Climate change and squid range expansion in the North Sea
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ABSTRACT

Aim Studies focussing on long-term changes in squid populations are rare due to limited availability of fisheries-independent data. However, squid play an important role as predator and prey in marine food-webs and have also become an increasingly important target for fisheries. Their short life history is thought to make them particularly sensitive to changes in the environment, potentially leading to strong fluctuations in population size. Here, we investigate whether squid have increased in the North Sea, in terms of distribution and abundance, and whether these patterns are related to variability in environmental and climatic factors.

Location North Sea, north-east Atlantic Ocean.

Methods We extracted squid catches from a unique 35-year time series of bottom trawl survey data in the North Sea (1980–2014), collected during late summer (August–September). Changes in distribution and abundance were compared with climatic variables known to be linked with various ecosystem components in the area.

Results We found that squid distribution across the North Sea increased over the 35-year time series. Loligo expanded southward from a predominantly north-easterly distribution, compared to northward expansions by Alloteuthis and the Ommastrephidae from their core distributions in the southern and central North Sea respectively. In addition, all squid species studied here displayed an overall increase in biomass over the time series and there were large annual fluctuations. Significantly positive relationships were found between this increase and climate variables for each of the dominant individual taxa studied and when all species were combined.

Main conclusions The results suggest a strong causal relationship between climate variability, notably warming sea temperatures, and squid populations. At least for the last 35 years, climate change appears to have been largely favourable for squid and with changes in climate set to continue, squid may end up beneficiaries where many finfish struggle.

Keywords Alloteuthis, Atlantic multidecadal oscillation, climate change, Loligo, North Atlantic oscillation, North Sea, Ommastrephidae, sea surface temperature, time series, Todaropsis

INTRODUCTION

As short-lived, fast-growing members of the molluscan class Cephalopoda, squid play an important trophic role in all marine ecosystems, feeding on pelagic and demersal fishes, other cephalopods and crustaceans (Parry, 2006), and in turn, providing prey for many apex predators (Montevecchi & Meyers, 1995). World-wide catches of cephalopods
including squid have increased considerably over the last two decades (Hunsicker et al., 2010). With several of the main commercial finfish stocks dwindling, squid has been identified as a valuable alternative fishing target (Caddy & Rodhouse, 1998). As with all developing fisheries, it is important to understand population dynamics and possible approaches to assessment and management before these stocks become the target of large-scale fisheries (Pierce & Boyle, 2003). However, management of short-lived species such as squid can be complex, and many traditional methods of population estimation are unsuitable (Pierce & Guerra, 1994; Young et al., 2004, 2006a,b). Critically, annual stock size depends almost entirely on recruitment success and, as in other short-lived species, is therefore expected to be strongly affected by environmental conditions. Consequently, squid abundance appears to respond quickly to changes in the environment and squid catches can be highly variable from year to year (Pierce et al., 2008). A better understanding of the dependency between squid populations and their environment is therefore key to sustainable management of a targeted squid fishery in the future.

The North Sea in the north-east Atlantic Ocean has seen temperature increases in the last three decades at much higher rates than the global average (MacKenzie & Schiedek, 2007). This has been linked to changes in North Sea fish distributions with many species shifting northward (Perry et al., 2005) and into deeper waters (Dulvy et al., 2008). Changes to the pelagic fish community structure have also been linked to climatic warming (Beare et al., 2004; Montero-Serra et al., 2015) with more warm-water dominated assemblages increasing in recent decades. Studies in several sub-areas of the north-east Atlantic Ocean have shown that temperature plays an important role in squid distribution, abundance (Robin & Denis, 1999; Challier et al., 2005), timing of breeding and size at maturity (Pierce et al., 2005). Squid generally favour warmer waters in the winter and cooler waters in the summer. Previous studies of squid populations in the northern North Sea and to the west of Scotland have shown that population size links to larger scale climatic variation, such as the North Atlantic Oscillation (Pierce & Boyle, 2003). This relationship holds for populations further south towards French and Portuguese waters (Pierce et al., 2008). Although survey and landings data from the English Channel have received some scientific interest in recent years (Challier et al., 2005), no studies have been able to investigate squid populations in the whole of the North Sea over multiple decades. Commercial squid catches in the North Sea have been variable but show a growing trend over recent decades (Fig. 1), and there is uncertainty whether this trend reflects abundance, or is due to fishing effort on squid (Pierce et al., 2008).

Several species of squid are documented from the North Sea, predominantly belonging to two families: short-finned squid, Ommastrephidae, and long-finned squid, Loliginidae. Ommastrephid squid tend to be oceanic and more pelagic (Dawe et al., 2007) so, although present in the North Sea in small numbers, they are less likely to be caught by the demersal gears currently used in most of the North Sea mixed fisheries (Pierce et al., 2010). In contrast, loliginid squid are generally demersal and found in relatively shallow water, and are therefore a much more likely bycatch. The North Sea is thought to represent the distributional boundary of several loliginid species, including the veined squid, Loligo forbesii Steenstrup, 1857, which is commercially the most important species in the UK. Although the biogeographical range of L. forbesii is extensive, including both temperate and subtropical waters of the eastern Atlantic from 60° to 20° N, the species is near its northern limit in Irish and British waters. The closely related European squid, Loligo vulgaris Lamarck, 1798 has been found in waters to the west of Scotland, and in the English Channel, and specimens have also been recorded in the southern North Sea (Tinbergen & Verwey, 1945; de Heij & Baayen, 2005). A third loliginid species, the European common squid, Atloteuthis subulata (Lamarck, 1798), is thought to be the most abundant squid species in the North Sea and has been shown to undertake seasonal migrations between the southern North Sea in the summer and northern North Sea in winter (Oesterwind et al., 2010). Despite its abundance, A. subulata is not a valuable commercial species due to its smaller size. Preliminary observations on the environment and squid in the North Sea have been made (e.g. de Heij & Baayen, 2005), but longer term patterns in squid distribution and abundance have not been examined in this area.

In this study we explore patterns in squid distribution and abundance using a unique 35-year survey data set from the North Sea. The principal aim is to expand our understanding of squid and the dependency of population size and distribution and assess the effect of climate change. We distinguish between the possible effects of large-scale climate drivers and local environmental variability (sea temperature). We hypothesize that squid distribution and abundance in the North Sea have increased and that these patterns are related to variability in climatic factors.
MATERIALS AND METHODS

Survey data

Data collection

Squid catches were collated from bottom trawl hauls from the North Sea International Bottom Trawl Survey (IBTS: ICES, 2013). It is a long-running, internationally coordinated survey, which aims at providing fisheries-independent data to underpin management of demersal fish species. Although several nations contribute to this survey, in this study only catches from the English component were included. This annual survey takes place in August and September (Quarter 3) and samples the same 74 stations across the North Sea between 51° and 62° N latitude (Fig. 2). The stations are designed in a regular grid to achieve one fishing sample in each 0.5° latitude x 1° longitude grid cell. Sampling takes place during daylight hours only. All fish species caught are identified, weighed and measured. Other organisms, including squid, were traditionally identified (often to species level, except in some of the earliest years of the survey), and the total catch per species weighed and counted. Length measurements on squid have only been made routinely since 2004. The survey dates back to 1980 and although the programme has deliberately been standardized as much as possible, some changes in the sampling programme have occurred over time. Most significantly, in 1992 the trawl design was changed from a Granton to a Grande Ouverture Verticale (GOV). The GOV has a higher headline height than the Granton (c. 5 m vs. 4 m) but, as many squid species are nocturnal predators and are likely to reside close to the seabed during the day (i.e. well within 4 m from the seafloor), both gears were assumed here to sample squid equally effectively.

Species identification

Over the course of the survey, nine categories of squid were recorded [at species (six), genus (two) or ‘generic’ (one) level] that reflect improvements to squid identification over time, but which had to be adjusted and re-categorized for
our analysis. For this study, we distinguished four taxonomic groupings.
1. Total squids, including all loliginid and ommastrephid species combined.
2. Loligo, including the dominant species Loligo forbesii and L. vulgaris, which unfortunately were not always distinguished reliably prior to 1998. Given that L. vulgaris were only encountered in very small numbers, the Loligo category was assumed to consist predominantly of L. forbesii.
3. Alloteuthis subulata was recorded in some earlier years (1980, 1983–1984, 1994) and frequently from 1997 onwards. The lack of records in many of the early years was likely due to A. subulata not being distinguished as a separate species rather than being absent. A second species in this genus, Alloteuthis media, has been previously recorded in the southern North Sea in summer. However, there are difficulties in separating the two species based on morphological characteristics, and ongoing uncertainties about the taxonomic status led us to refer to both species as A. subulata (Laptikhovsky et al., 2005; Jereb et al., 2015).
4. Ommastrephidae, consisting predominantly of Todaropsis eblanae (Ball, 1841), although at least one other species – Illex coindetti (Verany, 1839) – was confirmed in 1 year (2005). Given the more pelagic lifestyle of ommastrephid squid, the survey data were expected to sample this group less adequately and with genus- or species-level data lacking for many earlier years in the time series, analyses were only carried out at family level.

Data analysis
For each of the four squid categories, we calculated two variables; one representing abundance and one distribution. As a proxy for abundance, the annual mean catch rate was calculated, (standardized as kg per hour), and averaged over all stations; including only the time where the trawl was in contact with the seafloor. Distribution was calculated as the proportion of stations at which squid were found in a given year, also referred to as occurrence.

Environmental data
Long-term environmental data series were collated from different sources. As a descriptor of water temperatures experienced by the squid within the North Sea, we collated data on sea surface temperature (SST) from the Met Office Hadley Centre observations data set (HadISST; www.metoffice.gov.uk), through the Met Office Marine Data Bank (MDB), and from the International Comprehensive Ocean-Atmosphere Data Set (ICOADS). The spatial resolution of SST was a 1° latitude by 1° longitude grid. For the North Sea (ICES Sub-area IV, Fig. 2), we calculated both annual mean SST, and summer- and winter SST, where summer was defined as the months June–July–August, and winter as December–January–February (with December referring to the year prior to the focal year). We also included the lagged effects (−1 year), the annual- and summer SST of the previous year. Although exploratory analyses included spring and autumn SST, these variables were removed owing to their strong correlations with SST in consecutive seasons (as opposed to weaker correlations between summer and winter SST).

As well as local conditions, three climate indices of wider scale than the North Sea were examined. The Atlantic multi-decadal oscillation (AMO) index was used as a proxy for North Atlantic Ocean-wide sea temperature conditions. It is a climate mode that manifests itself as a 20–30 year cycle in de-trended sea surface temperature series for the North Atlantic Ocean (Enfield et al., 2001). These data were obtained from the National Oceanic and Atmospheric Administration Centre (NOAA) at www.esrl.noaa.gov/psd/data/correlation/amon.us.data. The North Atlantic oscillation (NAO) index (Hurrell, 1995) was used as a proxy for atmospheric conditions. The NAO is defined here as the normalized (atmospheric) sea level pressure difference between the Azores (high) and Iceland (low). A positive winter index is characterized by stronger westerly winds bringing relatively warm conditions to western Europe. Winter NAO indices (December–March) were obtained from the Climatic Research Unit of the University of East Anglia (www.cru.uea.ac.uk/cru/data/nao). Finally, inflow into the northern North Sea from the North Atlantic Current has been associated with regional climate variability, productivity and changes in species distribution and migration (e.g. Reid et al., 2003). We used monthly predictions of northern inflow (between Orkney, Scotland and Utsira, Norway) derived from a coupled physical, chemical and biological model system (NORWECOM, Skogen et al., 1995), and collated through the ICES Oceanography Data Portal (http://ocean.ices.dk/iroc/IROC.aspx).

Statistical analysis of squid-climate relationships
We conducted a correlation analysis to explore which individual climate variables were associated with changes in the abundance and distribution of each of the four taxonomic groups of squid: total squid, Loligo, Alloteuthis and Ommastrephidae. Pearson cross-moment correlations \((r_p)\) were used, as the variables did not show distributions significantly different from normality (one-sample Kolmogorov–Smirnov tests, \(P > 0.05\)) except squid catch rates which were log-transformed to achieve normality. To include zero catch rates, a small value was added before log transformation, equal to half the smallest non-zero value (\(\text{sensu}\) Maxwell & Jennings, 2005). There was, however, moderate to weak autocorrelation within several of the time series variables. To account for this, the test procedure for significance of correlations was adjusted (Pyper & Peterman, 1998) by reducing the effective degrees of freedom (increasing the \(P\)-values) according to the degree of autocorrelation; adjusted \(P\)-values are hereafter referred to as \(P_{adj}\).

We used generalized linear models (GLM) to examine the relative importance of different climatic variables on both
metrics of squid abundance (log catch rate and occurrence) for each of the four taxonomic categories. Climatic variables included were annual mean SST, previous year’s SST, AMO index, NAO winter index and North Sea inflow. In addition, the models included year as a variable, to account for possible temporal autocorrelation. A backward selection procedure was used. Starting with a full model that included all environmental variables plus the year effect, gradually all variables not contributing significantly to the fit were removed (P > 0.05). After a final model was obtained it was checked whether adding second-order interactions would significantly improve its fit (F-test with P < 0.05). Where catch rate was the response variable, the GLM of the following form was considered:

$$\log (\text{catch rate} + i) \sim \text{SST} + \text{SST}_{y-1} + \text{AMO} + \text{NAO} + \text{Inflow} + \text{Year}$$

(1)

where $i$ was calculated as half the smallest non-zero catch rate. Where occurrence (% of sampling stations where caught) was the response variable the GLM was a logistic regression of quasibinomial family, of the following format:

$$\text{logit (occurrence)} \sim \text{SST} + \text{SST}_{y-1} + \text{AMO} + \text{NAO} + \text{Inflow} + \text{Year}$$

(2)

RESULTS

Trends in squid populations

We found that squid biomass and distribution (occurrence) across the North Sea have increased over the 35-year time series (Fig. 3). Although strong fluctuations are apparent, the mean catch rate of squid by weight (all species combined), as monitored between 1980 and 2014 during the Summer IBTS, has increased significantly (Fig. 3a, $r^2 = 0.255$ on log-transformed catch rates, $P = 0.003$). Squid occurrence in the North Sea has also seen a strongly significant increase as indicated by the proportion of stations where squid were encountered (Fig. 3b, $r^2 = 0.594$, $P < 0.0001$).

Figure 3 Long-term trends in annual mean catch rates (on log scale; a, c) and occurrence (% of sampling stations where caught; b, d) of all squid species combined, and *Loligo* (a, b); and of *Alloteuthis subulata* and the family Ommastrephidae (c, d) in the North Sea.
Loligo accounted for the greatest proportion of observed squid biomass in the North Sea, in many years well over 90% (Fig. 3a). Accordingly, there was an increasing trend in Loligo log catch rates ($r^2 = 0.192$, $P = 0.016$) closely resembling the trend for total squid. Likewise, occurrence of Loligo increased (Fig. 3b, $r^2 = 0.264$, $P = 0.004$). Within the genus Loligo, species identification was only routinely done from 1998 to 2014; during that period L. vulgaris accounted, on average, for only 1.6% of all Loligo biomass caught in the survey. The Loligo biomass in the North Sea presented here was overwhelmingly dominated by L. forbesii (98.4%).

There were also increasing, albeit variable, trends for Alloteuthis (Fig. 3c,d; log catch rate, $r^2 = 0.329$, $P = 0.005$; occurrence, $r^2 = 0.417$, $P = 0.001$). Ommastrephid squid abundance also increased (log catch rate, $r^2 = 0.502$, $P < 0.0001$; ommastrephid occurrence, $R^2 = 0.45$, $P < 0.0001$). While the possibility exists that the lack of records of ommastrephids during the earlier period was due to incorrect identification, very few specimens were present when it was first recorded which suggests that misidentification did not play a major role.

Squids in general have become more widely distributed within the North Sea; in the early 1980s squid were mainly recorded in the north-western and southernmost parts, but they are now almost ubiquitously present (Fig. 4a). The genus Loligo, mainly recorded in the northern North Sea during the 1980s, has been widespread also in the southern and central North Sea during the most recent two decades (Fig. 4b). Records of Alloteuthis were more widespread in the southern and central North Sea after the mid-1990s than before, acknowledging that during 1985–1989 the taxon was not distinguished in the survey data (Fig. 4c). Ommastrephids, rarely recorded before 1995, were recently observed in many of the deeper parts of the central-western North Sea (Fig. 4d).

**Changes in climate and environment in the North Sea**

The annual mean sea surface temperature (SST) in the North Sea has risen significantly from 1980 to 2014 ($r^2 = 0.45$, $P < 0.0001$), from c. 10 °C in the early 1980s to a record 11.7 °C in 2014 (Fig. 5a). There has, however, been some short-term variability; cooler periods in 1984–1986, in 1996, and recently between 2010 and 2013. When broken up by season the rising trend in SST was less clear for winter SST ($r^2 = 0.120$, $P = 0.042$), which showed very high interannual variability (Fig. 5b), but was strong for summer SST ($r^2 = 0.423$, $P < 0.0001$; Fig. 5c).

The Atlantic multidecadal oscillation (AMO) index has also increased significantly from 1980–2014 ($r^2 = 0.519$, $P < 0.0001$), displaying mostly negative values before 1997 followed by predominantly positive values (Fig. 5d). By contrast, there was no long-term trend in the North Atlantic oscillation (NAO) winter index between 1980 and 2014 ($r^2 = 0.029$, $P = 0.327$; Fig. 5e). In most years the NAO winter index was predominantly positive interspersed with only a few mildly negative values, apart from in 1996 and 2010 when it was strongly negative. Inflow from the North Atlantic Ocean into the northern North Sea was highest (most negative values) between the late 1980s and mid-1990s (Fig. 5f). The general trend from 1985 to 2014 showed a decreasing inflow into the North Sea ($r^2 = 0.314$, $P = 0.001$).

The AMO index was strongly correlated with the North Sea’s annual mean SST ($r = 0.59$, $P_{adj} = 0.0015$, adjusted for temporal autocorrelation in both variables). However, neither variable was correlated with the NAO winter index (AMO: $r = –0.205$, $P_{adj} = 0.238$; SST: $r = –0.267$, $P_{adj} = 0.121$). Seasonal measures of North Sea SST were strongly correlated with each other when consecutive seasons were compared (i.e. autumn with winter SST, winter with spring SST, etc.; all $r > 0.6$, $P_{adj} < 0.001$); the correlation between winter and summer SST was less strong, although still significant ($r = 0.355$, $P_{adj} = 0.038$). Influx of Atlantic water into the northern North Sea was not correlated with either the North Sea SST or the NAO index ($P_{adj} > 0.05$), but weaker inflow was associated with a more positive AMO index ($r = 0.442$, $P_{adj} = 0.02$).

**Climate response**

Both measures of combined squid abundance, log catch rate and occurrence, were positively correlated with annual mean SST in the North Sea (Fig. 6, Table 1), and with the AMO index. Strong positive correlations were also found for both squid abundance and occurrence, with North Sea SST during the previous year, and with seasonally averaged SST values (Table 1). There was no correlation with the NAO winter index or with the Atlantic inflow into the northern North Sea (Table 1).

All three taxa, Loligo, Alloteuthis and Ommastrephidae, showed strongly positive correlations (Fig. 6) with North Sea SST, North Sea SST lagged by 1 year, and seasonal (summer and winter) SST (Table 1). Loligo and ommastrephids showed significant correlations with the AMO in contrast to Alloteuthis. None of the taxa showed a significant relationship with the NAO winter index. Ommastrephids were significantly related to a weaker Atlantic inflow into the North Sea (Table 1). No such relationship was found with either Loligo or Alloteuthis.

Using generalized linear models (GLMs) the relative importance of the various climatic variables for the abundance of squid was examined (Table 2). These revealed that annual North Sea SST was the most important variable explaining abundance and occurrence, for the combined squid assemblage as well as the individual taxa: Loligo, Alloteuthis and Ommastrephidae. Following a backward selection procedure from a full model containing all climatic variables, SST was always retained (Table 2). The variable ‘year’, included in the full model to take account of temporal autocorrelation, was always rejected if SST was included as explanatory variable; this implied that both the long-term...
Figure 4  Changes in the spatial distribution within the North Sea of (a) all squid combined, (b) Loligo, (c) Alloteuthis and (d) ommastrephids, shown per 5-year period between 1980 and 2014. Surface area of symbols proportional to catch rate (kg h$^{-1}$) derived from the International Bottom Trawl Survey (IBTS) fishing stations sampled by Cefas vessels. Please note that the absence of ommastrephids (d) between 1980–1989 was due to this species not being caught in the trawls rather than 'no data'.

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SST trend (also captured by ‘year’) and short term, interannual variability in SST (not captured by ‘year’) significantly explained the variability in squid catches (Table 2). For total squid occurrence and *Alloteuthis* abundance, a positive 1-year lagged SST effect was also important. The AMO significantly contributed to explaining total squid catch rate and ommastrephid occurrence, but was rejected in most models that also contained SST. Inflow of Atlantic water into the northern North Sea was retained as a significant predictor of ommastrephid abundance and occurrence. The NAO index was always rejected (Table 2). Finally, gear type was included in the models as a categorical variable to investigate whether the lower squid catch rates in the earlier years of the time series were caused by a reduced catchability due to the slightly lower headline height of the Granton trawl used until 1991. In all cases, gear type was rejected in favour of SST, with the exception of the model explaining *Alloteuthis* occurrence, where the model including SST performed as well as the model including both SST and gear type (not shown). These results indicate that climatic responses by squid are primarily driven by current and previous (1-year lagged) sea surface temperature effects, and in addition by the AMO (in the case of total squid and ommastrephids) and North Sea influx (ommastrephids only).

**DISCUSSION**

This is the first comprehensive study that examines patterns in long-term squid distribution and abundance in the entire North Sea. Both squid distribution and abundance increased in the North Sea over a 35-year study period. We present evidence that these patterns are closely linked with the long-term climatic warming trends in the North Sea as well as with more short-term inter-annual temperature variability. This was found to be the case for all squid combined and for the individual taxa examined (*Loligo, Alloteuthis*, and...
ommastrephids), although the responses to climatic and short-term temperature variability appeared to be species specific.

**Squid responses to climate**

The most widely distributed squid species in the North Sea and the one dominating the *Loligo* category was *Loligo forbesii*. Over the time series, *Loligo* gradually expanded from the north-western and very southern parts of the North Sea to occupy nearly the entire basin. This expansion and increase in abundance were correlated with several climatic variables, including the AMO, but most strongly with a direct effect of annual North Sea SST. This was expected given the short life cycle of squid, and close links demonstrated between the spatial distribution of *Loligo* and warmer sea temperatures in Scottish waters (Waluda & Pierce, 1998; Viana et al., 2009) and the Celtic Sea (Denis et al., 2002). During winter in waters around Scotland, *L. forbesii* was shown to be absent from areas with temperatures lower than 7 °C (Pierce et al., 1998). Within-year variation in catch rates of *L. forbesii* around Scotland was also related with SST (Bellido et al., 2001). The predominantly southward expansion from northern waters may be unexpected given the positive relationship with temperature. It is, however, consistent with the temperature gradient present in the North Sea during the winter when the shallow southern parts are colder than the deeper and more constant temperatures in the north. This suggests that severe winter conditions may have previously rendered southern areas unsuitable for *Loligo*. Similar patterns have been observed in warm-water-associated fish species in the North Sea (Beare et al., 2004; Engelhard et al., 2011b). As expected, the related species *L. vulgaris* was also found although in much smaller numbers (contributing up to 1.6% of the total *Loligo* biomass) and only in the southern part of the North Sea (Oesterwind et al., 2010). We did not observe any years with high *L. vulgaris* abundances, as reported previously in the southern North Sea (Tinbergen & Verwey, 2010).

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**Figure 6** Relationships between North Sea SST (annual mean) and the log catch rates of (a) all squid, (b) *Loligo*, (c) *Alloteuthis* and (d) *Ommastrephidae*, and with occurrence (% of sampling stations where observed) of the same taxonomic groups (e–h). Symbols filled white indicate the years 1980–1989; grey the years 1990–1999; and black the years 2000–2014. Linear regression lines (a–d) and logistic regression curves (e–f) are indicated; all relationships significant ($P < 0.005$).
Table 1 Correlation coefficients between environmental variables and abundance measures (log catch rate and occurrence) of total squid, *Loligo*, *Alloteuthis* and ommastrephids in the North Sea. Environmental variables include: North Sea annual mean sea surface temperature (SST), previous year’s SST (SST<sub>y−1</sub>), the AMO index, NAO winter index (NAO<sub>win</sub>) and North Sea inflow; as well as seasonally averaged SST (winter, summer and previous year’s summer). Statistically significant correlations are emboldened: *P < 0.05; **P < 0.01; ***P < 0.005.

|          | SST       | SST<sub>y−1</sub> | AMO   | NAO<sub>win</sub> | Inflow | SST<sub>win</sub> | SST<sub>sum</sub> | SST<sub>sum−1</sub> |
|----------|-----------|-------------------|-------|-------------------|--------|------------------|-----------------|-------------------|
| All squid| Log catch rate | 0.663*** | 0.581*** | 0.484** | 0.115  | 0.108 | 0.456** | 0.513*** | 0.490** |
|          | Occurrence | 0.811*** | 0.700*** | 0.696*** | -0.072 | 0.178 | 0.474** | 0.690*** | 0.644*** |
| *Loligo* | Log catch rate | 0.514*** | 0.474** | 0.420* | 0.058  | 0.061 | 0.347 | 0.415* | 0.412* |
|          | Occurrence | 0.595*** | 0.441*  | 0.462* | -0.083 | -0.048 | 0.320 | 0.490** | 0.291 |
| *Alloteuthis* | Log catch rate | 0.825*** | 0.797*** | 0.438* | 0.163  | 0.180 | 0.625*** | 0.597*** | 0.716*** |
|          | Occurrence | 0.803*** | 0.665*** | 0.594* | -0.099 | -0.005 | 0.442* | 0.614*** | 0.616*** |
| Ommastrephidae | Log catch rate | 0.586*** | 0.460*  | 0.578*** | -0.167 | 0.425* | 0.375* | 0.603*** | 0.435* |
|          | Occurrence | 0.591*** | 0.493** | 0.659*** | -0.208 | 0.429* | 0.415* | 0.523** | 0.531*** |

There was weak or moderate autocorrelation within several of these variables. To account for this, the test procedure for significance of correlations was adjusted according to autocorrelation following Pyper and Peterman (1998; equation 1). Correlations different from zero at P < 0.05 are emboldened; *P < 0.05; **P < 0.01; ***P < 0.005.

1945), probably because the majority of those observations were from earlier in the year, and were restricted to coastal waters.

*Alloteuthis* dominated the shallow waters (< 50 m depth) of the southern and south-eastern parts of the North Sea during August and September. Its abundance and distribution have increased over the time series, extending, during peak abundance in the early 2000s, into the north and north-west of the North Sea. The observed correlations between *Alloteuthis* abundance and distribution, and SST of the current as well as the previous year were stronger than in any of the other squid categories studied. The above results can be explained by the particularly short life-cycle of *Alloteuthis* (Arkhipkin & Nekludova, 1993), hence a more direct effect of SST on recruitment is to be expected. The absence of detailed commercial landings data on *Alloteuthis* in the North Sea has led to very few previous studies on this species, in particular focussing on the effects of climate. The time series presented here provides, to our knowledge, the first insight into the long-term dynamics of *Alloteuthis* and evidence for strong links to climate.

The Ommastrephidae were typically associated with deeper (> 50 m) waters of the central North Sea. Despite high variability, the prevailing trend over the time series showed an increase in ommastrephid distribution with a northward expansion in years of high abundance. Of all the groups, ommastrephids were most closely linked to large-scale climate variability, including a strong positive relationship observed with the AMO, which represents North Atlantic Ocean-wide temperature conditions. The dominant species recorded in this family was *Todaropsis eblanae*, which occupies more demersal habitats, displays limited migratory behaviour and is likely to also be driven by local conditions. This was reflected by a strong correlation with SST as also reported in Pacific ommastrephid species (Alabia et al., 2016). Our results suggest a significant negative link between inflow and ommastrephids. This appears contrary to previous speculations that sporadic events of high *T. eblanae* abundance in the northern North Sea may be positively linked to hydrographical anomalies such as incursions of warm, high salinity Atlantic Seawater (Hastie et al., 1994). However, the oceanographical characteristics of inflow differ between winter and summer; the relatively constant temperature conditions of the North Atlantic Ocean are warmer than those in the North Sea in the winter and cooler in the summer, because the shallow North Sea responds more quickly to seasonal temperature changes. This negative link also suggests that migration through active transport from Atlantic waters into the North Sea is unlikely. Instead, the results indicate that a reduced inflow combined with warmer local and regional temperatures increased the spatial extent of the species’ potential habitat, which is subsequently occupied through density-dependent processes.

The long-term warming trend in North Sea SST and interannual temperature variability strongly influenced squid abundance and distribution. These long-term patterns in expansion and increased abundance were in part masked by periodic episodes of cooling and warming. For example, a persistent cooler period at the end of the time series, between 2010 and 2013, caused a retraction in distribution and abundance of all squid categories. In the following year, the warmest year of the time series, this retraction in distribution was reversed as demonstrated by an increase in abundance and distribution. Squid in the southern North Sea showed the strongest association with SST alone, whereas squid associated with the deeper waters of the central and northern North Sea were also influenced by large-scale climatic features such as the AMO and inflow of Atlantic water.
Expansion of squid in the North Sea

The increase in squid abundance and distribution is yet more evidence of potentially significant changes occurring in marine ecosystems in response to climate change. The close relationships between squid and climatic variables described here demonstrate unequivocally that squid are to be added to the growing list of marine biota known to be impacted by climate change, ranging from phyto- and zooplankton (Reid et al., 2003; Pitois & Fox, 2006) and jellyfish (Lynam et al., 2011) to fish (Hiddink & ter Hofstede, 2008) in the North Sea. Responses include northward distribution shifts of fish species (e.g. Perry et al., 2005; Rindorf & Lewy, 2006), population expansion originating from local remnant populations (Petitgas et al., 2012) and occupancy of deeper water by fish species associated with colder water (Dulvy et al., 2008). The expansion of squid associated with warm temperatures, appears to mirror the dramatic abundance increases in a large number of warm-water fish species characterized by small body sizes in the North Sea, contrasting with declining trends in a range of boreal, on average larger sized, fish species (ter Hofstede & Rijnsdorp, 2011) and a shift from a predominance of demersal to pelagic species (Kenny et al., 2009; Engelhard et al., 2011a). Therefore, observed prevalence of squid might represent another element in the general reorganization of the marine community structure within the North Sea, as already described for phyto- and zooplankton, jellyfish and fish (Reid et al., 2003; Hiddink & ter Hofstede, 2008; Kenny et al., 2009; Lynam et al., 2011). The recent shift from a cool to a warm biological regime, took place around 1989 (Reid et al., 2001), and a second regime shift was documented for the late 1990s (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014).

In addition to climate change, fishing has also profoundly affected the North Sea fish community (e.g. Jennings et al., 2002; Engelhard et al., 2014), with implications for the balance of the ecosystem. It was beyond the scope of this study to investigate the contribution of over-fishing, specifically the

### Table 2

Results from generalized linear models on the relative importance of different climatic variables for the abundance responses (log catch rate and occurrence) of total squid, *Loligo*, *Alloteuthis* and Ommastrephidae in the North Sea. Climatic variables included were SST (annual mean); previous year’s SST (SST<sub>-1</sub>); AMO index; NAO winter index; and North Sea inflow. For each response variable, the final model is shown following a backward selection procedure, from a full model that included all environmental variables, plus the year effect to account for temporal autocorrelation.

| Response variable | Predictor | Estimate | SE | t   | P     |
|-------------------|-----------|----------|----|-----|-------|
| All squid, log catch rate | SST | 0.588 | 0.121 | 4.845 | < 0.0001 |
| All squid, occurrence | SST | 0.653 | 0.147 | 4.442 | 0.0001 |
|                      | SST<sub>-1</sub> | 0.370 | 0.134 | 2.765 | 0.0010 |
|                      | AMO     | 1.158 | 0.398 | 2.914 | 0.0069 |
| *Loligo*, log catch rate | SST | 0.542 | 0.171 | 3.167 | 0.004 |
| *Loligo*, occurrence | SST | 0.694 | 0.179 | 3.886 | 0.006 |
| *Alloteuthis*, log catch rate | SST | 0.638 | 0.142 | 4.491 | 0.0002 |
|                      | SST<sub>-1</sub> | 0.467 | 0.119 | 3.921 | 0.0009 |
| *Alloteuthis*, occurrence | SST | 1.197 | 0.238 | 5.024 | < 0.0001 |
| Ommastrephidae, log catch rate | SST | 1.087 | 0.286 | 3.794 | 0.0008 |
|                      | Inflow  | 3.538 | 1.129 | 3.134 | 0.004 |
| Ommastrephidae, occurrence | SST | 1.549 | 0.410 | 3.782 | 0.0009 |
|                      | AMO     | 4.713 | 1.324 | 3.561 | 0.0015 |
|                      | Inflow  | 2.834 | 1.183 | 2.395 | 0.024 |

Final models were selected by removing insignificant terms (P > 0.05) and based on lowest Akaike's information criterion. The variables ‘year’ and ‘NAO index’ were rejected from all models. In cases where catch rate was the response variable, the GLM was a simple linear regression on log-transformed values. In cases where occurrence (%) of sampling stations where caught) was the response variable, the GLM was a logistic regression, using a logistic link function and of quasibinomial family.

into the northern North Sea. No evidence was found for an effect of the NAO index on squid, which was surprising as this is generally considered the most pronounced climate signal over the North Atlantic on decadal timescales (Hurrell & Deser, 2010). Previous studies have linked observed temperature dependence by squid to larger scale climatic variables, specifically the NAO (Sims et al., 2001; Zuur & Pierce, 2004; Pierce et al., 2005; Chen et al., 2006). The lack of a clear NAO signal in this study might relate to the recent dis-association between the NAO and temperature as a result of a complex series of changes in the atmospheric and marine climate in the mid-1990s (Alheit et al., 2012). As a consequence, the previous link between a positive NAO index and warmer (milder) Atlantic temperatures ceased to exist and although the NAO entered a negative phase in the mid-1990s, the North Sea temperature has continued to rise (Alheit et al., 2012).

While we have demonstrated that climatic indices and warming sea temperatures have been closely associated with the increased distribution and abundance of squid in the North Sea, the underlying mechanisms remain to be explored. The consistent importance of the SST in explaining squid population dynamics suggests that direct local effects on recruitment and survival played a key role, as opposed to, for example, large-scale immigration from beyond the North Sea. This was also demonstrated by the lack of a positive relationship with North Sea inflow. The strongest evidence for a direct effect on squid recruitment success was found in *Alloteuthis*, where SST of the previous year (lag) was positively related to increased biomass and distribution. Although other studies have found negative temperature-recruitment relationships (Challier et al., 2005), the North Sea represents the northern boundary for some species where cooler temperatures may well be limiting. Future work should focus further on the mechanisms that may account for the population expansion of squid in the North Sea.

Implications for the North Sea ecosystem

The increase in squid abundance and distribution is yet more evidence of potentially significant changes occurring in marine ecosystems in response to climate change. The close relationships between squid and climatic variables described here demonstrate unequivocally that squid are to be added to the growing list of marine biota known to be impacted by climate change, ranging from phyto- and zooplankton (Reid et al., 2003; Pitois & Fox, 2006) and jellyfish (Lynam et al., 2011) to fish (Hiddink & ter Hofstede, 2008) in the North Sea. Responses include northward distribution shifts of fish species (e.g. Perry et al., 2005; Rindorf & Lewy, 2006), population expansion originating from local remnant populations (Petitgas et al., 2012) and occupancy of deeper water by fish species associated with colder water (Dulvy et al., 2008). The expansion of squid associated with warm temperatures, appears to mirror the dramatic abundance increases in a large number of warm-water fish species characterized by small body sizes in the North Sea, contrasting with declining trends in a range of boreal, on average larger sized, fish species (ter Hofstede & Rijnsdorp, 2011) and a shift from a predominance of demersal to pelagic species (Kenny et al., 2009; Engelhard et al., 2011a). Therefore, observed prevalence of squid might represent another element in the general reorganization of the marine community structure within the North Sea, as already described for phyto- and zooplankton, jellyfish and fish (Reid et al., 2003; Hiddink & ter Hofstede, 2008; Kenny et al., 2009; Lynam et al., 2011). The recent shift from a cool to a warm biological regime, took place around 1989 (Reid et al., 2001), and a second regime shift was documented for the late 1990s (Alvarez-Fernandez et al., 2012; Beaugrand et al., 2014).

In addition to climate change, fishing has also profoundly affected the North Sea fish community (e.g. Jennings et al., 2002; Engelhard et al., 2014), with implications for the balance of the ecosystem. It was beyond the scope of this study to investigate the contribution of over-fishing, specifically the
removal of predatory fish or fish that compete with squid, to the increasing abundance of squid in the North Sea. However, the potentially changing role of gelatinous species is of considerable interest (Attrill et al., 2007). Driven by their ability to rapidly respond to favourable environmental conditions, combined with human-induced large-scale changes (e.g. overfishing), these species could significantly benefit from and perpetuate changes in the marine foodweb structure, as has been demonstrated for jellyfish in the Black Sea (Daskalov et al., 2007).

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All authors are involved in research to assess the impacts of fisheries exploitation and climate change on the sustainable management options for commercial fisheries in the NE Atlantic.

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