Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

CrossMark

Long-term variability of the siphonophores *Muggiaea atlantica* and *M. kochi* in the Western English Channel

Michael Blackett [a,b,*], Priscilla Licandro [b], Steve H. Coombs [c], Cathy H. Lucas [a]

[a] *Ocean and Earth Science, National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK*
[b] *Sir Alister Hardy Foundation for Ocean Science, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*
[c] *The Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK*

ARTICLE INFO

ABSTRACT

We investigated long-term variability of the calycophoran siphonophores *Muggiaea atlantica* and *Muggiaea kochi* in the Western English Channel (WEC) between 1930 and 2011. Our aims were to describe long-term changes in abundance and temporal distribution in relation to local environmental dynamics. In order to better understand mechanisms that regulate the species' populations, we identified periods that were characteristic of *in situ* population growth and the environmental optima associated with these events. Our results show that between 1930 and the 1960s both *M. atlantica* and *M. kochi* were transient components of the WEC ecosystem. In the late 1960s *M. atlantica*, successfully established a resident population in the WEC, while the occurrence of *M. kochi* became increasingly sporadic. Once established as a resident species, the seasonal abundance and distribution of *M. atlantica* increased. Analysis of environmental conditions associated with *in situ* population growth revealed that temperature and prey were key determinants of the seasonal distribution and abundance of *M. atlantica*. Salinity was shown to have an indirect effect, likely representing a proxy for water circulation in the WEC. Anomalies in the seasonal cycle of salinity, indicating deviation from the usual circulation pattern in the WEC, were negatively associated with *in situ* growth, suggesting dispersal of the locally developing *M. atlantica* population. However, our findings identified complexity in the relationship between characteristics of the environment and *M. atlantica* variability. The transition from a period of transiency (1930–1968) to residency (1969–2011) was tentatively attributed to structural changes in the WEC ecosystem that occurred under the forcing of wider-scale hydroclimatic changes.

Introduction

Blooms of jellyfish (pelagic Cnidaria and Ctenophora) are a characteristic feature of planktonic ecosystems (Boero et al., 2008; Condon et al., 2012) and have been for millennia (e.g. Hagadorn et al., 2002). However, dramatic shifts in the spatio-temporal distribution and abundance of blooms have been identified in numerous marine habitats over recent decades (Mills, 2001; Purcell et al., 2007). Jellyfish are important predators (Mills, 1995), with complex ecosystem-level effects (Pitt et al., 2009) and a range of socio-economic impacts (Purcell et al., 2007; Lucas et al., 2014). Therefore developing our understanding of factors affecting their populations is of high importance (Condon et al., 2012).

Both biological and physical factors influence jellyfish populations. Changes in abundance may occur through reproduction and mortality, or through physical processes of aggregation and redistribution (Graham et al., 2001). Environmental factors, including temperature, food availability and salinity, have been shown to directly affect jellyfish populations (Purcell, 2005); thus localised environmental variability may regulate populations. However, fluctuations may also occur indirectly, as a result of changes to circulation patterns, i.e. through advection (e.g. Decker et al., 2013

and references therein). Differentiating these 'real' and 'apparent' events (Graham et al., 2001) is important for developing a mechanistic understanding of how jellyfish populations respond to variable environmental conditions (Lucas and Dawson, 2014).

The calycophoran siphonophores *Muggiaea atlantica* (Cunningham, 1892) and *Muggiaea kochi* (Will, 1844) are holoplanktonic colonial jellyfish. They have a metagenic life cycle, comprising an alteration of generations between an asexual polygastric colony and a sexual monogastric eudoxid. Under favourable conditions, short generation times and simultaneous sexual and asexual reproduction can facilitate rapid population growth (Mackie et al., 1987). Typically inhabiting superficial waters (<200 m; Pugh, 1999), *Muggiaea* are also particularly susceptible to transport in ocean surface currents (Mackie et al., 1987), which may facilitate the formation of 'apparent' blooms or aggregations.

In the Atlantic Ocean and adjacent seas, *M. atlantica* and *M. kochi* inhabit predominantly neritic waters between 55°N–37°S and 48°N–36°S, respectively (Alvariño, 1971; Pugh, 1999). The congeners rarely co-occur at comparable densities (Mackie et al., 1987 and references therein) and are considered cool-temperate and warm-temperate analogues, respectively (Alvariño, 1971). However, recent findings suggest that *M. atlantica* has expanded its distributional range. Since the mid-1980s *M. atlantica* has progressively colonised the Western Mediterranean (Riera et al., 1986; Licandro and Ibañez, 2000; Licandro et al., 2012) and Adriatic (Kršinic and Njire, 2001; Batistić et al., 2007), probably in response to hydrological variability that occurred under the forcing of large-scale climate oscillations (Licandro and Ibañez, 2000; Licandro et al., 2012). Around the same time, unprecedented blooms of *M. atlantica* were also reported in coastal regions of the North Sea (Greve, 1994; Fosså et al., 2003).

Large blooms of *M. atlantica* can cause significant ecological and economic impacts. Predation by *M. atlantica* caused a restructuring of the copepod community during its invasion of the Adriatic (Kršinic and Njire, 2001) and produced cascading ecosystem effects in the German Bight (Greve, 1994). *M. atlantica* has also been identified as the causative agent of mass mortalities in farmed fish (Baxter et al., 2011), causing significant economic loss for aquaculture operations in Norway (Fosså et al., 2003) and Ireland (Cronin et al., 2004). The geographical expansion of *M. atlantica* may have significant impacts on the ecological and economic productivity of newly colonised regions.

The present study is based on long-term observations from the early 20th Century in the Western English Channel (WEC). As a biogeographical transition zone and a boundary region between neritic and oceanic waters (Southward et al., 2005) the WEC ecosystem is highly sensitive to hydroclimatic change (Southward et al., 1995). Previous studies have suggested multi-decadal oscillations of the WEC ecosystem between two quasi-stable states, characterised by northern cold- and southern warm-water planktonic assemblages (see Southward, 1980; Southward et al., 1995, 2005 for reviews). *M. atlantica* and *M. kochi* have been considered transient southwest species (Gough, 1905; Southward, 1962) indicative of the influx of water from the south (Russell, 1935; Corbin, 1947; Southward, 1962). More recent studies (Southward et al., 1995; Coombs and Halliday, 2009) indicate that *M. atlantica* abundance has increased dramatically since the late 1960s. However, the congeners have not been the focus of a rigorous analysis and more recent records have not been investigated.

Here we use the updated *Muggiaea* time-series to describe its long-term variability in the WEC and to verify its relationship with local environmental dynamics. In order to better understand mechanisms that regulate the species' populations, we identify annual blooms characteristic of *in situ* population development, and the environmental optima associated with these events.

Methods

Study site

The Marine Biological Association of the United Kingdom (MBA) has routinely collected data on the abundance of *Muggiaea* in the Western English Channel (WEC) since the early 20th Century. Physical environmental data were collected at an open-shelf station (E1: 50.03°N, 4.37°W) located approximately 30 km off Plymouth (UK), in proximity to the 75 m isobath (Fig. 1). At station E1 the water column is well stratified in summer (Pingree and Griffiths, 1978), with the pycnocline typically occurring at ~20 m depth (Smyth et al., 2010). Biological data were collected primarily at the adjacent station L5 (50.18°N, 4.30°W), which has a depth of 65 m (Fig. 1). This station is usually less strongly stratified in summer than E1 (Southward et al., 2005 and references therein). Samples were also collected from E1 and, occasionally, some other local sampling sites (see Southward et al., 2005). Both stations E1 and L5 are free from direct estuarine influence (Southward et al., 2005) and are considered to be representative of the wider WEC area (Southward, 1962).

Muggiaea data

Data on the abundance of *M. atlantica* and *M. kochi* were collected at the sampling stations on a quasi-monthly basis between 1930 and 2011 (with major interruptions during 1941–1945 and 1988–1995). These data were collected using double oblique hauls from ~65 m depth to the surface. A range of sampling gears has been employed; mostly 1 m and 2 m diameter ring nets during the early years then variants of a 0.9 m square inlet net (700–800 μm mesh size; see Southward et al., 2005 and references therein). After estimating the total volume of water filtered (assuming 100% filtration efficiency), all counts were adjusted to represent a nominal 4000 m^{-3} sample volume (see Southward and Boalch, 1986 for further methodological details). For the present study data were expressed as ind. 100 m^{-3}. Records of *Muggiaea* only concern polygastric colonies; eudoxids were not recorded.

Plankton exhibit heterogeneous spatial distributions (Graham et al., 2001) and sampling effort can influence estimates of jellyfish
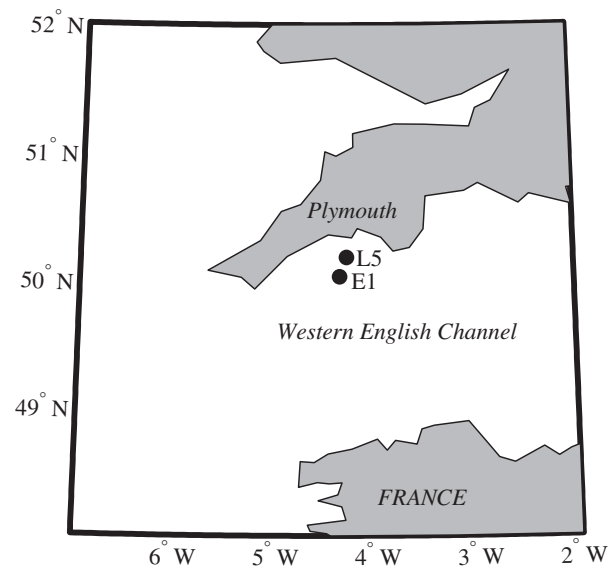

Fig. 1. Map of the Western English Channel with the locations of the sampling sites L5 and E1.

abundance (e.g., Lynam et al., 2011). Despite this, Southward et al. (2005) have shown that the samples collected in the present study accurately represent seasonal changes in abundance in the wider northern Channel region. The use of different sampling equipment may have also influenced estimates of abundance (Southward, 1970), however, it has been shown that nets with a mouth diameter of ~1 m and a mesh size of ~700 μm produce quantitative estimates of colonial gelatinous zooplankton abundance (Braconnot, 1971). Standardising counts to unit volume of water sampled mitigates these factors, but some bias undoubtedly still exists (Coombs and Halliday, 2009). Nevertheless, seasonal patterns of variability remain representative (Southward, 1970; Coombs et al., 2005).

Environmental data

Sea surface temperature (SST, °C), depth-integrated salinity (0–50 m) and copepod abundance (ind. 100 m^{-3}) were considered as descriptors of *Muggiaea*'s ambient environment.

Temperature and salinity data at 10 m depth intervals (0–50 m) were collected by the MBA at station E1 using a thermometer and salinity bottles between 1930 and 1987 and conductivity, temperature, depth (CTD) probes thereafter (see Smyth et al., 2010 for additional methodological details). Temperature at surface was highly correlated with temperature at 50 m depth (Pearson's correlation, >0.85). Therefore, considering the lower number of missing values in the SST dataset, we used SST, rather than depth-integrated sea temperature, to investigate the long-term variability of seawater temperature in the WEC. This also facilitated comparisons with long-term SST records from the wider area (50°N to 50.5°N, 4°W to 4.5°W) obtained from the British Atmospheric Data Centre (BADC) HADISST 1.1 dataset (http://badc.nerc.ac.uk).

Data on the abundance of copepods from a 1° by 2° grid in the study region (49°N to 50°N, −3°W to −5°W) were extracted from the Continuous Plankton Recorder (CPR) database for the period 1958–2011 (see Batten et al., 2003 for details of the sampling methodology). Considering the size range of *M. atlantica* prey (0.1–1.0 mm; Purcell, 1981) and the predominance of copepod stages in its diet (Purcell, 1982) we considered data on total copepods <2 mm (ind. 100 m^{-3}). Although the CPR only provides an estimate of the copepod standing stock in surface waters, these data provide a good representation of seasonal patterns of copepod variability in the WEC (John et al., 2001).

Numerical analyses

Treatment of missing data

Extensive gaps due to sampling interruptions, and numerous random missing data (due to weather constraints, equipment failure, etc.), prevented the use of traditional time-series analysis tools and necessitated pre-treatment of the data. Sampling frequency was adjusted to monthly values by taking the arithmetic mean when the number of data for a given month was greater than 1. In order to homogenise annual sampling effort, descriptors (excluding SST) were processed in two steps: (1) years comprising less than 7 months of data, or containing more than 4 months consecutive missing data were removed; (2) random missing data (MD) remaining in the truncated data series' were predicted using the eigenvector filtering (EVF) method (Colebrook, 1978; Ibañez and Conversi, 2002). The EVF method involves a Principal Component Analysis (PCA) performed on an autocovariance matrix composed of the original series (with MD) lagged progressively. The MD are then predicted through iterative computation of the autocorrelation function (Ibañez and Conversi, 2002). Although our descriptors represent discontinuous time-series, the EVF provided a suitable method as all variables exhibited strong seasonal cycles

and the windows of prediction were small (<4 consecutive missing data). In the case of SST, missing data were replaced by their corresponding HadISST values after verifying the high correlation of the two series (Pearson's correlation, $r = 0.97$, $p = <0.001$).

Temporal variability

Monthly values of biological data collected between 1930 and 2011 were transformed (log 10 [$x + 1$]) to reduce data variance. These data were then represented together with environmental data as contour plots to show the main patterns of seasonal and interannual variability. Interannual variability was also represented by standardised anomalies (z-scores), computed as deviations from the mean of the time-series divided by the standard deviation of the time-series.

In situ population growth of Muggiaea

Following the methodology described in Licandro et al. (2006), we distinguished gradual population increases characteristic of biological production *in situ* from random events. First, peaks and troughs of abundance (turning points) were identified following Kendall's information theory (Kendall, 1976). Second, the quantity of information (QI) associated with the probability to observe a turning point was calculated using the algorithm of Ibañez (1982). Turning points with high QI represent gradual changes over time, whereas those with low QI reflect abrupt (random) events. Ibañez (1982) demonstrated that turning points characterised by QI > 4.3 bits can be considered non-random at the 95% significance level.

We considered consecutive months between a significant trough and peak as an informative period (IP), i.e. a period in which the population was developing *in situ* under the influence of local environmental conditions. Conversely, turning points characterised by low QI were considered random events, indicative of lateral advection from surrounding areas. To ensure that only chronological months contributed to IPs, turning points identified close to the boundaries of missing data were disregarded.

Environmental preferences of Muggiaea

Considering the informative periods (IP), environmental conditions associated with high abundance were identified using the method proposed by Perry and Smith (1994). This method compares the cumulative distribution function (CDF) of the environmental conditions during the IP, against the CDF of the environmental data that have been weighted by species abundance. Similar CDFs imply a random association between abundance and environmental conditions, whereas dissimilar CDFs indicate a consistent association between species abundance and particular environmental conditions. The maximum difference between the two CDFs represents the environmental condition associated with maximal species abundance; this was considered to represent the optimal environmental condition. The significance of the association was tested using a randomisation test with 10,000 permutations.

Environmental influence on seasonal distribution of Muggiaea

We explored the influence of local environmental variability (SST, salinity and copepod abundance) on the seasonal distribution of *Muggiaea* using the multi-table STATIS method (Lavit et al., 1994). STATIS is an extension of Principal Component Analysis designed to analyse multiple data tables describing sets of variables measured on the same observations. STATIS has been used previously in the field of ecology, mainly to assess spatial (e.g. Gaertner et al., 1998) or temporal (e.g. Licandro and Ibañez, 2000) variability in species assemblages. In the present study we utilised STATIS to investigate interannual variability in the seasonal structure of the local environment. Relationships between environmental characteristics and the seasonal distribution of

Muggiaea were explored by incorporation of *Muggiaea* as supplementary variables.

Records of SST, salinity and copepod abundance were arranged into yearly data tables with columns describing environmental variables and rows describing monthly observations. The variables of each table were centred and normalised and each table was then normalised to ensure all tables participated equally in the analysis. The STATIS analysis proceeded in three steps, which are described below, following the methodology of Abdi et al. (2012):

Interstructure. The interstructure analysis involves the eigen-decomposition of the tables' similarity structure. This provides an ordination of the years, identifying similarities based on their environmental characteristics. The first eigenvector of this eigenanalysis also provides table weights used to compute the compromise.

Compromise. For the compromise analysis the individual tables are gathered to form the compromise table. The generalised singular value decomposition of this table, under the constraints of the table weights, provides an ordination of the tables' global structure. This represents the information common to all the tables, in our case the average seasonal environmental cycle. At this step we also projected the average seasonal cycle of *Muggiaea* as supplementary variables by computing correlation coefficients with the axes of the compromise.

Trajectories. The trajectories analysis involves the projection of the individual tables onto the axes of the compromise. This step allows visualisation of the similarities and differences amongst the years' structures, i.e. environmental cycles. At this step *Muggiaea* were incorporated as supplementary variables by computing correlation coefficients with the axis of the compromise. Both the compromise and trajectories analyses were presented in two-dimensional maps inside a circle of correlation (radius = 1).

At the interstructure step we also included a cluster analysis; average linkage hierarchical agglomerative clustering based on the Euclidean distance was used to identify groups of similar years. Also, in addition to projecting *Muggiaea* species as supplementary variables, months characterised by *in situ* growth (IPs) were superimposed on plots of the trajectories.

In summary, the STATIS analysis produced three main results: (1) the interstructure, which identifies the similarity between years' environmental characteristics; (2) the compromise, which represents the typical annual environmental cycle; (3) the trajectories, which reveal the similarities and differences amongst the years.

All analyses were programmed using MATLAB® (R2013b 8.2.0.701), with the exception of the informative periods which utilised the PASTECS library (Ibañez et al., 2009) for R (R Development Core Team, 2012).

Results

Temporal variability of environmental conditions

The mean annual sea surface temperature (SST) was generally below or around the long-term mean (12.63 ± 0.42 °C) from 1930 to 1994 (with the exception of 1949, 1959–1960, and 1989–1990), while values consistently higher were recorded afterwards (Fig. 2A). The highest positive anomalies were recorded in 1959, 1989 and 2007, while the lowest were in 1963 and 1986.

The seasonal cycle of SST was characterised by a sinusoidal pattern, with minimum values in February and maxima in August (Fig. 3A). Temperature at surface ranged from 8.80 °C to 10.55 °C in winter (January–March), 10.52–12.90 °C in spring (April–June), 14.80–17.55 °C in summer (July–September) and 11.97–14.10 °C

in autumn (October–December). Maximum SST values were recorded in August 1976 (19.10 °C) and July 1983 (19.26 °C), while minima were recorded in February 1947 (7.42 °C) and March 1986 (7.50 °C).

Mean annual depth-integrated salinity (0–50 m) was generally below the long-term average (35.21 ± 0.10) during the 1930s (with the exception of 1934, 1935 and 1938) and from 1977 to 1985 (except 1979, Fig. 2B). On the other hand, salinity was mostly close to, or above the long-term average from 1948 to 1976, and constantly above average after 2005. Minimal yearly averages of salinity were recorded in 1936 and 1982, while maxima occurred in 1956 and 1965.

Maximum values of depth-integrated salinity were typically observed during the winter months. Minima generally occurred in summer, although pulses of reduced salinity were common throughout the years, particularly in 1936, 1977, 1982 and 1983 (Fig. 3B). Salinity varied on average from 35.10 to 35.46 during winter, 34.94–35.40 in spring, 34.91–35.38 in summer and 35.08–35.47 in autumn.

From 1958–1990 copepod abundance was generally above or around the long-term average (20268 ± 9010 ind. 100 m^{-3}), except during 1963–1968 and 1972–1974 (Fig. 2C). After 1990 copepod abundance was variable until stabilising around the long-term mean after 2001.

A common seasonal feature of copepod abundance was a recurrent spring peak (Fig. 3C). Secondary peaks were also common in summer, particularly from 1980 to 2000. Since 2001 copepods typically peaked in May and their abundance remained high throughout the summer. Lowest densities were normally observed in January–February. Particularly high copepod abundance was observed during spring of 1959 and 1987, summer of 1964 and autumn 1978 and 1987.

Temporal variability of Muggiaea

During the study period *M. atlantica* was the dominant species of *Muggiaea* in the Western English Channel (WEC), being recorded in 74% of the 636 months sampled (Fig. 3D). The appearance of the congeneric *M. kochi* was infrequent, occurring in only 19% of sampled months (Fig. 3E).

From 1930 until 1968 *M. atlantica* abundance was low; its mean annual abundance being consistently below the long-term average (Fig. 2D). During the 1970s *M. atlantica* abundance was close to the long-term mean. Then, after 1980, its abundance increased considerably, with yearly averages consistently above the long-term mean. Maxima were observed in 1996, 2005, 2006 and 2009 (Fig. 2D).

M. atlantica seasonal distribution was highly variable (Fig. 3D). Prior to the late 1960s its appearance was episodic. High seasonal abundance was recorded during August–December, with maxima typically recorded in September–October (max 300 ind. 100 m^{-3}). A noticeable change took place after the late 1960s, when *M. atlantica* started to be regularly recorded in the WEC. In the 1970s *M. atlantica* distribution became predominantly bimodal, with seasonal maxima occurring in August and secondary peaks developing in the autumn. Particularly high densities of *M. atlantica* were observed in August 1970 (1000 ind. 100 m^{-3}) and 1978 (1100 ind. 100 m^{-3}), whilst 1979 exhibited unusually low annual abundance. Years following 1980 were characterised by an extended seasonal occurrence, with *M. atlantica* being consistently recorded from April to December. Throughout the 1980s maximum abundance was observed in June-July with secondary peaks in autumn. From the late 1990s abundance typically remained high through summer and autumn after seasonal maxima in June-July. High amplitude seasonal maxima were recorded in 1996, 2005 and 2010 (max 1100–2200 ind. 100 m^{-3}).
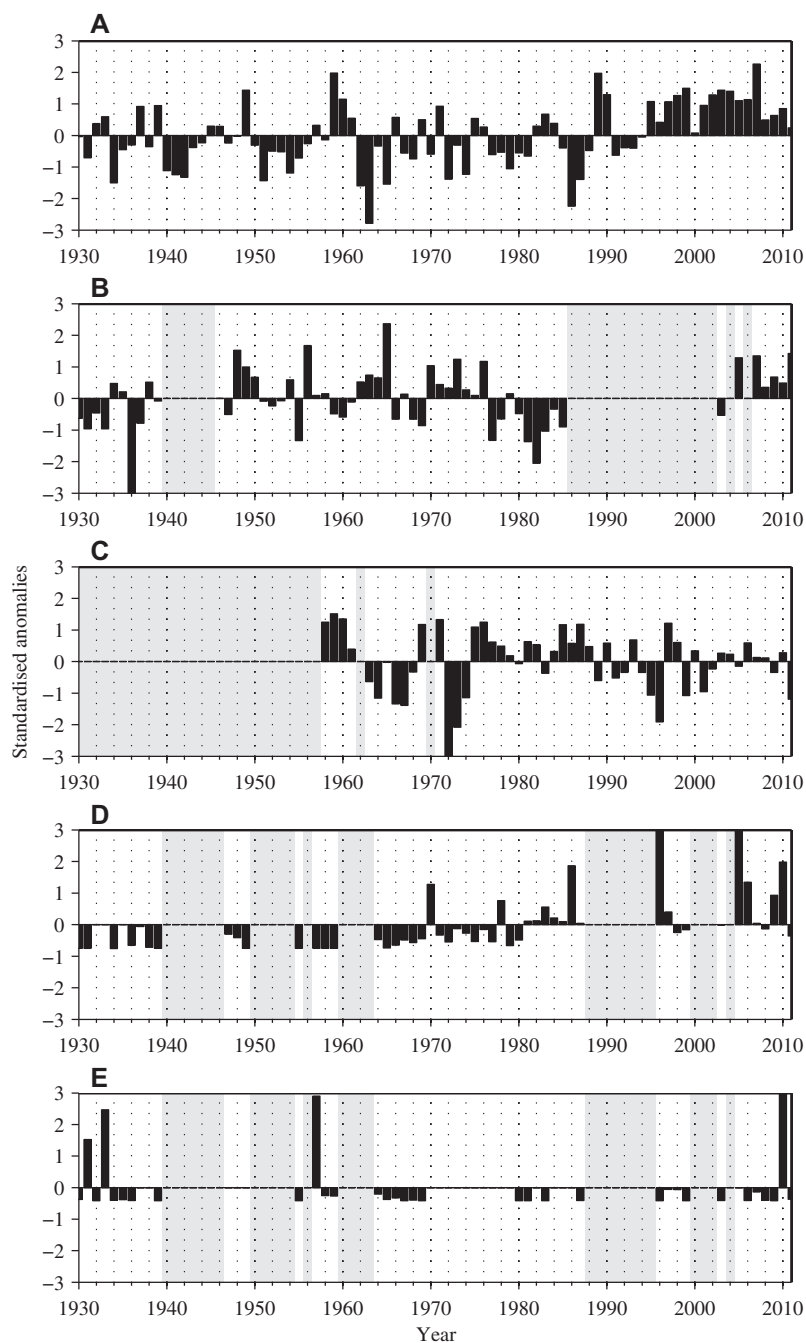
Fig. 2. Standardised anomalies of mean annual (A) sea surface temperature, (B) depth-integrated salinity (0–50 m), (C) copepods, (D) *Muggiaea atlantica*, and (E) *M. kochi*. Grey areas represent missing data.

From 1930 to 2011 *M. kochi* was occasionally recorded in high abundance in the WEC (i.e. in 1931, 1933, 1957-59, 1964, 1997–1998, 2007 and 2010) (Fig. 3E). Maximal annual anomalies were recorded in 1931, 1933, 1957 and 2010 (Fig. 2E). High seasonal abundance of *M. kochi* typically developed during August–November (max 2.5–88 ind. 100 m^{-3}; Fig. 3E). Whilst not mutually exclusive, *M. kochi* displayed a strong tendency to occur when *M. atlantica* was absent or scarce.

In situ population growth

From 1930–2011 a total of 137 peaks and troughs were identified in the seasonal abundance of *M. atlantica* (Fig. 4). Before the late 1960s the majority of peaks and troughs were not statistically

significant (75% and 81%, respectively), which we attribute to advection events and not *in situ* population growth. However, the population was developing *in situ* during May and October in 1936, 1937, 1938, 1948 and 1967 and during July–October in 1966 and 1969. During the 1970s seasonal patterns were predominantly related to *in situ* growth (73% of peaks and 50% of troughs were significant), with IPs observed in all but two years (1971 and 1972). Excepting 1979, IPs encompassed two peaks, indicating that the population diminished slightly between successive peaks. The onset of IPs varied from February (1975) to June (1974 and 1978) and extended to September-November. Primary peaks generally occurred in August with secondary peaks developing in autumn. From the 1980s onwards *M. atlantica* exhibited consistent *in situ* population growth every year (58% and 49% significant peaks and
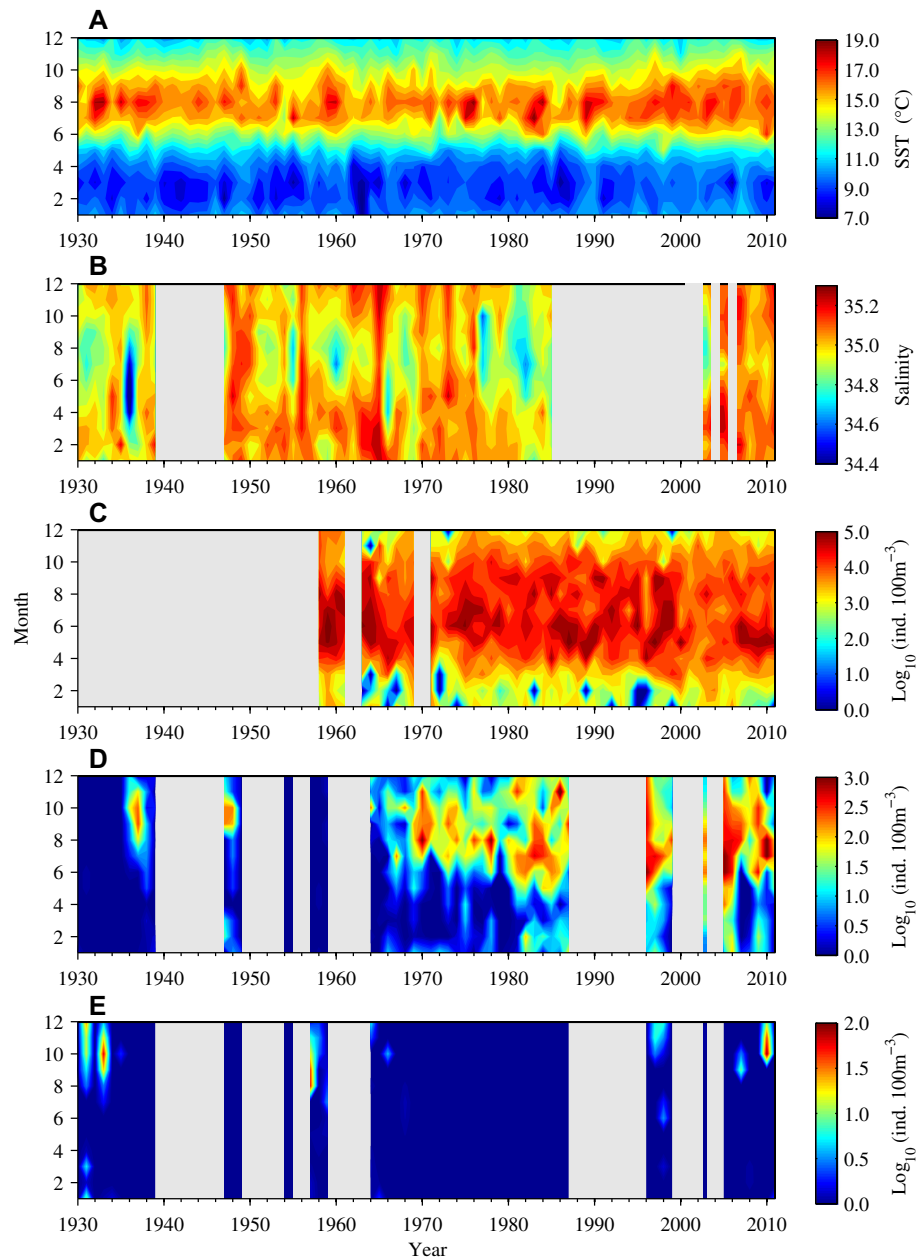
Fig. 3. Interannual and seasonal variability of (A) sea surface temperature, (B) depth-integrated salinity (0–50 m), (C) copepods, (D) *Muggiaea atlantica* and (E) *M. kochi*. Grey areas represent missing data.
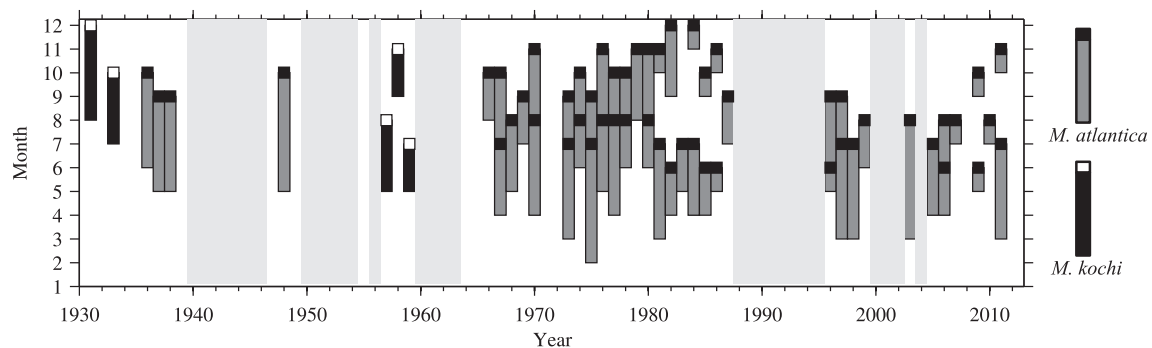

Fig. 4. *In situ* population growth of *Muggiaea* in the Western English Channel. Bars represent informative periods, i.e. months during which the population was developing *in situ*, while squares represent significant peaks of abundance. *Muggiaea atlantica*: grey bars and black squares; *Muggiaea kochi*: black bars and white squares. Light grey areas represent missing data.

troughs, respectively). During the 1980s (not including 1987) the *M. atlantica* annual cycle was characterised by two distinct IPs, which were separated by a significant decrease in abundance. Primary peaks occurred in June–July while the onset of IPs was generally in April–May. The timing of IPs was variable. From the late 1990s onward the onset of IPs was variable but generally occurred in March–April, with peaks developing in June–August. Some years exhibited IPs with connected (1996 and 1997), or disconnected peaks (2009 and 2011), while single IPs were observed in 1999, 2003, 2005 and 2006. *In situ* growth was highly ephemeral in 2007 and 2010, lasting only two months (July–August). No IPs were identified in 2008.

The *M. kochi* population developed *in situ* in 1931, 1933, 1957, 1958 and 1959 (Fig. 4). Respectively, only 13% and 14% of the 54 peaks and 55 troughs identified over the whole study period were associated with significant QI. This suggests that the *M. kochi* population was developing in the area of study only rarely. The timing of *M. kochi* IPs was highly variable, with peaks occurring from June to December. No IPs were found in 1997, 1998 or 2010, despite relatively high abundance. *In situ* population growth of *M. kochi* and *M. atlantica* was mutually exclusive.

Association of environmental descriptors with informative periods

The IPs of *M. atlantica* and *M. kochi* were characterised by similar environmental conditions. The *M. atlantica* population was developing *in situ* within a SST range of 8.9–19.3 °C, a depth-integrated salinity range of 34.52 and 35.46, and prey (copepod) abundance between 666 and 180,330 ind. 100 m^{-3}. The environmental conditions recorded during *in situ* development of the *M. kochi* population were SST between 11.2 and 18.8 °C, salinities of 35.02–35.27, and prey densities between 12,061 and 198,100 ind. 100 m^{-3}, respectively.

Both temperature and prey abundance significantly influenced the distribution of *M. atlantica* informative periods (Fig. 5A and B). Peaks of abundance were significantly associated with temperatures of 14.6–15.5 °C (p = <0.005) and copepod abundance of 20,400–22,100 ind. 100 m^{-3} (p = <0.1; Table 1). No association with salinity was apparent (Table 1, Fig. 5C). High abundance of *M. kochi* was related to slightly higher temperatures than *M. atlantica*, i.e. SST of 15.0–16.0 °C (p = <0.1; Table 1, and Fig. 5D). Although few prey data were available during the IPs of *M. kochi*, the data that were available did not show any significant association between peaks of *M. kochi* and prey abundance (n = 9; Fig. 5E). Salinity preferences were not considered, due to the narrow salinity range observed during periods of *M. kochi* population growth *in situ*.

Environmental influence on seasonal distribution of Muggiaea

Interstructure analysis

The interstructure identifies the similarity between years based on their environmental characteristics. The first principal component (PC1) explained 71% of the total variation and the second principal component (PC2) explained 5% (Fig. 6). Cluster analysis identified 4 separate groups of years and a single individual year. The groups G2 (1964, 1967, 1984 and 2005) and particularly G1 (1968, 1975, 1977, 1978, 1979, 1980, 1981, 1982 and 2003) exhibited strong association with PC1, indicating similar structures and

Table 1
Environmental preferences of *Muggiaea atlantica* and *Muggiaea kochi* identified by analysis of environmental descriptors during periods of *in situ* population growth. Asterisks indicate optimal conditions significantly associated with an increase in the abundance of the species.

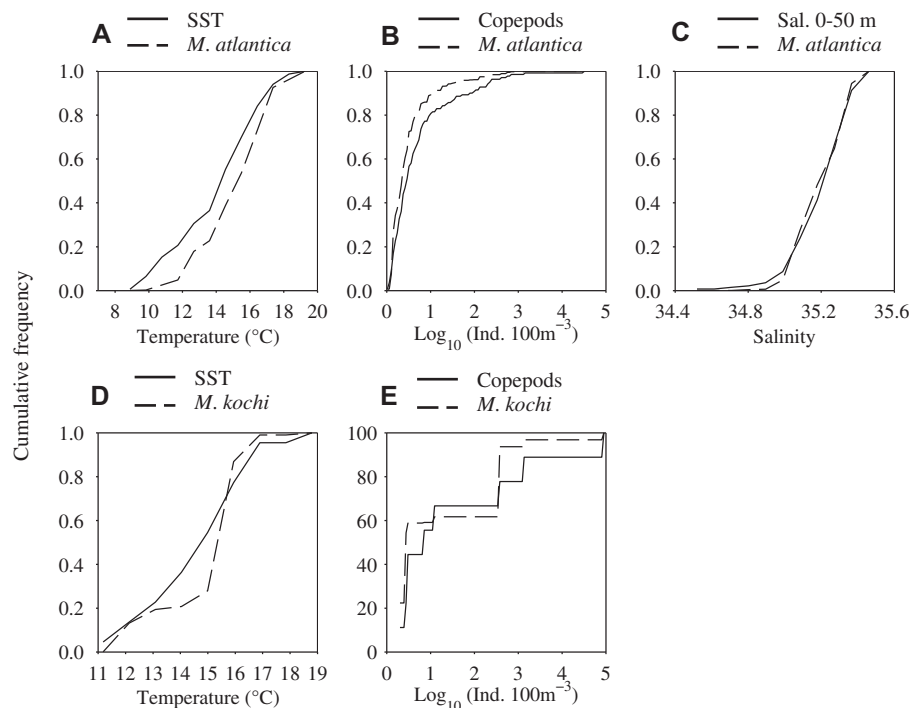| Species	SST (°C)	Salinity (0–50 m)	Copepods (ind. 100 m^{-3})
Muggiaea atlantica	14.6–15.5[**]	35.18–35.27	20,400–22,100[*]
Muggiaea kochi	15.0–16.0[*]	N/A	17,600–19,500

[*] $p < 0.1$.
[**] $p < 0.005$.

Fig. 5. Cumulative distribution functions (CDFs) of siphonophore abundance (dashed lines) in relation to environmental conditions (solid lines) during periods of *in situ* population growth. (A) *Muggiaea atlantica* and sea surface temperature, (B) *Muggiaea atlantica* and copepod abundance, (C) *Muggiaea atlantica* and depth-integrated salinity (0–50 m), (D) *Muggiaea kochi* and SST, and (E) *Muggiaea kochi* and copepod abundance.
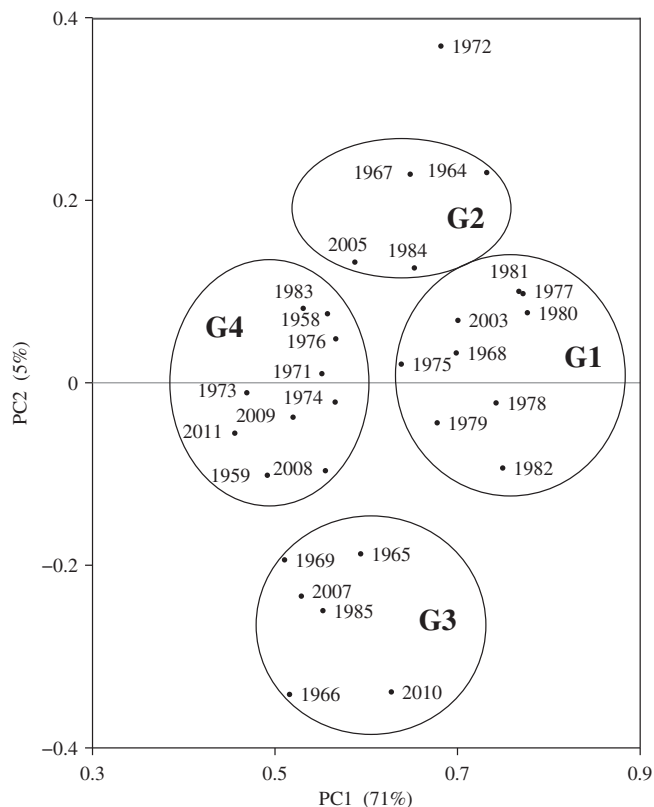
Fig. 6. Interstructure of the STATIS analysis. This plot shows the similarity of the 30 years based on their environmental characteristics (sea surface temperature, salinity and copepod abundance). The importance of each year in the compromise is indicted by the strength of association with the first principal component (PC1). Groups of similar years have been identified using hierarchical cluster analysis.
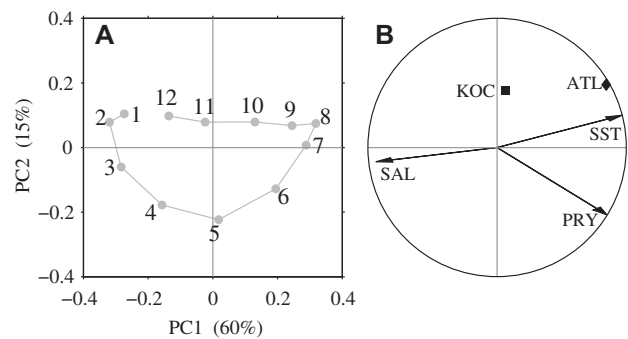

Fig. 7. The compromise of the STATIS analysis. This plot represents the typical annual environmental structure in the Western English Channel. (A) The position of the months (January = 1–December = 12) in the compromise space. (B) The association of the environmental descriptors (sea surface temperature, SST; salinity, SAL; copepod abundance, PRY) and species abundance (*Muggiaea atlantica*, ATL; *Muggiaea kochi*, KOC) with the axes of the compromise. The x-axis is the first principal component (PC1) and the y-axis is the second principal component (PC2).

good representation by the compromise. The years of G3 (1965, 1966, 1969, 1985, 2007 and 2010) represented an intermediate group, associated moderately to PC1 and negatively to PC2. The group G4 (1958, 1959, 1971, 1973, 1974, 1976, 1983, 2008, 2009 and 2011) displayed reduced association with PC1 and contained years with more distinctive environmental structures. The year 1972 was unusual, with a particularly strong link to PC2.

Compromise analysis

The compromise analysis (Fig. 7) represents the typical annual environmental structure common throughout the years. PC1 accounted for 60% of the total variance and differentiated the winter and summer months, while PC2 (14% of the total variance) separated spring and autumn (Fig. 7A). Examination of the relationships between descriptors (SST; salinity, SAL; copepod abundance, PRY) and the principal components (Fig. 7B) reveals the underlying structure of the compromise. Overall, SST was positively related to PC1 whilst salinity (SAL) was negatively associated, confirming that winter months were typically characterised by high salinity and low temperature whilst summer months exhibited the inverse relationship. Copepod abundance (PRY) was linked positively to PC1 and negatively to PC2, indicating a general pattern of high prey abundance in spring/summer and minimal abundance in late autumn/winter.

The seasonal distribution of *M. atlantica* (ATL) was positively related to PC1, revealing an overall positive relationship with SST and copepod abundance, and a negative link with salinity (Fig. 7B). Overall, *M. atlantica* was most abundant in the summer months when temperature and copepod abundance were high and salinity was low. In contrast, *M. kochi* (KOC) associated weakly

with PC2, indicating a tendency to occur in autumn, but with high variability. A weak link was found between *M. kochi* seasonal distribution and SST, while salinity and copepod abundance appear unrelated to the seasonal occurrence of this species.

Trajectories

The trajectories show the structures of the individual years, revealing similarities and differences between them. The trajectories (Figs. 8–11; and Fig. 1_Supplementary material) revealed high interannual variability in the seasonal structure of the environment. However, three broad typologies were evident, corresponding to groups of years clustered in the interstructure. Differences in the shape of trajectories between years were predominantly driven by high variability in the annual cycle of salinity, whereas SST and copepod abundance displayed less variability. The analysis revealed interesting associations between environmental typologies and specific patterns of *M. atlantica* seasonal growth and distribution.

Typology 1 (Fig. 8) resembled the characteristic structure of the compromise and characterised the years of groups G1 (1968, 1975, 1977, 1978, 1979, 1980, 1981, 1982 and 2003) and G2 (1964, 1967, 1984 and 2005). This typology was consistently associated with *in situ* development of the *M. atlantica* population, which took place in all G1 years and G2 except for 1964. Typically (years 1968, 1975, 1977, 1980, 1981, 2003) the *M. atlantica* population began developing in early spring when conditions were cool and saline (Fig. 8), and peaked in summer, when temperatures were maximal and salinity was minimal. However, in 1978, 1979 and 1980 population growth *in situ* started relatively late, despite similar environmental characteristics (Fig. 1_Supplementary material). During G2 years (except 1964) the *M. atlantica* population was developing in phase with copepods (Fig. 8).

Two alternative typologies were characterised by their distinct annual salinity patterns. Typology 2 (Fig. 9) comprised the years of G3 (1965, 1966, 1969, 1985, 2007 and 2010) and exhibited salinity minima in spring and maxima in autumn. This typology corresponded to atypical patterns of growth and distribution of the *M. atlantica* population. *In situ* population growth was late and ephemeral (1966, 1969, 2007 and 2010), or did not occur (1965), and was out of phase with the peak of prey abundance, suggesting these conditions were unfavourable for growth (Fig. 9). It is noteworthy that 1966, 1969 and 2007 exhibited intense freshening events in spring, with salinities as low as 34.62 (2007).

Typology 3 (Fig. 10) was characterised by salinity maxima in early spring and minima in early autumn. This typology
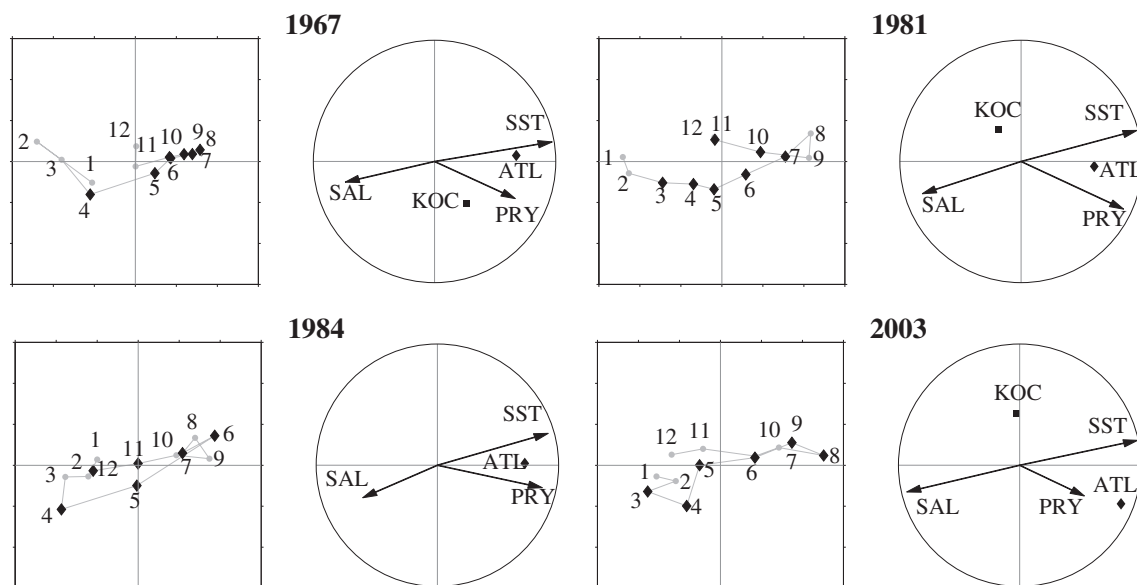
Fig. 8. Environmental typology 1 trajectories. Typical annual environmental conditions associated with consistent *in situ* population growth of *M. atlantica*. Months during which the *M. atlantica* population was developing *in situ* are represented by black diamonds.

Fig. 9. Environmental typology 2 trajectories. Annual environmental conditions characterised by spring salinity minima and restricted *in situ* population growth of *M. atlantica*. Months during which the *M. atlantica* population was developing *in situ* are represented by black diamonds.
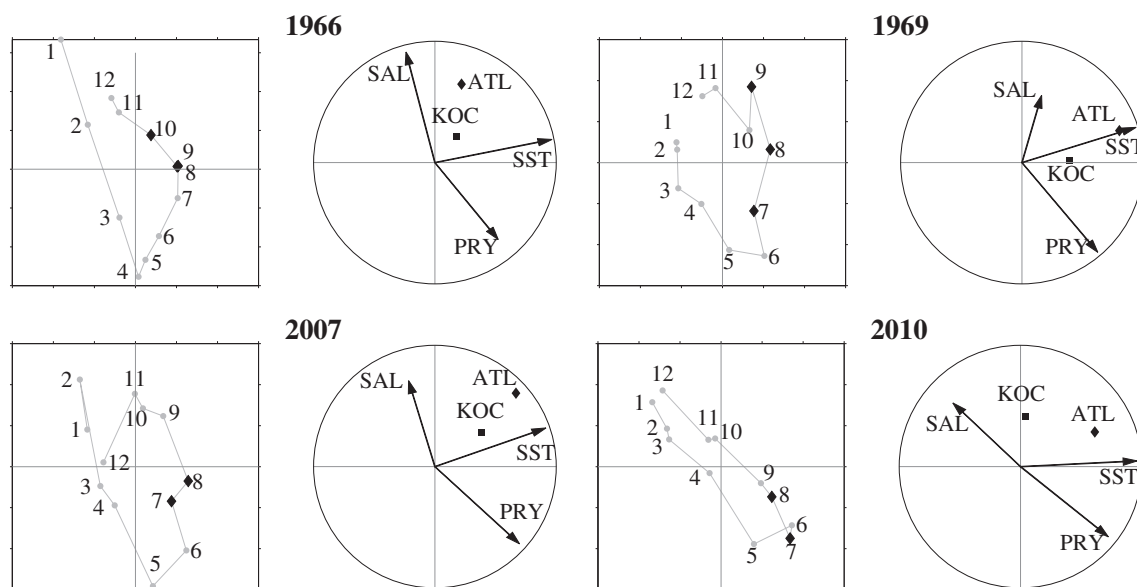
characterised the majority of G4 years (1958, 1959, 1971, 1974, 2008, 2009), which were also associated with peaks of *M. atlantica* abundance out of phase with prey abundance. Under these conditions *M. atlantica* was reproducing *in situ* only during 2 of the 6 years (1974 and 2009; Fig. 1_Supplementary material).

Some years of group G4 (1973, 1976, 1983, 2011) exhibited trajectories dissimilar to the regular typologies. These years were characterised by relatively stable salinity patterns and consistent *in situ* growth periods of *M. atlantica* (Fig. 11). The year 1972 displayed a distinctive trajectory due to particularly late seasonal abundance of copepods. The *M. atlantica* population was not recorded developing *in situ* during this year.

In situ population growth of *M. kochi* was only recorded in two of the thirty years analysed by the STATIS technique (1958 and

1959). Both years were categorised as typology 3 conditions, displaying highly similar environmental characteristics but dissimilar patterns of growth and distribution (Fig. 10).

The annual peak of *M. atlantica* generally occurred in summer or autumn under all environmental typologies (except 1958), while *M. kochi* tended to exhibit peaks in all four seasons under a wide range of environmental conditions.

In summary, the STATIS analysis highlighted (1) a tendency for *M. atlantica* populations to develop *in situ* with stable salinity conditions and abundance of prey; (2) restricted population growth under atypical salinity conditions and low prey concentration; (3) that the seasonal distribution of *M. atlantica* was generally associated with defined hydroclimatic conditions, while this was not the case for *M. kochi*.
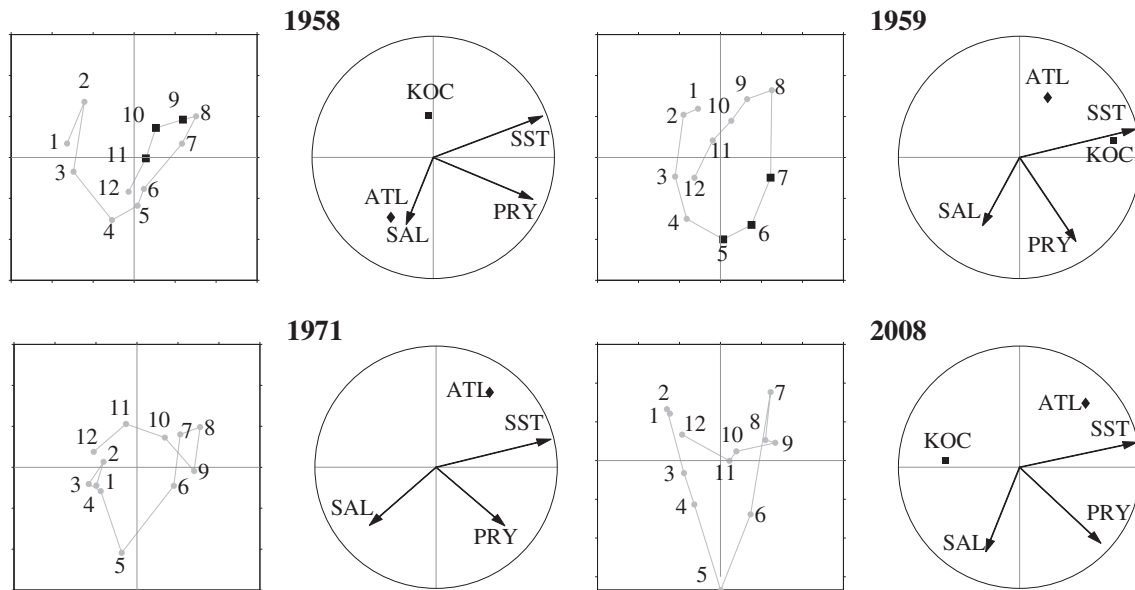
Fig. 10. Environmental typology 3 trajectories. Annual environmental conditions characterised by spring salinity maxima and restricted *in situ* population growth of *M. atlantica* and *M. kochi*. Months during which the *M. kochi* population was developing *in situ* are represented by black squares.
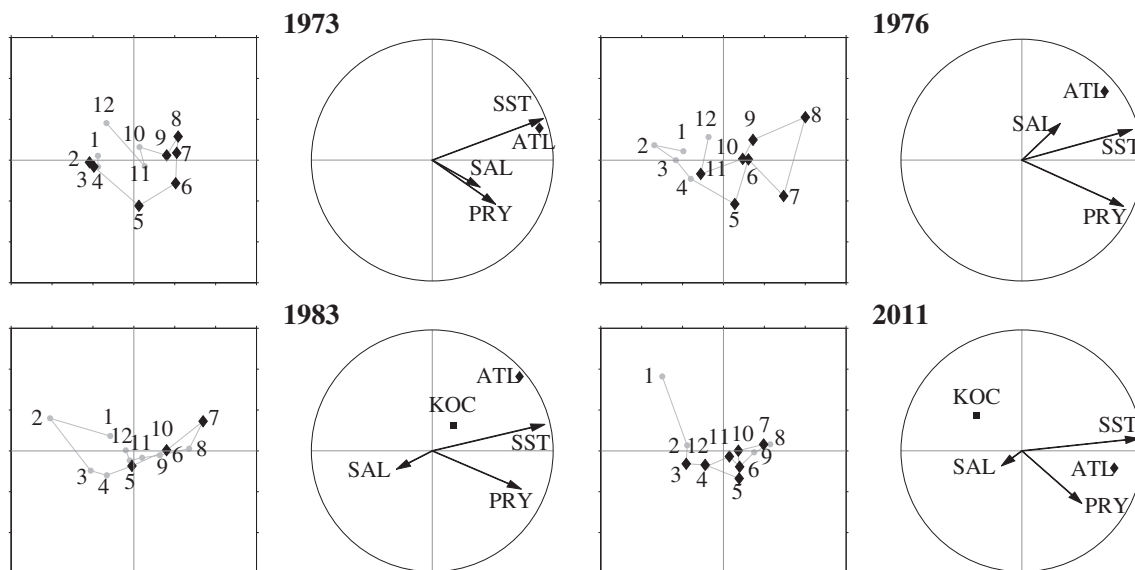

Fig. 11. Stable environmental trajectories. Annual environmental conditions characterised by stable salinity patterns and consistent *in situ* population growth of *M. atlantica*. Months during which the *M. atlantica* population was developing *in situ* are represented by black diamonds.

Discussion

Our study shows that between 1930 and the late 1960s *Muggiaea atlantica* and *Muggiaea kochi* were transient components of the Western English Channel (WEC) ecosystem. Their sporadic occurrence and infrequent *in situ* population development at this time indicated the influence of advection, probably from source populations to the south (Corbin, 1947; Southward, 1962). Following this period dramatic changes were identified. From the late 1960s the occurrence of *M. kochi* became increasingly sporadic and *in situ* population development of this species was no longer recorded. In contrast, after 1968 the *M. atlantica* population was regularly developing *in situ* and this species was observed throughout the seasons of every year, with a progressive expansion of seasonal abundance. These results provide strong evidence that *M. atlantica*

established a self-sustaining population in the WEC and suggest that, as documented in several species of phytoplankton (Hays et al., 2005) and copepods (Beaugrand et al., 2002), *M. atlantica* has undergone a northwards distributional shift in recent decades.

The STATIS compromise analysis suggested that sea surface temperature (SST), salinity, and to a lesser extent, prey (copepod) abundance were key factors determining the seasonal occurrence of *M. atlantica* in the WEC. In contrast, *M. kochi* was only correlated with SST, albeit weakly. Experimental studies have shown that the reproductive capacity of *Muggiaea* is positively related to temperature and food availability (Purcell, 1982; Carré and Carré, 1991). Analysis of the environmental descriptors associated with informative periods confirmed the significance of temperature as a determinant of *Muggiaea*'s seasonal distribution. Both *M. atlantica* and *M. kochi* populations were successfully developing *in situ* when

SST was within species-specific temperature ranges, i.e. 9–19 °C for *M. atlantica* and 11–19 °C for *M. kochi*. Within these tolerable reproductive ranges we identified optimal temperatures (SST), i.e., 14.6–15.5 °C for *M. atlantica* and 15.0–16.0 °C for *M. kochi,* that were consistently associated with rapid population growth.

Increased temperatures promote faster lifecycles and higher reproductive rates in *M. kochi* (Carré and Carré, 1991) and many other species of jellyfish (Purcell, 2005 and references therein). The thermal optima (SST) we identified for *M. kochi* are lower than those reported from the Mediterranean (17–21 °C; Patriti, 1964; Licandro et al., 2012), but represented the most commonly available maximal SST range in the WEC (<20% of SST values were >16 °C). The relatively low *M. kochi* abundance observed in the present study, compared to other regions (e.g. Licandro et al., 2012), may therefore be explained by a restricted reproductive capacity due to the temperature regime in the WEC. Carré and Carré (1991) suggested that in response to low temperature (13 °C) in the Mediterranean, *M. kochi* employs a suspended reproductive phase that facilitates overwintering of the polygastric population. In the present study the lower limit of *M. kochi*'s tolerable reproductive range (11 °C) suggests the threshold at which it enters this phase in the WEC. These results indicate that the species is able to acclimate to some extent, an adaptation that is well known for certain species of jellyfish (e.g. Lucas, 2001). However, winter temperatures in the WEC (average SST 1930–2011, 9.6 °C) are likely below a critical thermal limit for *M. kochi* survival. Consequently the polygastric stage of this species cannot successfully overwinter in the WEC and the population must rely on annual re-colonisation via advective transport.

In contrast, the thermal optima (SST) identified for *M. atlantica* in the present study are in close agreement with results from warmer regions, (e.g. Licandro et al., 2012). At more southerly latitudes *M. atlantica* typically exhibits annual peak abundance 1–2 months earlier than observed in the WEC in recent years (Patriti, 1964; Moreno and Fdez-Alcazar, 1984). The WEC has experienced a pronounced increase in sea surface temperature since the 1980s (Smyth et al., 2010; Fig. 2) and earlier seasonal maxima of *M. atlantica* observed in the region during this period are concomitant with temperature changes. This suggests that *M. atlantica* has a well-defined thermal niche that dictates its reproductive phenology. In the present study we found that the *M. atlantica* population did not develop *in situ* when SST was below 9 °C. This is in accordance with preliminary experimental results from the Mediterranean that identified the threshold for suspended reproduction as around 10 °C (Pagès et al., unpublished data from the north-western Mediterranean). Evidently minimal sea temperature in the WEC does not go below critical thermal limits for *M. atlantica* survival, as polygastric stage *M. atlantica* can successfully overwinter in the region.

Copepods form the dominant component of the diet of calycophorans (Purcell, 1981, 1982). However, our results show that high abundance of *Muggiaea* is often, but not necessarily associated with high abundance of copepods. This suggests that copepods form an important dietary component at specific times, but that other prey sources must also be important, particularly during autumn, when copepods are scarce but the *M. atlantica* population is often developing *in situ*. The importance of other prey sources is also highlighted when considering that *M. kochi* exhibited no significant association with copepod abundance when developing *in situ*. Furthermore, years in which the *M. atlantica* population was developing in phase with copepods, did not exhibit increased abundance, which could be expected given access to a rich prey resource. Other prey resources, such as meroplankton (Mapstone, 2009), that were not considered in the present study, may have been important factors influencing the congeners temporal distribution and abundance.

We found that high seasonal abundance of *M. atlantica* in the WEC occurred under lower salinity conditions in the summer. Siphonophores are generally considered strictly oceanic (Pugh, 1999) and intolerant of low salinity waters (Mackie et al., 1987). However, the neritic *M. atlantica* can exploit both low salinity (Kitamura et al., 2003; Marques et al., 2008; Primo et al., 2012) and high salinity waters (Licandro et al., 2012). Salinity may however have an indirect effect, representing a proxy for physical processes. Annual trajectories of the STATIS analysis showed that summer periods characterised by lower salinity corresponded to extensive periods of *in situ* population development. These conditions correspond to highly stratified waters (Smyth et al., 2010) and represent the typical annual cycle in the WEC (Pingree, 1980; present study). Previous studies have already suggested that calm conditions and intense stratification may favour the accumulation and reproduction of *M. atlantica* (Graham et al., 2001; Licandro et al., 2012; Batistić et al., 2013).

Annual trajectories of the STATIS analysis revealed that deviation from the characteristic annual salinity cycle negatively influenced the *in situ* population development of *M. atlantica*. In particular, low salinity events occurring in the spring were associated with late and restricted development of the *M. atlantica* population *in situ*. Salinity represents a proxy for water circulation in the WEC (Southward et al., 2005). For instance, in the southern region of the Channel low salinity events in spring represent the intrusion of low salinity surface waters (LSSW; <35) originating from freshwater plumes of the Loire and Gironde rivers in the Bay of Biscay (Kelly-Gerreyn et al., 2006). Gough (1905) and Corbin (1947) identified LSSW as a vector for the transport of *M. atlantica* into the WEC. However, our results indicate that during the period of study, high abundances of *M. atlantica* were not associated with the occurrence of LSSW. Considering that this species is tolerant of very low salinities (i.e. down to nearly 20; Primo et al., 2012) a negative relationship between low salinity and *M. atlantica* abundance in spring suggests that anomalies in the usual circulation patterns may have dispersed the locally developing population. The arrival of *M. atlantica* in the WEC has also been attributed to the intrusion of high salinity Atlantic waters from the southwest (Southward, 1962). However, we only found one instance when the sudden appearance of high *M. atlantica* abundance coincided with these high salinity events (2008; data not shown). In general *M. atlantica* was sparse or absent throughout the duration of high salinity events in spring, suggesting a similar dispersal effect as speculated during the occurrence of low salinity events.

We identified three main environmental typologies that were associated with the *in situ* development of the *M. atlantica* population. Those conditions occurred at different times without temporal continuity, indicating that the establishment of *M. atlantica* as a resident species of the WEC was not due to a persistent shift in local temperature, salinity or prey availability. Rather, community composition changes that occurred during the study period in response to different hydroclimatic regimes (Edwards et al., 2013; Alheit et al., 2014) may have determined the establishment of a resident *M. atlantica* population in the WEC. During the period of *M. atlantica* transiency (1930–1968) the WEC ecosystem was characterised by a low abundance of warm-water southwestern plankton species and low intermediate trophic level diversity (Southward et al., 2005). Intense predation by an abundant pilchard (*Sardina pilchardus*) population during this period has been suggested as a driver of low zooplankton abundance and diversity (Southward, 1980). Limited prey resource and strong competitive, and perhaps predatory pressure (e.g. Mapstone, 2009 and references therein) from pilchards may have therefore limited the success of the *M. atlantica* population. During this period the WEC represented a 'sink' habitat (Pulliam, 1988) where *in situ* reproduc-

tion was insufficient to balance local mortality, and the population relied on immigration from nearby 'source' areas.

The establishment of the *M. atlantica* population in the late 1960s occurred after a transition to a cool-water community characterised by an abundant and diverse northwestern plankton assemblage and a rapid decline in pilchard abundance (see Southward et al., 1995, 2005 for detailed reviews). A reduction in competitive pressure from pilchards, and increased prey resources may have contributed to the establishment of the *M. atlantica* population. Similar structural changes in the Irish Sea ecosystem following a decline in the herring (*Clupea harengus*) population have been linked to the increased frequency of cnidarian material present in CPR samples after 1970 (Lynam et al., 2011). After 1968 the WEC likely transformed from a 'sink' to a 'source' habitat for *M. atlantica* (Pulliam, 1988), with local reproduction outweighing mortality and immigration.

However, changes to prevailing wind patterns in the WEC may have also contributed to the establishment of *M. atlantica*. During the 1970s there was a reduction in westerly wind strength and a strengthening of southerly winds (Smyth et al., 2010). Southerly winds drive waters of a southern origin into the WEC (Pingree and Griffiths, 1980). Increased southerly winds during the 1970s could have transported increased numbers of *M. atlantica* from the Armorican Shelf region, where source populations exist (Mackie et al., 1987 and references therein). Changing wind conditions has been shown to be an important factor influencing planktonic community composition through bio-physical interactions (e.g. Hinder et al., 2012). Therefore, increased immigration combined with improved habitat suitability may have facilitated the establishment of the *M. atlantica* population in the WEC.

Around 1985 the WEC ecosystem switched back to its current warm-water state, but without the low in zooplankton abundance and diversity associated with the first warm-water period (see Southward et al., 1995, 2005 for detailed reviews). During this period *M. atlantica* exhibited a pronounced increase in abundance and seasonal distribution concomitant with an increase in sea surface temperature. Historically, both *M. atlantica* and *M. kochi* have been considered as southwestern indicator species, indicative of the influx of warm southern waters (Russell, 1935; Southward et al., 2005). However, we found no temporal association between *M. atlantica* variability and the predominance of southwestern warm- or northwestern cool-water plankton community composition. *M. atlantica* was transient during the first warm-water community period, then established a resident population during the cool-water community period and subsequently proliferated after transition back to the current warm-water community period. Therefore *M. atlantica* should no longer be considered as an indicator of southern water inflow in the WEC. However, *M. kochi* was mostly absent during the cold-water state, in accordance with its warm-water affinity and transient nature, and may still provide utility as an indicator species in the WEC.

During the period 1930 to the late 1960s *M. atlantica* and *M. kochi* underwent alternating periods of dominance, a phenomenon that has also been observed in other regions (Mackie et al., 1987 and references therein). During this early period both *M. atlantica* and *M. kochi* were transient components of the plankton, probably dependent upon advection into the area, which suggests that patterns of dominance in the sink habitat of the WEC should mirror patterns of dominance in lower latitudinal regions supporting source populations. Evidence promoting this hypothesis is found by comparing records from our study area and other Atlantic coastal regions. For instance, *M. kochi* was dominant in the region of Gibraltar in the early 1930s (Leloup, 1933), as it was in the WEC (Russell, 1934; present study), while in the 1910s *M. atlantica* predominated in both regions (Russell, 1934; Bigelow and Sears, 1937). Since establishment of a resident *M. atlantica* population

in the WEC, *M. kochi* has failed to predominate. This could be possibly due to competitive exclusion by *M. atlantica*, given the latter's greater reproductive fitness in the WEC temperature regime.

Our study provides useful information about the environmental parameters that are associated with the maintenance of resident populations of *M. atlantica* and *M. kochi*. Although the interactive effects of environmental conditions are complex, our study confirms that temperature plays a fundamental role in determining species' geographical distributions (e.g. Beaugrand et al., 2002; Hays et al., 2005). Predicted future increases in sea surface temperature (IPCC, 2007) could result in other more northerly latitudes providing suitable environments for the establishment of *M. atlantica* populations. For example, Greve et al. (1996) hypothesised that low winter temperatures in the German Bight prevented *M. atlantica* residency after its invasion in 1989 (Greve, 1994). Our results suggest that if temperatures continue to increase *M. atlantica* could successfully overwinter and establish a resident population, a situation also applicable to the wider North Sea.

Changes in the abundance of other species of jellyfish have already been reported in neighbouring ecosystems of the Irish Sea and North Sea (e.g. Lynam et al., 2004, 2011). Whilst sea temperature consistently emerges as a key driver of changes in these regions (Licandro et al., 2010; Lynam et al., 2011) the influence of variable hydroclimatic conditions is complex and often region- and species-specific (e.g. Lynam et al., 2004). The WEC is a highly dynamic biophysical environment prone to shifts of community equilibria that show complex, non-linear responses to climatic oscillations (Southward, 1980; Alheit et al., 2014). Further research and continuing observations are required to decipher whether changes in the WEC and neighbouring areas represent actual shifts in baseline conditions or oscillations associated with long-term hydroclimatic variability (Condon et al., 2013).

Acknowledgements

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pocean.2014.07.004.

References

Abdi, H., Williams, L.J., Valentin, D., Bennani-Dosse, M., 2012. STATIS and DISTATIS: optimum multitable principal component analysis and three way metric multidimensional scaling. Wiley Interdisciplinary Reviews: Computational Statistics 4, 124–167.

Alheit, J., Licandro, P., Coombs, S., Garcia, A., Giráldez, A., Santamaría, M.T.G., Slotte, A., Tsikliras, A.C., 2014. Atlantic Multidecadal Oscillation (AMO) modulates dynamics of small pelagic fishes and ecosystem regime shifts in the eastern North and Central Atlantic. Journal of Marine Systems 131, 21–35.

Alvariño, A., 1971. Siphonophores of the pacific with a review of the world distribution. Bulletin of the Scripps Institution of Oceanography of the University of California 16, 1–432.

Batistić, M., Jasprica, N., Carić, M., Lučić, D., 2007. Annual cycle of the gelatinous invertebrate zooplankton of the eastern South Adriatic coast (NE Mediterranean). Journal of Plankton Research 29, 671–686.

Batistić, M., Lučić, D., Marina, C., Garić, R., Licandro, P., Jasprica, N., 2013. Did the alien calycophoran *Muggiaea atlantica* outcompete its native congeneric *M. kochi* in the marine lakes of Mljet Island (Croatia)? Marine Ecology 34, 3–13.

Batten, S.D., Clark, R., Flinkman, J., Hays, G.C., John, E., John, A.W.G., Jonas, T., Lindley, J.A., Stevens, D.P., Walne, A., 2003. CPR sampling: the technical background,

materials and methods, consistency and comparability. Progress in Oceanography 58, 193–215.

Baxter, E.J., Rodger, H.D., McAllen, R., Doyle, T.K., 2011. Gill disorders in marine-farmed salmon: investigating the role of hydrozoan jellyfish. Aquaculture Environment Interactions 1, 245–257.

Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296, 1692–1694.

Bigelow, H.B., Sears, M., 1937. Siphonophorae. Report on the Danish Oceanographical Expeditions 1908–10 to the Mediterranean and Adjacent Seas, vol. 2, Copenhagen, pp. 1–144.

Boero, F., Bouillon, J., Gravili, C., Miglietta, M.P., Parsons, T., Piraino, S., 2008. Gelatinous plankton: irregularities rule the world (sometimes). Marine Ecology Progress Series 356, 299–310.

Braconnot, J.C., 1971. Contribution à l'étude biologique et écologique des Tuniciers pélagiques Salpides et Doliolides I. Hydrologie et écologie des Salpides. Vie et Milieu 22, 257–286.

Carré, C., Carré, D., 1991. A complete life cycle of the calycophoran siphonophore *Muggiaea kochi* (Will) in the laboratory, under different temperature conditions: ecological implications. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 334, 27–32.

Colebrook, J.M., 1978. Continuous plankton records: zooplankton and environment, North–East Atlantic and North Sea 1948–1975. Oceanologica Acta 1, 9–23.

Condon, R.H., Duarte, C.M., Pitt, K.A., Robinson, K.L., Lucas, C.H., Sutherland, K.R., Mianzan, H.W., Bogeberg, M., Purcell, J.E., Decker, M.B., Uye, S., Madin, L.P., Brodeur, R.D., Haddock, S.H.D., Malej, A., Parry, G.D., Eriksen, E., Quiñones, J., Acha, M., Harvet, M., Arthur, J.M., Graham, W.M., 2013. Recurrent jellyfish blooms are a consequence of global oscillations. Proceedings of the National Academy of Sciences of the United States 110, 1000–1005.

Condon, R.H., Graham, W.M., Duarte, C.M., Pitt, K.A., Lucas, C.H., Haddock, S.H.D., Sutherland, K.R., Robinson, K.L., Dawson, M.N., Decker, M.B., Mills, C.E., Purcell, J.E., Malej, A., Mianzan, H., Uye, S., Gelcich, S., Madin, L.P., 2012. Questioning the rise of gelatinous zooplankton in the world's oceans. BioScience 62, 160–169.

Coombs, S.H., Halliday, N.C., 2009. An update and review of trends in zooplankton and fish larvae off Plymouth 1924–2009. Marine Biological Association Occasional Publication, 24, 27pp.

Coombs, S.H., Halliday, N.C., Southward, A.J., Hawkins, S.J., 2005. Distribution and abundance of sardine (*Sardina pilchardus*) eggs in the English Channel from Continuous Plankton Recorder sampling, 1958–1980. Journal of the Marine Biological Association of the United Kingdom 85, 1243–1247.

Corbin, P.G., 1947. The spawning of mackerel, *Scomber scombrus* L., and pilchard, *Clupea pilchardus* Walbaum, in the Celtic Sea in 1937–39. Journal of the Marine Biological Association of the United Kingdom 27, 65–132.

Cronin, M., Cusack, C., Geoghegan, F., Jackson, D., McGovern, E., McMahon, T., O'Beirn, F., Cinneide, Ó., Silke, J., 2004. Salmon mortalities at Inver Bay and Mc Swynes Bay finfish farms, County Donegal, Ireland during 2003. Marine Environment and Health Series. Series 15, 129pp.

Cunningham, J.T., 1892. On a species of siphonophore observed at Plymouth. Journal of the Marine Biological Association of the United Kingdom 2, 212–215.

Decker, M.B., Liu, H., Ciannelli, L., Ladd, C., Cheng, W., Chan, K.-S., 2013. Linking changes in eastern Bering Sea jellyfish populations to environmental factors via nonlinear time-series models. Marine Ecology Progress Series 494, 179–189.

Edwards, M., Beaugrand, G., Helaouët, P., Alheit, J., Coombs, S., 2013. Marine ecosystem response to the Atlantic Multidecadal Oscillation. PLoS ONE 8 (2), e57212.

Fosså, J.H., Flood, P.R., Olsen, A.B., Jensen, F., 2003. Små og usynlige, men plagsomme maneter av arten *Muggiaea atlantica* (Small and invisible, but troublesome jellyfish of the species *Muggiaea atlantica*). Fisken Havet 2, 99–103 (In Norwegian).

Gaertner, J.C., Chessel, D., Bertrand, J., 1998. Stability of spatial structures of demersal assemblages: a multitable approach. Aquatic Living Resources 11, 75–85.

Gough, L.H., 1905. On the distribution and the migrations of *Muggiaea atlantica*, Cunningham, in the English Channel, the Irish Sea, and off the south and west coasts of Ireland, in 1904. Conseil Permanent International pour l'Exploration de la Mer, Publications de Circonstance 29, 1–13.

Graham, W.M., Pagès, F., Hamner, W.M., 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451, 199–212.

Greve, W., 1994. The 1989 German Bight invasion of *Muggiaea atlantica*. ICES Journal of Marine Science 51, 355–358.

Greve, W., Reiners, F., Nast, J., 1996. Biocoenotic changes of the zooplankton in the German Bight: the possible effects of eutrophication and climate. ICES Journal of Marine Science: Journal du Conseil 53, 951–956.

Hagadorn, J.W., Dott, R.H., Damrow, D., 2002. Stranded on a Late Cambrian shoreline: medusae from central Wisconsin. Geology 30, 147–150.

Hays, G.C., Richardson, A.J., Robinson, C., 2005. Climate change and marine plankton. Trends in Ecology and Evolution 20, 337–344.

Hinder, S.L., Hays, G.C., Edwards, M., Roberts, E.C., Walne, A.W., Gravenor, M.B., 2012. Changes in marine dinoflagellate and diatom abundance under climate change. Nature Climate Change 2, 271–275.

Ibañez, F., 1982. Sur une nouvelle application de la théorie de 1'information à la description des séries chronologiques planctoniques. Journal of Plankton Research 4, 619–632.

Ibañez, F., Conversi, A., 2002. Prediction of missing values and detection of 'exceptional events' in a chronological planktonic series: a single algorithm. Ecological Modelling 154, 9–23.

Ibañez, F., Grosjean, P., Etienne, M., 2009. Pastecs: Package for Analysis of Space-Time Ecological Series. R package version 1.3-8. <http://www.sciviews.org/pastecs>.

Intergovernmental Panel on Climate Change, 2007. Climate Change 2007. The Physical Science Basis. Cambridge University Press, Cambridge.

John, E.H., Batten, S.D., Harris, R.P., Hays, G.C., 2001. Comparison between zooplankton data collected by the Continuous Plankton Recorder survey in the English Channel and by WP-2 nets at station L4, Plymouth (UK). Journal of Sea Research 46, 223–232.

Kelly-Gerreyn, B.A., Hydes, D.J., Jégou, A.M., Lazure, P., Fernand, L.J., Puillat, I., García-Soto, C., 2006. Low salinity intrusions in the western English Channel. Continental Shelf Research 26, 1241–1257.

Kendall, M., 1976. Time-Series. Charles Griffin, London.

Kitamura, M., Tanaka, Y., Ishimaru, T., 2003. Coarse scale distributions and community structure of hydromedusae related to water mass structures in two locations of Japanese waters in early summer. Plankton Biology and Ecology 50, 43–54.

Kršinic, F., Njire, J., 2001. An invasion by *Muggiaea atlantica* Cunningham 1892 in the northern Adriatic Sea in the summer of 1997 and the fate of small copepods. Acta Adriatica 42, 49–59.

Lavit, C., Escoufier, Y., Sabatier, R., Traissac, P., 1994. The ACT (STATIS method). Computational Statistics and Data Analysis 18, 97–119.

Leloup, E., 1933. Siphonophores calycophorides provenant des campagnes du Prince Albert ler de Monaco. Résultats des Campagnes Scientifiques, vol. 87, Monaco, pp. 1–12.

Licandro, P., Ibañez, F., 2000. Changes of zooplankton communities in the Gulf of Tigullio (Ligurian Sea, Western Mediterranean) from 1985 to 1995. Influence of hydroclimatic factors. Journal of Plankton Research 22, 2225–2253.

Licandro, P., Ibañez, F., Etienne, M., 2006. Long-term fluctuations (1974–1999) of the salps Thalia democratica and Salpa fusiformis in the northwestern Mediterranean Sea: relationships with hydroclimatic variability. Limnology and Oceanography 51, 1832–1848.

Licandro, P., Conway, D.V.P., Daly Yahia, M.N., Fernandez de Puelles, M.L., Gasparini, S., Hecq, J.H., Tranter, P., Kirby, R.R., 2010. A blooming jellyfish in the northeast Atlantic and Mediterranean. Biology Letters 6, 688–691.

Licandro, P., Souissi, S., Ibañez, F., Carré, C., 2012. Long-term variability and environmental preferences of calycophoran siphonophores in the Bay of Villefranche (north-western Mediterranean). Progress in Oceanography 97, 152–163.

Lucas, C.H., 2001. Reproduction and life history strategies of the common jellyfish, *Aurelia aurita*, in relation to its ambient environment. Hydrobiologia 451, 229–246.

Lucas, C.H., Dawson, M.N., 2014. What are jellyfish and thaliaceans and why do they bloom? In: Pitt, K.A., Lucas, C.H. (Eds.), Jellyfish Blooms. Springer, Netherlands, pp. 9–44.

Lucas, C.H., Gelcich, S., Uye, S., 2014. Living with jellyfish: management adaptation strategies. In: Pitt, K.A., Lucas, C.H. (Eds.), Jellyfish Blooms. Springer, Netherlands, pp. 129–150.

Lynam, C.P., Hay, S.J., Brierley, A.S., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnology and Oceanography 49 (3), 637–643.

Lynam, C.P., Lilley, M.K.S., Bastian, T., Doyle, T.K., Beggs, S.E., Hays, G.C., 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? Global Change Biology 17, 767–782.

Mackie, G.O., Pugh, P.R., Purcell, J.E., 1987. Siphonophore biology. Advances in Marine Biology 24, 97–262.

Mapstone, G.M., 2009. Siphonophora (Cnidaria: Hydrozoa) of Canadian Pacific Waters. NRC Research Press, Ottawa, Ontario, Canada.

Marques, S.C., Azeiteiro, U.M., Leandro, S.M., Queiroga, H., Primo, A.L., Martinho, F., Viegas, I., Pardal, M.A., 2008. Predicting zooplankton response to environmental changes in a temperate estuarine ecosystem. Marine Biology 155, 531–541.

MATLAB® (R2013b 8.2.0.701), 2013. The MathWorks Incorporated. Natick, Massachusetts, United States.

Mills, C.E., 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES Journal of Marine Science 52, 575–581.

Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451, 55–68.

Moreno, I., Fdez-Alcazar, J., 1984. Estudio del zooplancton epiplanctonico de la zona costera de gijon. VI. sifonoforos. Cuadernos de Investigación Biológica 5, 21–28.

Patriti, G., 1964. Les siphonophores du Golfe de Marseille. Recueil des Travaux de la Station Marine d'Endoume Bulletin 35, 185–258.

Perry, R.I., Smith, S.J., 1994. Identifying habitat associations of marine fishes using survey data: an application to the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 51, 589–602.

Pingree, R., 1980. Physical Oceanography of the Celtic Sea and English Channel. Elsevier, Amsterdam.

Pingree, R.D., Griffiths, D.K., 1978. Tidal fronts on shelf seas around British-Isles. Journal of Geophysical Research-Oceans and Atmospheres 83, 4615–4622.

Pingree, R.D., Griffiths, D.K., 1980. Currents driven by a steady uniform wind stress on the shelf seas around the British-Isles. Oceanologica Acta 3, 227–236.

Pitt, K., Welsh, D., Condon, R., 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. Hydrobiologia 616, 133–149.

Primo, A.L., Marques, S.C., Falcao, J., Crespo, D., Pardal, M.A., Azeiteiro, U.M., 2012. Environmental forcing on jellyfish communities in a small temperate estuary. Marine Environmental Research 79, 152–159.

Pugh, P.R., 1999. Siphonophorae. In: Boltovsky, D. (Ed.), South Atlantic Zooplankton. Backhuys Publishers, Leitlen.

Pulliam, H.R., 1988. Sources, sinks, and population regulation. American Naturalist 132, 652–661.

Purcell, J.E., 1981. Dietary-composition and diel feeding patterns of epipelagic siphonophores. Marine Biology 65, 83–90.

Purcell, J.E., 1982. Feeding and growth of the siphonophore *Muggiaea atlantica* (Cunningham 1893). Journal of Experimental Marine Biology and Ecology 62, 39–54.

Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. Journal of the Marine Biological Association of the United Kingdom 85, 461–476.

Purcell, J.E., Uye, S., Lo, W.-T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology-Progress Series 350, 153–174.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Riera, T., Gili, J.M., Pagès, F., 1986. Estudio cuantitativo y estacional de dos poblaciones de cnidarios plactónicos frente a las costas de Barcelona (Mediterráneo Occidental): Ciclos entre 1966–67 y 1982–83. Miscellanea Zoologica 10, 23–32.

Russell, F.S., 1934. On the occurrence of the siphonophores *Muggiæa atlantica* (Cunningham) and *Muggiæa kochi* (Will) in the English Channel. Journal of the Marine Biological Association of the United Kingdom (New Series) 19, 555–558.

Russell, F.S., 1935. On the value of certain plankton animals as indicators of water movements in the English Channel and North Sea. Journal of the Marine Biological Association of the United Kingdom 20, 309–332.

Smyth, T.J., Fishwick, J.R., Al-Moosawi, L., Cummings, D.G., Harris, C., Kitidis, V., Rees, A., Martinez-Vicente, V., Woodward, E.M.S., 2010. A broad spatio-temporal view of the Western English Channel observatory. Journal of Plankton Research 32, 585–601.

Southward, A.J., 1962. The distribution of some plankton animals in the English Channel and Approaches. II. Surveys with the Gulf III high speed sampler, 1958–60. Journal of the Marine Biological Association of the United Kingdom 42, 275–375.

Southward, A.J., 1970. Improved methods of sampling post-larval young fish and macroplankton. Journal of the Marine Biological Association of the United Kingdom 50, 689–712.

Southward, A.J., 1980. The Western English Channel – an inconstant ecosystem? Nature 285, 361–366.

Southward, A.J., Boalch, G.T., 1986. Aspects of long-term changes in the ecosystem of the western English Channel in relation to fish populations. International Symposium of Long Term Changes in Marine Fish Populations, Vigo, 415–446.

Southward, A.J., Hawkins, S.J., Burrows, M.T., 1995. 70 years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the Western English Channel in relation to rising sea temperature. Journal of Thermal Biology 20, 127–155.

Southward, A.J., Langmead, O., Hardman-Mountford, N.J., Aiken, J., Boalch, G.T., Dando, P.R., Genner, M.J., Joint, I., Kendall, M.A., Halliday, N.C., Harris, R.P., Leaper, R., Mieszkowska, N., Pingree, R.D., Richardson, A.J., Sims, D.W., Smith, T., Walne, A.W., Hawkins, S.J., 2005. Long-term oceanographic and ecological research in the western English Channel. Advances in Marine Biology 47, 1–105.

Will, J.G.F., 1844. Horae tergestinae oder beschreibung und anatomie der im herbste 1843 bei triest beobachteten akalephen. Leipzig.