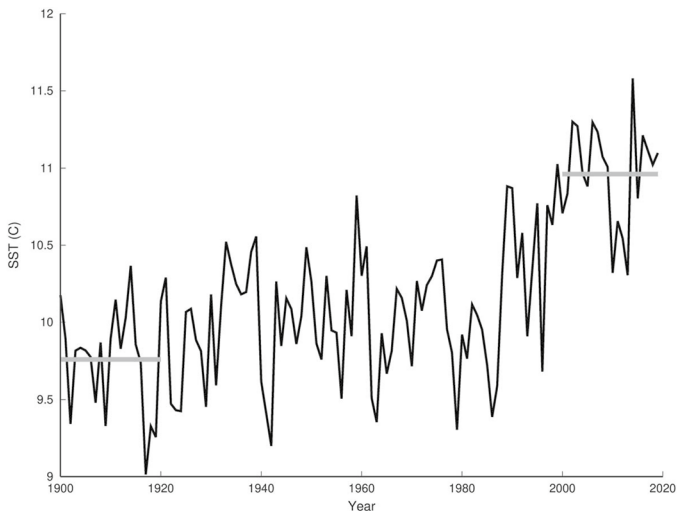


Fig. 8 Annual average SST changes in the North Sea for the last century. Horizontal grey lines are the averages for the 20y periods 1900–1920 and 2000–2020

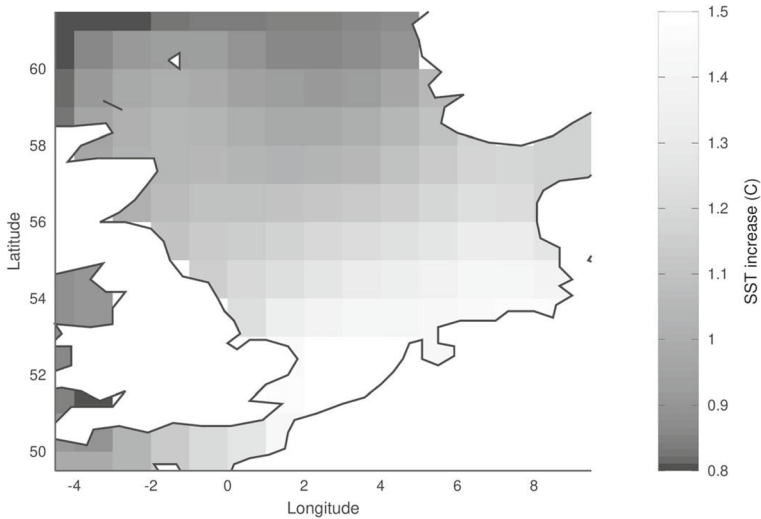


Fig. 9 Annual (J–D) Hadley SST increase between periods 1900–1920 and 2000–2020

Devon but nowhere close to the North Sea (<https://www.glaucus.org.uk/Homepage.html>). In contrast, it seems that the current distribution of *E. cirrhosa* has not changed within the last century (Oesterwind et al. 2010, 2011; Goud et al. 2019).

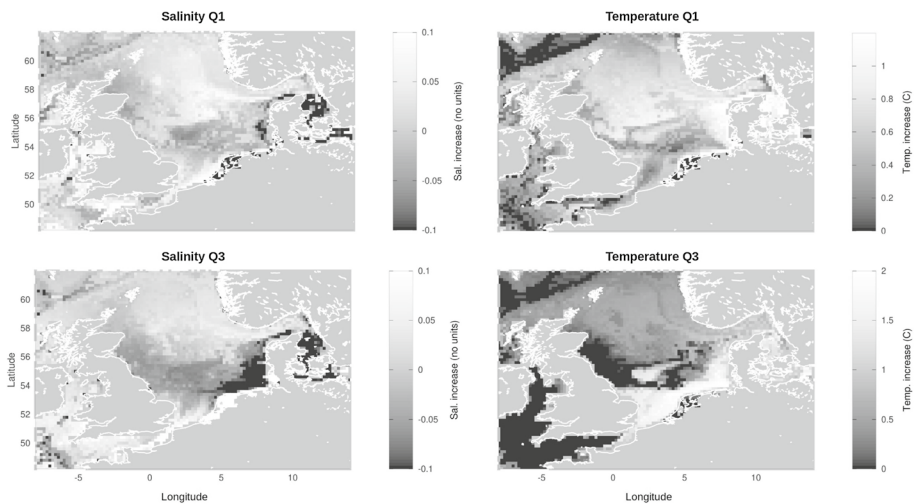


Fig. 10 Changes of Adjusted Hydrography Optimal Interpolation (AHOI) bottom temperatures and bottom salinities for Q1 (January–March) and Q3 (July–September) between 1950–1960 and 2007–2017. Left panels: salinities; right panels: temperature; upper panels: Q1; bottom panels: Q3. Note different grey scales for Q1 and Q3

Environmental changes

The updated average annual SST reveals similar results as described by Huthnance et al. (2016). Average SST increased by more than 1 °C, from 9.8 °C in 1900–1920 to almost 11 °C in 2000–2020 (Fig. 8). The SST changes are strongest in the southern North Sea with an increase of more than 1.5 °C (Fig. 9).

SBT increased since 1950 with a maximum of 2 °C in summer in the southern area. In winter the maximum increase is about 1.2 °C at the coastal waters of Belgium, Netherlands and Denmark, but an increase of about 1 °C is also observable in the deeper parts of the North Sea especially north of the Dogger Bank, Fladen Ground and the Norwegian Trench (Fig. 10).

A comparison between 1950–1960 and 2007–2017 shows that SBS increased around 0.1 in the northern parts of the North Sea and in coastal waters but decreased up to 0.1 in the central part of the North Sea especially in the German and Dutch coast in summer (Fig. 10). In winter (Q1), SBS increased especially around the Fladen Ground and close to the English Channel (Fig. 10). These changes agree with similar increases of salinity almost everywhere in the North Sea from 1971 to 2012 as reported by Huthnance et al. (2016).

Scarce North Sea water velocity observations does not allow a similar analysis of centennial or multi-decadal variability like with temperature. An alternative to the observations is the hydrodynamic models, which despite being widely applied to the North Sea, still need improvement to reach the accuracy needed to isolate the climate scale from the multi-decadal and shorter time scales (see for instance, Huthnance et al. 2016). Moreover, hydrodynamic models need information about atmospheric changes like wind and sea level pressure, which were either not available or very scarce in the early twentieth century. However, considering that strong inflows into the North Sea correspond frequently to high-salinity events (Sundby and Drinkwater 2007) multi-decadal trends of salinity could be used as a rough proxy for changes of Atlantic inflow. The salinity changes indicate a salinity increase, especially in winter in the central North Sea, which could indicate an increasing inflow of Atlantic waters to east of the Shetlands. Increase of temperature in the deep Norwegian trench also suggests an increase of deep warm Atlantic inflow.

Discussion

Unavailable, uninterrupted long-term data of North Sea cephalopods hinders a species-specific analysis of the dynamics of changes in the cephalopod biodiversity as a response to climate change. Yet, our results illustrate that historical studies in combination with recent data can help to fill this gap, and enable a description of ecological changes in the absence of a long data time series. We were able to illustrate significant changes in the cephalopod community of the North Sea within the last 100 years, underpinning the high adaptability and plasticity of cephalopods (e.g. Boyle et al. 1995; Collins et al. 1995; Doubleday et al. 2016) and indicating that the last century has been a period of pronounced cephalopod expansion in the North East Atlantic.

Fishing methods used for the cephalopod documentation have been somewhat different between both centuries, but both datasets are based on demersal fishing. While the recent dataset included standardized beam trawls and bottom trawls for the last 20 years, Grimpe (1925) analysed preserved and fresh samples and all fishing reports which were

documented and provided within 18 years of fishery research on the imperial research steamer, Poseidon. Furthermore, he included different publications and observations in his study (Grimpe 1925). Hence, abundances or biomasses cannot be compared quantitatively based on the available data sets so that we have focused on the distribution and species' biology. However, we could illustrate an increasing landing biomass of cephalopods within the North Sea, and even though it is unknown whether landings are predominantly driven by species abundance, economic developments or changes in policy (Probst and Oesterwind 2014), they might indicate an increasing abundance.

Grimpe (1925) did not provide any effort data, 'zero' catches or detailed gear information (e.g. mesh size). This information would allow a better estimation of the comparison of both data sets, because maximum length and species documentation (occurrence) are depending on the sampling effort and gear selectivity. However, his analyses summarized recordings of cephalopod presence independently of the gear (including various different bottom trawls). Grimpe (1925) did not provide length data for all observations and in the past VML was the standard measure, so the comparison of maximal mantle length should be interpreted with caution. He confirmed that the whole North Sea had been sampled up to several times a year and is convinced that his conclusions are not biased through an insufficient sample size in space and time (a compiled map is given in the electronic supplementary material; esm1). Indeed, the lack of information illustrates somewhat the limitation of the study but even though a quantitative statistical analysis with robust data would obviously be ideal, such analysis is unfortunately impossible because the needed data does not exist for the entire time period targeted here (i.e., since the 1920s). The goal of our study is, however, to make a semi-qualitative comparison within the limitations of the available data, i.e., those data collected by Grimpe (1925). He observed small species like Sepiolidids and paralarvae of *A. subulata* and assumed that larger areas of no records within 18 years represent areas where the respective species is absent. Grimpe (1925) generally reported about a wide range of length data and in some cases (e.g. *A. subulata*) he provides comprehensive length measurements, which (i) are directly comparable to the data for the recent decades and (ii) illustrate that small (even Sepiolidida) and large individuals were fished. Consequently, it can be assumed that presence and absence information of smaller life stages like small *L. forbesii* are generally reliable and that a comparison between both datasets and his observations of the different species is valid. Another limitation might be due to the different life cycle knowledge and the resulting assumptions about 100 years ago. In Grimpe's period, it was generally assumed that the life span of cephalopods lasts longer than what we now know is realistic, which might have led to misinterpretation of different observations (e.g. migration routes). An annual life cycle for *L. forbesii* for example, was first published in 1974 (Holme 1974); until that, wrong ideas about its life span were assumed. A current study illustrates a maximum age of ~480 days for *L. forbesii* in the North Sea (Oesterwind et al 2019). However, Grimpe (1925) already assumed an annual life cycle for *A. subulata* and most Loliginids but was unsure about the lifespan of *L. forbesii* because both, an annual but also multi-years lifecycle was theoretically possible for him. Consequently, Grimpe's (1925) description of the historical migration pattern of *L. forbesii* and *A. subulata* is realistic for us.

A detailed analysis of the influence of environmental factors on the cephalopods (as through habitat models) is unfortunately not possible due to the time lag between both observation periods. However, it is very likely that temperature change is a strong driver for our observed changes. Cephalopod populations are suggested to be highly responsive to climate change (Sims et al. 2001; Hastie et al. 2009) especially temperature alterations, which seems to explain the variation in abundance distribution and migration (Brodziak

and Hendrikson 1999; Bellido et al. 2001; Pierce and Boyle 2003). For example, the distribution patterns of *Loligo* in the North Sea in February appeared to be strongly related to bottom temperature and salinity (Pierce et al. 1998). However, abundance and seasonal migration in combination with environmental conditions are also discussed for other North Sea cephalopods (Oesterwind et al. 2010, 2015).

The increase of 1 °C in average SST in the last century (Fig. 8) is one considerably larger than the standard deviation of inter-annual SST changes, which is approximately 0.4 °C. The two study periods (1900–1920 and 2000–2020) also include the lowest and highest SST values recorded in the last century, accounting for an increase of 2.5 °C: Minimum SST of 9 °C occurred in 1918, while maximum SST of 11.5 °C was recorded in 2015. These remarks indicate that our centennial SST changes are a significant increase which appears plausible to have had an impact on the biology of North Sea cephalopods. Spatial distribution of both, the cephalopods and temperature changes, correlate and also speak for an impact of climate. In many cases of the twentieth century, there was a higher cephalopod species richness in the southern North Sea with a higher presence of cephalopods and a lower biodiversity with less presence of cephalopods in the north. In the twenty-first century the situation has been mostly inverted, especially due to the northward expansion of *L. forbesii* and *A. subulata*, as well as due to the establishment of *T. eblanae* and *I. coindetii*. Similar northward displacements of biomass, as assumed for the cephalopods, had been already documented and explained with temperature changes (e.g. IPCC 2014). While in the twentieth century the temperatures in the northern North Sea might have been too cold for some cephalopods, the increased temperatures seem to be more adequate now and it seems that at least the newcomers *T. eblanae* and *I. coindetii* are linked to the Atlantic inflow from the north (Barrett et al. 2021).

Our results somewhat contradict van der Kooij et al. (2016) who described a southward migration of *Loligo* and a northward expansion of *Alloteuthis* and ommastrephids within the North Sea. Here, we did not observe a similar southward shift for *Loligo*, because Grimpe (1925) already mentioned a southern occurrence of *L. forbesii* (Fig. 3), similar to the illustrated distribution map presented by van der Kooij et al. (2016). In a broader scale, a decreasing abundance for *L. forbesii* in its southern distribution (France and Portugal) and an increasing abundance in its northern distribution (Scotland) has been described by Chen et al. (2006).

Our different results are most likely due to the different datasets and their potential. Van der Kooij et al. (2016) based their conclusions on a 35 years data series of only the CEFAS portion of the ICES-NS-IBTS, which were sampled in Q3. In addition, their analyses were integrated on higher taxonomic level and species with different physiological characteristics were not differentiated. For example, *L. vulgaris*, which is associated to warmer waters compared to *L. forbesii* (Chen et al. 2006; Anderson et al. 2008) were pooled with *L. forbesii* to *Loligo* spp. Consequently, the observed southern expansion of *Loligo* by van der Kooij et al. (2016) might also be explainable by a higher presence of *L. vulgaris* in the southern North Sea.

Recently, *L. forbesii* is year-around present and has been shown to reproduce in winter and summer in the North Sea (Pierce et al. 2005). Two different spawning forms were supposed to exist in the last century (*L. forbesii typica* as spring spawner and *L. forbesii moulinsi* as autumn spawner), but Grimpe (1925) excluded the occurrence of the spring spawners in the North Sea. Consequently, we can conclude that the second spawning season in the North Sea established within the last century and that the spawning has shifted from spring and autumn to summer and winter, whereby it seems that the summer breeding

population has declined since the 1970s and the winter breeding population now dominates (Pierce et al. 2005).

Changes in *A. subulata* are also substantial, but have to be interpreted with caution due to the differentiation problems with *A. media*, and should be verified through further genetic analyses. It seems that a North Sea stock has established within the last century and the species performs its total life cycle in the North Sea nowadays. Temperature dependent migration is evident in summer and winter for spawning and aging (Oesterwind et al. 2010). Increased water temperature might meanwhile allow the overwintering of *A. subulata* in the North Sea.

Impressive changes occurred also within the ommastrephids. First, evidence of a newly established stock of *I. coindetii* has recently been detected in the northern and central part of the North Sea (Oesterwind et al. 2020). The establishment of *T. eblanae* dated back to more than 35 years as van der Kooij et al. (2016) illustrate. They also observed changes in ommastrephids, but *T. eblanae* and *I. coindetii* were pooled together so that the establishment of *I. coindetii* could not be detected. The authors' conclusion of a northward expansion of ommastrephids is explainable by the new *I. coindetii* stock in the Northern North Sea, which underpins the importance of a species-specific analysis. *I. coindetii* spawning individuals and a large increase in biomass were first observed around 2015 (Oesterwind et al. 2020) when historical maximum SST was documented for the North Sea. Abundances are highest at the Fladen Ground, an area which is impacted by the East Shetland Atlantic Inflow and therefore characterized by warmer Atlantic waters. SBT shows a relatively high increase at the Fladen Ground compared to other areas, especially in winter.

Other potential drivers like a changing food web, especially the altered abundances of top predators or a combination of abiotic and food web changes are not evaluated within our study, but have to be considered as drivers of change in biodiversity as well. A changing abundance in fish predators is already observed (Temming and Hufnagl 2015), but the impact on the food web is more complex as it can be discussed here (Jennings et al. 2002).

One of the effects of the cephalopod expansion is that fishers have adapted to the new fishery resource in recent years, as e.g. *L. forbesii* exploitation has become commercially viable especially off the Scottish coast (Hastie et al. 2009; Pinnegar et al. 2016). Recreational fishery for these squids is also developing in the UK and Norway. Hence, because cephalopods have become a relevant fishery resource in the North Sea the need for a sustainable management of commercial relevant cephalopods increases. Furthermore, the described changes had and will have significant impact on the North Sea ecosystem and therefore need further investigations. It may already be inferred that trophic interactions and energy flow in the North Sea and adjacent waters have changed substantially due to the expansion of cephalopods.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-022-02403-y>.

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Data availability The data that support the findings of this study are openly available in ICES Datras at <http://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>.

Code availability Not applicable.

Declarations

Conflict of interest There is no conflict of interest or competing interest.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

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