Interannual variability of gelatinous mesozooplankton in a temperate shelf sea: greater abundance coincides with cooler sea surface temperatures

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Although gelatinous zooplankton are an important component of marine ecosystems, gelatinous mesozooplankton that are <2 cm are underrepresented in monitoring programmes. Here, the interannual variability of gelatinous mesozooplankton abundance and diversity was estimated from 167 zooplankton net samples that were collected in the Celtic Sea during seven fisheries surveys between 2007 and 2019 and analysed alongside environmental parameters. Compositional changes occurred interannually, including an overturn in the abundance ratio of two siphonophores (*Muggiaea atlantica* and *Agalma elegans*). Analysis of annual mean gelatinous abundance revealed no linear trend over time (Spearman, $r = -0.09$, $p = 0.287$); however, the interannual abundance varied by a factor of 33 (minimum mean abundance in $2013 = 7.36 \pm 4.86$ individuals m^{-3}; maximum in $2017 = 244.82 \pm 84.59$ individuals m^{-3}). Holoplanktonic taxa dominated the abundance of the gelatinous community (93.27%) and their abundance was negatively associated with summer sea surface temperature (represented by the 16°C isotherm in July), and the Eastern Atlantic Pattern index 3 months prior (April). Our data suggest that gelatinous mesozooplankton in the Celtic Sea may become less abundant with further ocean warming, and further highlight the need to monitor gelatinous mesozooplankton with a high taxonomic resolution moving forward.

Keywords: Celtic Sea, climate change, holoplankton, jellyfish, time series, zooplankton

Introduction

Shelf seas contain diverse and productive ecosystems (Lauria et al., 2012) that have undergone profound changes in recent times as a result of both natural and anthropogenic modes of climate variability (Southward et al., 1995; Beaugrand and Reid, 2003; Schmidt et al., 2020). Marine zooplankton are one of the most sensitive taxa to changes in environmental conditions and monitoring their long-term abundance and diversity has facilitated the detection of ecosystem-wide changes in several shelf basins (Southward et al., 1995; Beaugrand et al., 2009; Conversi

et al., 2010). The mechanisms that alter the interannual abundance and composition of zooplankton in shelf seas are complex and are possibly specific to each shelf region (Pershing *et al.*, 2010). These mechanisms can be an indirect consequence of changes in local oceanographic conditions (Beare *et al.*, 2000; Ershova *et al.*, 2015), the direct or indirect effects of hydroclimatic changes (Napp *et al.*, 2002; Pitois and Fox, 2006; Bedford *et al.*, 2020), or due to a combination of those factors (Southward *et al.*, 1995). It is important to understand the mechanisms which influence the long-term variability of zooplankton as they can drive trends in the abundance of higher trophic organisms, including commercially important fish (Beaugrand and Reid, 2003).

In the Northeast Atlantic, the second-largest shelf sea is the Celtic Sea. This sea spans 500 km from the northwest coast of France to the southern coast of Ireland, covering an area of ~130 000 km^2. As this shelf sea sustains the second most productive fishery in the North West European Shelf in terms of commercial fish landings (Pinnegar *et al.* 2002), the interannual variability of many taxonomic groups has been monitored there for several decades (Lauria *et al.*, 2012). Monitoring has documented considerable changes in the abundance and composition of phytoplankton (Schmidt *et al.*, 2020), zooplankton (Beaugrand *et al.*, 2000; Giering *et al.*, 2019), fish (Pinnegar *et al.*, 2002), and seabirds (Lauria *et al.*, 2012) in the Celtic Sea, which may reflect broad shifts in the entire shelf ecosystem. Despite this significant body of research, some groups of taxa remain underrepresented in monitoring programmes that cover this shelf sea, particularly the gelatinous zooplankton community (Gibbons and Richardson, 2009).

Since the 1990s, a surge of ecological research has revealed that gelatinous zooplankton have a more nuanced role in marine food webs as they provide regulating, provisioning, and supporting services to ecosystems (Doyle *et al.*, 2014). Large aggregations of pelagic tunicates graze on a wide range of organisms from large diatoms to particulate organic matter and microbes (Holland, 2016), while pelagic cnidarians and ctenophores mostly predate upon zooplankton populations (Purcell, 1991; Sabatés *et al.*, 2010). When bloom conditions subside, large mortality events known as "jellyfish falls" can occur, which represent an important transport pathway of carbon from the pelagic zone to the benthos (Lebrato *et al.*, 2012). The use of various techniques (DNA analysis, stable isotope analysis, stomach content analysis, and Remotely Operated Vehicles) has revealed that gelatinous zooplankton are also predated upon by a range of marine organisms including other gelatinous zooplankton, crustaceans, cephalopods, sea birds, turtles, and over 100 species of fish (Pauly *et al.*, 2009; Hays *et al.*, 2018). Although we now know that gelatinous zooplankton are a natural and important component of marine ecosystems (Hays *et al.*, 2018), there is still a lack of information available for the abundance and diversity of gelatinous mesozooplankton that are <2 cm in size (Gibbons and Richardson, 2009).

Zooplankton monitoring programmes that do include gelatinous mesozooplankton data often classify them into groups of low taxonomic resolution (e.g. "coelenterate tissue"), as some physical samplers can damage defining features of individuals. Equally, a historical lack of research interest in gelatinous zooplankton played a large role as well, even if gelatinous mesozooplankton were present in good condition (Gibbons and Richardson, 2009). The low taxonomic resolution for gelatinous mesozooplankton in many of these data removes the ability to observe changes in particular groups of taxa that differ in specific biological traits (Southward *et al.*, 1995). As a result, there are limited studies that explain the interannual variability of gelatinous mesozooplankton abundance with a high taxonomic resolution (Southward *et al.*, 1995; D'Ambrosio *et al.*, 2016; Guerrero *et al.*, 2018). Even the most comprehensive zooplankton monitoring survey in the North Atlantic (the Continuous Plankton Recorder survey) is selective when capturing gelatinous zooplankton (e.g. *Pelagia noctiluca*) (Baxter *et al.*, 2010), so gelatinous zooplankton data from the CPR survey should be supported by other forms of information such as genomics (Licandro *et al.*, 2015) or additional quantitative sampling (Baxter *et al.*, 2010).

Within this context of limited gelatinous mesozooplankton time series, summer mesozooplankton net samples were collected and analysed for the period 2007–2019 in the Celtic Sea region. These data are compared to in situ and satellite-derived physical parameters to determine the potential mechanisms that influence the interannual variability of gelatinous mesozooplankton abundance and diversity. The implications of any detected trends and mechanisms for change are discussed in the context of the Celtic Sea ecosystem.

Materials and methods
Zooplankton sample collection
All sampling was carried out in Irish and United Kingdom territorial waters aboard the RV Celtic Explorer (Marine Institute of Ireland). One hundred and sixty-seven zooplankton samples were collected in the Celtic Sea region during seven fisheries surveys over 13 years between 10 June and 27 July each year (mean sampling date was 1 July, 23.85 samples were collected per survey on average). As no single fisheries survey had an adequate temporal coverage of sampling in the Celtic Sea, mesozooplankton samples were collected from two fisheries surveys, the Irish Mackerel and Horse Mackerel Egg Survey (Irish MEGS) and the Western European Shelf Pelagic Acoustic Survey (WESPAS). The Irish MEGS surveys collected zooplankton samples in 2007, 2010, and 2013 and WESPAS surveys collected zooplankton samples in 2016, 2017, 2018, and 2019 (Figure 1). The Irish MEGS surveys used a Gulf VII sampler to sample zooplankton. This sampler had a 0.2 m diameter aperture, with a 250 µm mesh, and was towed on a double-oblique (v-shaped) profile at an average speed of ~2 m s^{-1} to within 10 m from the bottom (ICES, 2019). Samples were immediately preserved in 4% buffered formalin upon collection. Three hours after preservation, all fish eggs and larvae were carefully removed from the samples, and the remainder of each sample was placed in long-term storage [more information provided in ICES (2019)]. The WESPAS surveys used a ring net sampler to sample zooplankton. This net had a 1 m diameter aperture, a 200 µm mesh, and was deployed vertically at an average speed of ~0.5 m s^{-1} to within 10 m of the bottom (O'Donnell *et al.*, 2019). These samples were split using a 200 ml Folsom plankton splitter. One half was preserved immediately in 4% buffered formalin and stored (for the current study), while the other half was used to estimate the total dry weight of each zooplankton sample (presented in O'Donnell *et al.*, 2019). It was recently demonstrated that the Gulf VII net and the ring net provide similar estimates of gelatinous mesozooplankton abundance and diversity with exception that the Gulf VII underestimated the abundance of Appendicularia by a factor of 9.7 (Long *et al.*, 2020). As such, the abundance of this taxonomic group was
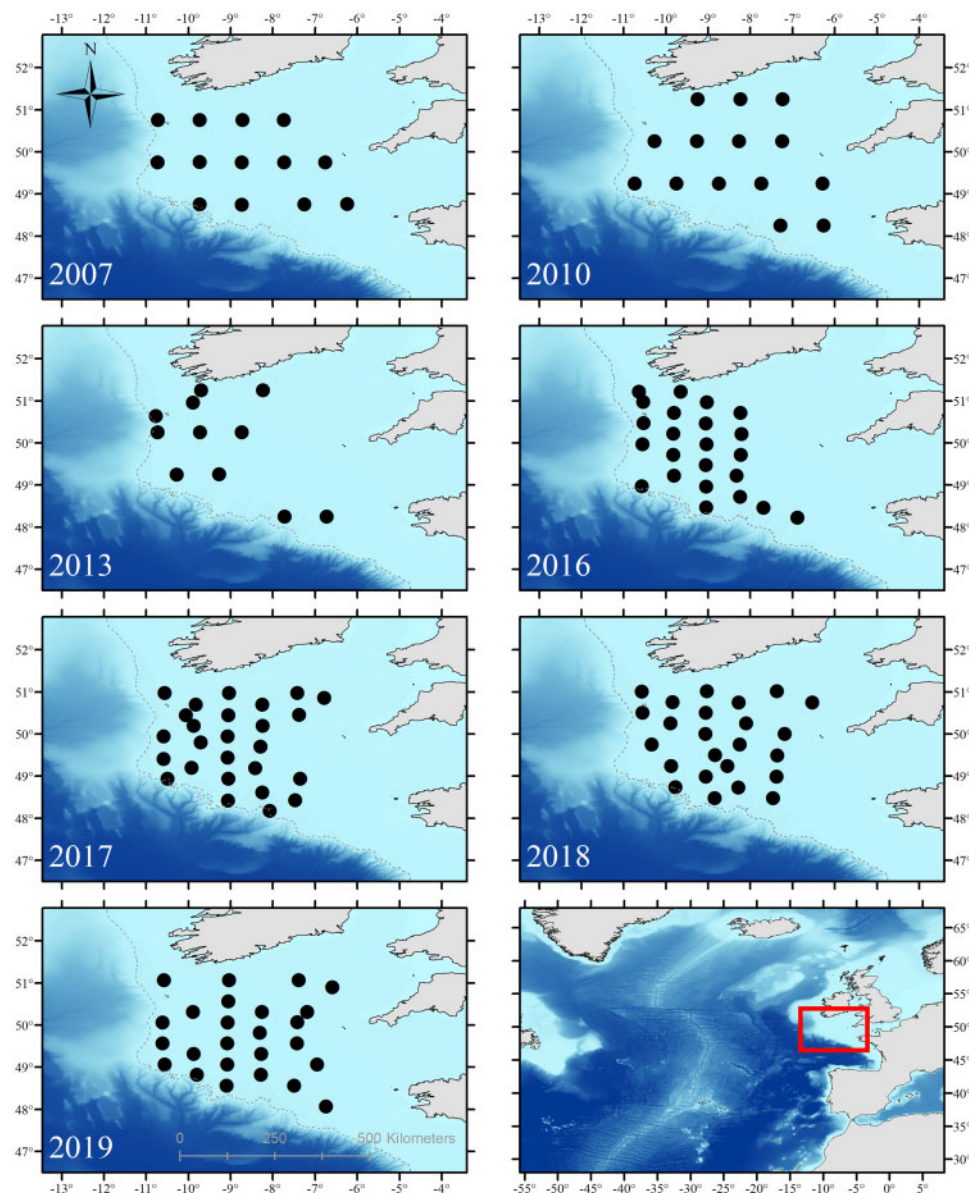
Figure 1. Spatial coverage of zooplankton net deployments and CTD deployments. 2007–2013 = Gulf VII net (Irish MEGS surveys). 2016–2019 = ring net (WESPAS surveys). Dashed contour = 200 m (edge of continental shelf). The extent map illustrates the limits of the Celtic Sea relative to the North Atlantic Ocean. The specific station information for each survey is presented in Supplementary File S1.

raised by this factor for samples which were collected by a Gulf VII sampler (Irish MEGS surveys) in this study. Otherwise, the difference in net type among the surveys was not considered as a sampling bias for our analysis. A comprehensive description of zooplankton sample collection is detailed in ICES (2019) for surveys that used a Gulf VII sampler, and in O'Donnell *et al.* (2019) for surveys that used a ring net. To further reduce station variability among survey years, stations with a bottom depth greater than 200 m and stations that were outside the limits of the Celtic Sea (48°N—52°N, 6°W—11°W) were removed from the analysis (32 stations were removed, 136 were retained).

Zooplankton sample processing

Gelatinous zooplankton present in each zooplankton sample were enumerated using a dark field microscope and were identified to

species level where possible (Mayer, 1912; Russell, 1953, 1970; Totton, 1965; Bone, 1998; Mills, 1998; Conway, 2012; Conway, 2015). Species that are difficult to identify using microscopy were identified to genus level (e.g. *Obelia* spp.). Doliolids were identified to order level (Doliolida) as the visual identification of doliolid species requires counting muscle bands on individuals, which was not feasible due to research time constraints. As many appendicularian individuals were damaged and lacked characterising features, this group was identified to class level (Appendicularia). Some other taxa were also identified to higher taxonomic levels as they lacked characterising features, due to damage incurred during sampling or preservation (e.g. unidentifiable anthomedusae). If one or more taxa were highly abundant in a sample (>100 individuals in 20 ml portion of a 200 ml sample), the sample was split up to four times (1/16th) using a

200 ml Folsom Plankton Splitter (note: WESPAS samples were already split once during sample collection). The entirety of each sample was analysed for gelatinous taxa that can be > or <2 cm (e.g. *Leuckartiara octona* or *Clytia hemisphaerica*). Calycophoran siphonophore abundances were estimated as the sum of anterior nectophores present per taxon. Physonect siphonophore colony abundances were estimated for each taxon using the equation $((X/\alpha) + Y)$, where X was the sum of nectophores in a sample, Y was the sum of physonect larval colonies in a sample, and α was a factor representing the average number of nectophores present on an adult physonect colony of each taxon. This factor (α) was obtained for each taxon from past studies of physonect morphology in the North East Atlantic region (e.g. $\alpha = 10$ for *Nanomia bijuga*; Totton, 1965; $\alpha = 15$ for *Agalma elegans*; Totton, 1965). As most ctenophores are very fragile (Hosia *et al.*, 2017) and most scyphozoans are greater than 2 cm in size (Russell, 1970), both of these groups were likely underrepresented in our samples (as we used small meshed nets) and as a result data for ctenophores and scyphozoans were excluded from any quantitative analyses.

Environmental data collection

Conductivity, Temperature and Depth (CTD) profiles were recorded during (Irish MEGS) or directly before (WESPAS) each zooplankton net haul (see Supplementary File S1 for full CTD deployment details). CTD data were processed to calculate sea surface temperature (SST; temperature at 5 m depth), thermocline depth, Schmidt stability index (SSI), and the centre of buoyancy of the water column at each station. The mean of these parameters was calculated per survey and these were compared over time. Computational analyses and visual outputs for CTD data were carried out in R program version 3.4.3 (R Core Team, 2016) using the "rLakeAnalyzer" (Winslow *et al.* 2019) and "oce" packages (Kelly *et al.*, 2020), and the Sea-bird software. To better understand the evolution of SST approaching each survey period over the Northwest European Shelf (NWES) region, Odyssea reprocessed SST data were also obtained (Autret *et al.*, 2019a, b). These satellite-derived, level 4, gap-free SST data are available at 0.04° spatial resolution and daily temporal resolution and are produced by the French Research Institute for Exploitation of the Sea (IFREMER) within the GHRSST framework (Group for High-Resolution Sea Surface Temperature). This product was accessed through the Copernicus Marine Environment Monitoring Service (http://marine.copernicus.eu). From this, SST data (°C) were calculated for each zooplankton station on the mean sampling day of the study (1 July, summer), the date 3 months before (1 April, spring), and the date 6 months before (1 January, winter). To understand the interannual variability of SST over the larger NWES region each summer, the mean latitude of the 16°C isotherm was also calculated for this large region on 1 July for each survey year. All satellite-derived data were analysed using ArcMap version 10.7.1 (2020). As long-term oscillations of ocean-atmospheric systems can affect the interannual variability of marine zooplankton populations (Eloire *et al.*, 2010), monthly mean data for the North Atlantic Oscillation and the Eastern Atlantic Pattern (EAP) were obtained for the study period (2007–2019) from the NOAA Climate Prediction Centre data repository (https://www.climate.gov). Both the North Atlantic Oscillation and the EAP are atmospheric pressure systems, which oscillate latitudinally in the northern hemisphere over multidecadal time

scales and these indices are strongly linked to long-term trends in SST and wind behaviour in the North East Atlantic (Cannaby and Hüsrevoğlu, 2009).

Data analysis

For the five most abundant taxa in the zooplankton samples, temporal trends in their relative contribution to total gelatinous mesozooplankton abundance were examined. This allowed any changes in gelatinous community composition to be detected. Taxa abundance data were also converted into a Bray-Curtis dissimilarity matrix (after it was subjected to Wisconsin double standardization to downweigh highly abundant taxa) and then plotted using non-metric dimensional scaling (NMDS). This was executed in R program version 3.4.3 (R Core Team, 2016) using the package "vegan" (Oksanen *et al.*, 2014). To gain an initial understanding of the interannual variability of gelatinous mesozooplankton abundance, the combined mean abundance of all gelatinous zooplankton taxa was calculated for each survey and these were compared to temporal characteristics of the environmental parameters. Additionally, gelatinous taxa abundance data were grouped based on their life history (meroplanktonic taxa vs holoplanktonic taxa) as taxa with different life histories can have unique responses to environmental change (Bedford *et al.*, 2020). Possible associations between the different abundance groupings and the environmental data were first estimated using pair-wise Spearman's rank correlations. To incorporate any random effects of our sampling design while quantifying the relationship between gelatinous abundance and environmental parameters, generalized linear mixed models (GLMMs) were constructed for the life history groups using the Laplace approximation method and a log-link function. Fixed effects were selected using a backward stepwise process, using the Akaike information criterion value to compare the goodness of fit among models. These included CTD parameters (centre of buoyancy, thermocline depth, SST), satellite SST parameters (SST at 0, 3, and 6 months before sampling, latitude of the 16°C isotherm in July), and hydroclimatic indices (EAP and NAO at 0, 3, and 6 months before sampling). If any fixed effects had a moderate-strong correlation (>0.5), the fixed effect with the highest estimate was retained, and other correlated effects were removed from the model. Response variables (holoplanktonic abundance and meroplanktonic abundance) both followed a gamma distribution. Fixed effects were rescaled to a mean of 0 and a standard deviation of 1 prior to the model selection process as we encountered issues with model convergence. The random effects that were explored for each model included survey year (seven levels) and net type used (two levels). All statistical analyses for models were carried out in R program version 3.4.3 (R Core Team, 2016) using the package "lme4" (Bates *et al.* 2020) and data distribution was explored using the package "fitdistrplus" (Delignette-Muller *et al.*, 2019).

Results

Temporal trends in environmental conditions

Over the Northwest European Shelf, the mean latitude of the 16°C isotherm in July (from satellite SST data) followed a similar trend to the mean SST for each survey (from CTD data), suggesting a good agreement between the CTD and satellite data (Figure 2). There was an incremental increase in mean SST and mean latitude of the 16°C isotherm from 2007 to a maximum in 2013 (temperature = 18.2°C, latitude = 51.3°N) and a

subsequent decrease from 2013 to a minimum mean in 2017 (temperature = 14.7°C, latitude = 49.9° N). The mean SST and latitude of the 16°C isotherm increased slightly from 2017 to 2019.

Other physical parameters such as thermocline depth, centre of buoyancy, and the SSI displayed different magnitudes of inter-annual variability. Mean centre of buoyancy inversely agreed with mean SST and the mean latitude of the 16°C isotherm over time (see Figure 2). The mean SSI was typically low for each survey (SSI <10 000) with exception to the 2013 survey, which had a mean SSI almost ten times higher than any other survey (95 525.4), suggesting there was particularly intense thermal stratification that summer. The trend in mean thermocline depth was different to the temporal trends of other physical parameters. The minimum mean thermocline depth was recorded in 2007 (32.16 m), and the maximum mean thermocline depth was recorded in 2017 (52.31 m). The mean thermocline depth during the 2013 and 2017 surveys was similar, even though these two surveys had the largest difference in mean SST.

Trends in diversity and community composition

A total of 33 gelatinous zooplankton taxa were identified in the Celtic Sea over the 13-year study period, which included 20 hydromedusae, 4 siphonophores, 2 scyphomedusae, 3 ctenophores (2 lobate and 1 cydippid taxa), 2 salps, 1 doliolid, and 1 appendicularian. Five additional taxa were unidentifiable as they were damaged during sampling or preservation. Despite this large overall diversity, the mean taxa richness of gelatinous zooplankton in each sample was much lower (8.67 ± 1.29; ± represents the 95% confidence interval of the mean for the remainder of the text). Six of these taxa were considered rare as they were only present in one sample of one survey and five of these were found in 2013. These were the hydromedusae, *Bougainvillia pyramidata* (2013), *Modeeria rotunda* (2013), and *Eutima gracilis* (2018), the siphonophore *Apolemia uvaria* (2013), the scyphomedusae *Cyanea lamarckii* (2013), and the salp *Soestia zonaria* (2013).

Five taxa dominated the abundance of gelatinous taxa in samples from each survey, and their relative contributions to total gelatinous abundance varied over time (Figure 3). Appendicularia was the most abundant taxon in five of the seven sample years and its mean abundance varied considerably over time [mean abundance; maximum in 2017 = 111.43 ± 34.65 individuals (ind.) m^{-3}, minimum = 2.04 ± 3.26 ind. m^{-3}]. In samples of the 2007 and 2010 surveys, the calycophoran siphonophore *Muggiaea atlantica* was the second most abundant gelatinous mesozooplankton taxon, with a mean abundance of 43.63 ± 14.85 ind. m^{-3} in 2007 and 7.36 ± 4.86 ind. m^{-3} in 2010. For the remainder of the study, *M. atlantica* abundances were low (mean abundance <0.5 ind. m^{-3}). Mean abundance in 2013 was dominated by an equal proportion of *Aglantha digitale*, Doliolida and Appendicularia, although the total mean gelatinous abundance was low this year (7.76 ± 5.19 ind. m^{-3}). Parallel to a reduction in the relative contribution of *M. atlantica* to total gelatinous abundance in samples from 2016 to 2019, there was a clear increase in the relative contribution of the siphonophore *A. elegans* in those years. A full list of the gelatinous taxa and their contributions to mean abundance each survey is provided in Table 1.

The temporal changes in community abundance and composition are further highlighted by plotting the taxa abundance matrix (Bray-Curtis dissimilarity, Wisconsin standardization) using
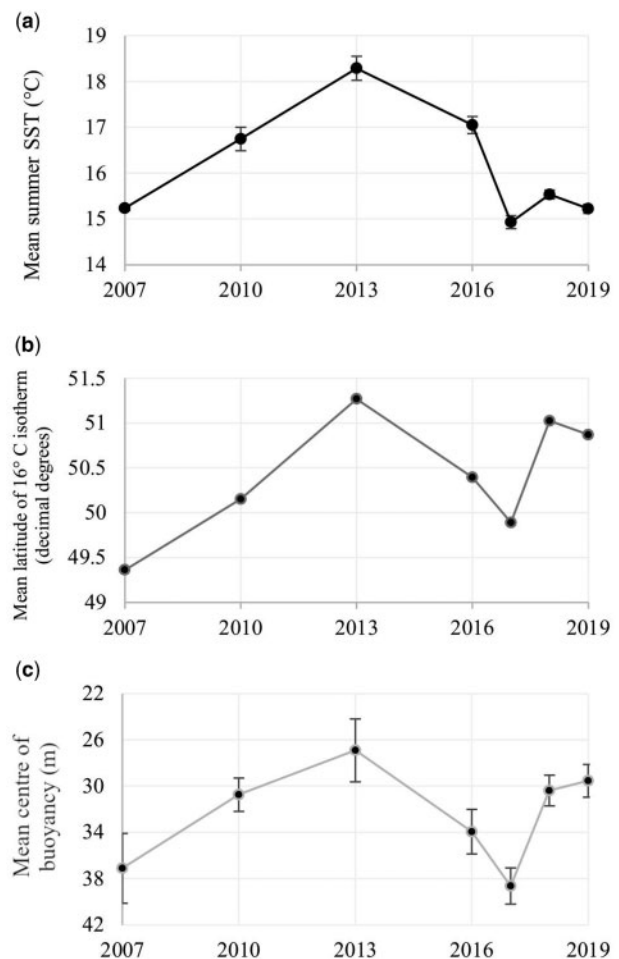

Figure 2. Mean values in the Celtic Sea per survey for (a) SST (°C) from CTD sampling, (b) latitude of the 16°C isotherm across the North West European Shelf in July (decimal degrees) from satellite data, and (c) centre of buoyancy (m) analysed from CTD data. *Note that the y-axis for (c) centre of buoyancy is inverted to highlight the similar trend to (a) and (b). Error bars indicate the standard error of the mean.

NMDS and grouping the samples by survey (Figure 4). Samples in the first two surveys (2007 and 2010) grouped together on the NMDS plot, the last four surveys formed a second grouping (2016, 2017, 2018, and 2019), while samples from 2013 plotted away from all other samples in the study. The stress of the analysis was moderate (0.24), which suggests weak clustering and confirms that subtle changes in community composition occurred over time.

Trends in gelatinous abundance

There was no increase or decrease in total gelatinous mesozooplankton abundance over the study period (Spearman, r = −0.09, p = 0.287). Total mean abundance varied considerably among the surveys, by as much as a factor of 33 (Figure 5). Total mean abundance decreased incrementally over the first three surveys of the time series from 129.742 ± 81.33 ind. m^{-3} in 2007 to 7.76 ± 5.19 ind. m^{-3} in 2013. Total mean abundance was incrementally higher over the next two surveys (2016 and 2017) reaching a maximum mean abundance in 2017 samples (244.87 ± 84.59 ind. m^{-3}).
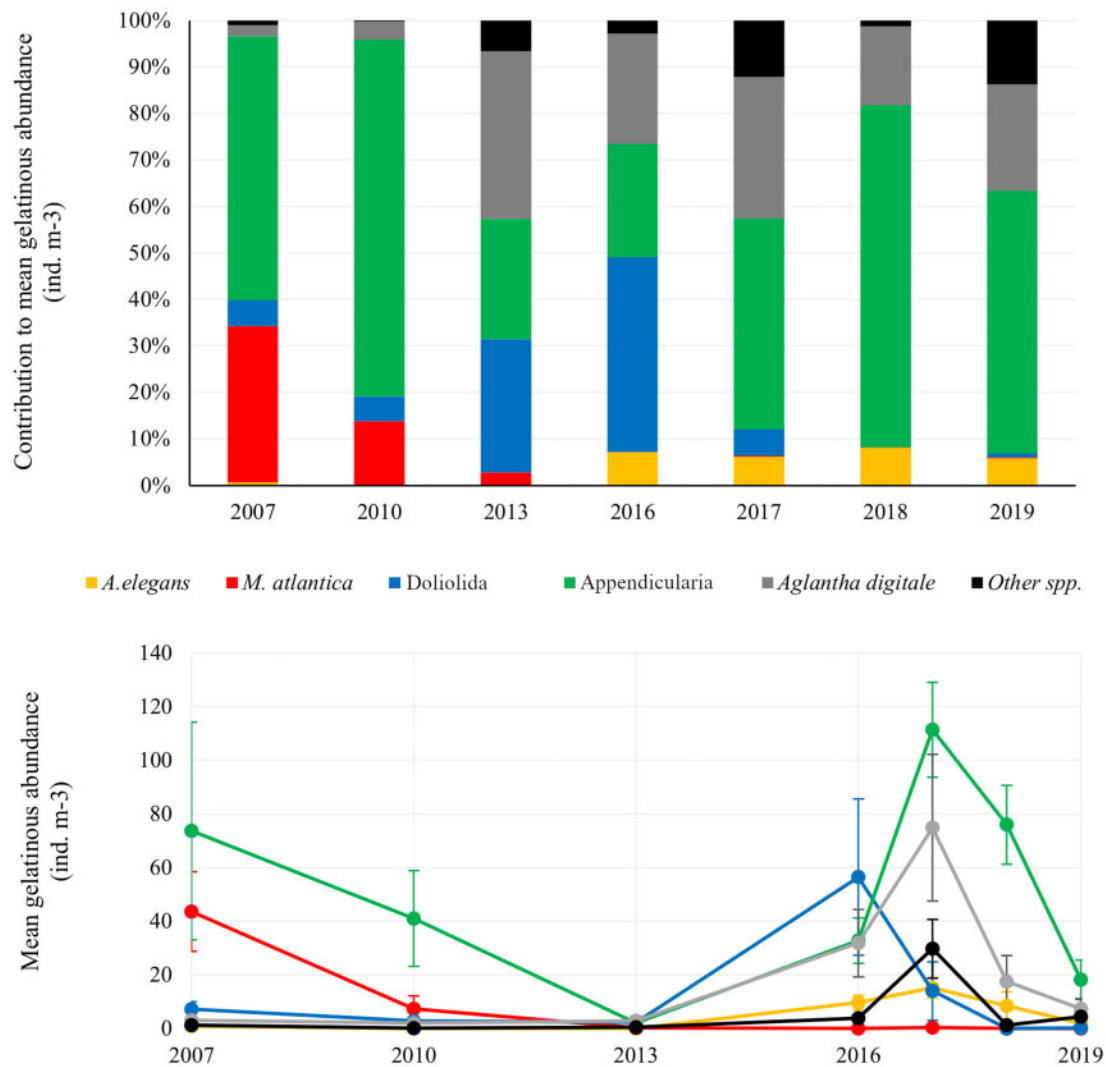
Figure 3. Top panel: High temporal variability in the relative contribution of the five most abundant gelatinous mesozooplankton species as a percentage of total gelatinous mesozooplankton abundance for each survey. Black = Other species, Grey = *Aglantha digitale*, Blue = Doliolida, Green = Appendicularia, Yellow = *A. elegans*, Red = *M. atlantica*. Bottom panel: Mean abundance (ind. m^{-3}) of the five most abundant species each survey. Appendicularia was the most abundant species in five of the seven surveys. The relative abundance (and mean abundance) of *M. atlantica* decreased considerably each year from 2007 to 2013 and is not visible in the last four sample years due to low abundances. At the same time, the relative abundance of *A. elegans* and *A. digitale* was higher in the last four surveys.

There was a step decrease in total mean abundance in samples of the last two surveys, returning to a relatively low mean abundance of 31.92 ± 16.29 ind. m^{-3} in 2019 samples.

When gelatinous taxa abundance data were grouped by life history, trends in the abundance of holoplanktonic and meroplanktonic gelatinous mesozooplankton in the Celtic Sea were different over the study period. The temporal trend of holoplanktonic taxa abundance was similar to that of total gelatinous mesozooplankton abundance as holoplanktonic taxa contributed to 93.27% of total gelatinous mesozooplankton abundance on average in samples (see Figure 5). Mean meroplanktonic taxa abundance remained below ~3 ind. m^{-3} in samples of each survey except for 2017 when mean meroplanktonic taxa abundance was at its study maximum (28.91 ± 21.55 ind. m^{-3}). Meroplanktonic taxa contributed to 6.73% of the total gelatinous mesozooplankton abundance in samples on average.

Relations between abundance groups and environmental data

The abundance of holoplanktonic and meroplanktonic gelatinous mesozooplankton had weak-moderate and significant ($p < 0.01$) Spearman rank correlations with several physical parameters over the study period. For holoplanktonic abundance, these included the latitude of the 16°C isotherm in July ($\rho = -0.40$, $p < 0.0001$) and the EAP index during the sampling period ($\rho = 0.227$, $p = 0.008$). The latitude of the 16°C isotherm in July ($\rho = -0.31$, $p < 0.0001$) and the NAO index 3 months before the sampling period ($\rho = 0.287$, $p < 0.001$) had weak but highly significant correlations with meroplanktonic abundance. When the abundance of all taxa are combined (as total gelatinous abundance), the strength of the negative association with the latitude of the 16°C isotherm in July is slightly greater ($\rho = -0.41$, $p < 0.001$). This is best illustrated

Table 1. Mean abundance (N m^{-3}) each survey for gelatinous zooplankton taxa identified in the study, ranked by their overall mean abundance over the study period (highest to lowest).

Taxon	2007 N m^{-3}	SD	2010 N m^{-3}	SD	2013 N m^{-3}	SD	2016 N m^{-3}	SD	2017 N m^{-3}	SD	2018 N m^{-3}	SD	2019 N m^{-3}	SD	Overall N m^{-3}	SD
Appendicularia	73.7	146.2	41.0	66.9	2.0	5.5	32.8	40.7	111.4	90.1	76.0	72.1	18.2	36.9	55.0	80.9
Aglantha digitale	3.1	4.3	2.1	5.4	2.8	6.1	31.9	60.4	74.9	139.5	17.5	47.3	7.4	19.0	24.9	73.1
Doliolida	7.2	10.5	2.9	4.1	2.3	6.4	56.5	139.6	14.0	55.3	<0.1	0.1	1.0	1.0	13.4	64.5
Agalma elegans	0.9	0.9	<0.1	<0.1	<0.1	<0.1	9.6	13.2	15.2	19.4	8.4	26.3	1.9	1.8	6.5	15.8
Muggiaea atlantica	43.6	53.6	7.4	18.2	0.2	0.5	<0.1	0.1	0.3	1.0	0.1	0.3	0.1	0.2	5.1	21.2
Lizzia blondina	–	–	–	–	–	–	–	–	26.9	55.4	0.2	1.2	<0.1	0.1	5.1	26.1
Salpa fusiformis	<0.1	<0.1	<0.1	<0.1	0.1	0.2	0.1	0.6	–	–	<0.1	0.1	3.1	9.8	0.6	4.3
Unidentifiable anthomedusae	0.3	0.4	<0.1	<0.1	0.2	0.5	2.5	4.8	0.6	1.9	<0.1	0.2	<0.1	0.1	0.6	2.3
Euphysa aurata	0.8	0.8	–	–	<0.1	<0.1	0.1	0.3	0.9	1.4	0.2	0.3	0.4	1.8	0.4	1.0
Pleurobrachia spp.	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.1	0.4	0.8	1.4	0.6	2.1	0.3	0.7	0.3	1.2
Unidentifiable Physonectidae	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.5	0.9	<0.1	<0.1	–	–	<0.1	<0.1	0.1	0.4
Nanomia bijuga	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	0.2	0.1	0.2	<0.1	<0.1	0.2	0.3	0.1	0.2
Unidentifiable leptomedusae	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	<0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.3s	0.1	0.2
Clytia hemisphaerica	–	–	–	–	–	–	<0.1	0.1	0.1	0.3	<0.1	0.1	–	–	<0.1	0.1
Corymorpha nutans	<0.1	<0.1	<0.1	<0.1	–	–	<0.1	<0.1	0.1	0.3	<0.1	0.1	<0.1	0.1	<0.1	0.1
Beroe spp.	–	–	–	–	–	–	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	0.1	0.3	<0.1	0.1
Leuckartiara octona	<0.1	<0.1	<0.1	<0.1	<0.1	0.1	<0.1	0.1	0.1	0.1	<0.1	<0.1	<0.1	0.1	<0.1	0.1
Unidentifiable ephyrae	–	–	–	–	–	–	0.1	0.3	–	–	–	–	–	–	<0.1	0.1
Laodicea undulata	–	–	–	–	–	–	<0.1	<0.1	<0.1	0.1	<0.1	<0.1	0.1	0.2	<0.1	0.1
Obelia spp.	–	–	–	–	–	–	–	–	0.1	0.1	<0.1	0.1	–	–	<0.1	0.1
Hydractinia borealis	–	–	–	–	–	–	–	–	<0.1	0.1	–	–	<0.1	0.1	<0.1	0.1
Solmaris corona	<0.1	0.2	–	–	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	0.1
Ectopleura dumortierii	<0.1	<0.1	–	–	–	–	–	–	<0.1	0.1	–	–	–	–	<0.1	<0.1
Bolinopsis infundibulum	–	–	–	–	–	–	–	–	<0.1	<0.1	<0.1	0.1	–	–	<0.1	<0.1
Eutima gracilis	–	–	–	–	–	–	–	–	–	–	<0.1	0.1	–	–	<0.1	0.1
Aequorea spp.	–	–	–	–	–	–	–	–	<0.1	0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Unidentifiable Diphyidae	–	–	<0.1	<0.1	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	<0.1
Soestia zonaria	–	–	–	–	<0.1	0.1	–	–	–	–	–	–	–	–	<0.1	<0.1
Liriope tetraphylla	–	–	–	–	<0.1	<0.1	–	–	<0.1	0.1	–	–	–	–	<0.1	<0.1
Coryne eximia	–	–	–	–	<0.1	<0.1	–	–	<0.1	0.1	–	–	–	–	<0.1	<0.1
Amphinema rugosum	–	–	–	–	<0.1	<0.1	–	–	<0.1	<0.1	–	–	<0.1	<0.1	<0.1	<0.1
Stauridiosarsia gemmifera	<0.1	<0.1	–	–	–	–	–	–	–	–	–	–	–	–	<0.1	<0.1
Pelagia noctiluca	–	–	–	–	–	–	<0.1	<0.1	<0.1	<0.1	–	–	–	–	<0.1	<0.1
Sarsia spp.	–	–	–	–	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	<0.1
Bougainvillia pyramidata	–	–	–	–	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	<0.1
Cyanea lamarckii	–	–	–	–	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	<0.1
Modeeria rotunda	–	–	–	–	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	<0.1
Apolemia uvaria	–	–	–	–	<0.1	<0.1	–	–	–	–	–	–	–	–	<0.1	<0.1

SD, standard deviation of the mean.

by mapping the spatial association between total gelatinous abundance and the 16°C isotherm in July for each survey (Figure 6). When the 16°C isotherm was further south (e.g. during the summers of 2007 and 2017), total gelatinous abundance was higher in the Celtic Sea, whilst total gelatinous abundance was lower when the 16°C isotherm was further north (e.g. during the summers of 2010 and 2013). Surveys 2016 and 2018 may represent intermediary years between high and low abundance and a moderately positioned 16°C isotherm.

Mixed-effects modelling highlighted the linkages underpinning the Spearman rank associations. It revealed that different physical parameters affected the abundance of the two functional groups of gelatinous mesozooplankton over time. The final model for holoplanktonic abundance included station latitude, the latitude of the 16°C isotherm in July and the EAP (East Atlantic Pattern) index 3 months before sampling as fixed effects, and year as a random effect. The random effect (year) explained 26.72% of among-group variation on average (intercept = 0.396, SD =

0.629). The variables with the largest effect on holoplanktonic abundance were the latitude of the 16°C isotherm in July (estimate = −0.862, t_{130} = −3.674, $p = 0.001$) and the EAP index 3 months before the sampling period (estimate = 0.475, t_{130} = 2.034, $p = 0.041$) and these effects were both significant. Station latitude had a small significant effect (0.229, t_{130} = 2.148, $p = 0.081$).

In the final model for meroplanktonic taxa abundance, the random effect (year) explained 77.28% of among-group variation (intercept = 9.935, SD = 3.152). The SST 3 months before sampling was the parameter that had the largest effect on the variability of meroplanktonic abundance (estimate = −1.354, t_{129} = −3.348, $p < 0.001$). Station latitude had a small significant effect on meroplanktonic abundance (estimate = −0.684, t_{129} = −2.176, $p = 0.029$), which represented some spatial correlation among surveys. The other fixed effect (NAO at time of sampling) did not have a significant effect on meroplanktonic abundance and the estimated effect was smaller than the other two variables

$(-0.456, t_{129} = -0.532, p = 0.594)$. It should be noted that net type (ring net vs Gulf VII sampler) was queried as a random effect in both sets of models and this variable did not explain any substantial random variation in the abundance of either groups of taxa between survey years, which is supported by the work of Long *et al.* (2020).
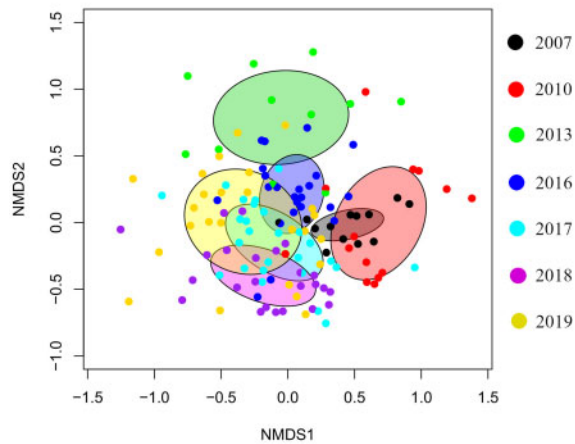

Figure 4. NMDS plot of the gelatinous mesozooplankton species abundance matrix (Bray–Curtis dissimilarity, Wisconsin standardisation, stress = 0.24) grouped by survey year. Ellipse = extent of 1 standard deviation from the centroid of the stations of a survey. The ellipses for 2007 (red) and 2010 (black) group close together, as do the ellipses for 2016, 2017, 2018, and 2019 (blue, cyan, purple, and yellow, respectively). The ellipse for 2013 (green) is in isolation. Points are individual stations coloured based on survey year.

Discussion

Over the past century, there has been a considerable body of work investigating the zooplankton dynamics of shelf seas in the North East Atlantic (Hays *et al.*, 2005). In contrast to the extensive research of crustacean zooplankton in the Celtic Sea (Fraser, 1955; Williams, 1985; Williams *et al.*, 1994; Beaugrand *et al.*, 2000), the interannual variability of gelatinous mesozooplankton abundance and diversity is vastly underrepresented in the literature (Gibbons and Richardson, 2009), despite their ecological and socio-economic importance (Doyle *et al.*, 2014). In reply to several recent calls for further monitoring of gelatinous zooplankton (Brodeur *et al.*, 2016; Aubert *et al.*, 2018; Long *et al.*, 2020), here we describe trends in the abundance and diversity of gelatinous mesozooplankton in the Celtic Sea.

One of the most important findings from this study was that there was no significant increase or decrease in gelatinous abundance over the study period (Spearman, $r = -0.09$, $p = 0.287$; Figure 5). In contrast, other research in the Celtic Sea and adjacent seas have reported an increase (Lynam *et al.*, 2011) or a decrease (Bedford *et al.*, 2020) in the abundance of certain zooplankton taxa over several years. In the Irish Sea (adjacent to our study region), Lynam *et al.* (2011) found that the abundance of scyphozoan jellyfish increased over a 15-year period, and this was linked to changes in climatic factors (SST, precipitation, and the North Atlantic Oscillation Index) and the overexploitation of certain commercial fish stocks such as Atlantic herring (*Clupea harengus*). A more recent analysis of plankton in the Celtic and North seas between 1956 and 2017 revealed that a decrease in the abundance of large diatoms and non-gelatinous holoplankton (mainly small copepods) and a concurrent increase in the abundance of non-gelatinous meroplankton have occurred in accordance with a gradual increase in mean SST (Bedford *et al.*, 2020). The trend of gelatinous mesozooplankton abundance in the Celtic Sea is therefore atypical of what has been reported for other
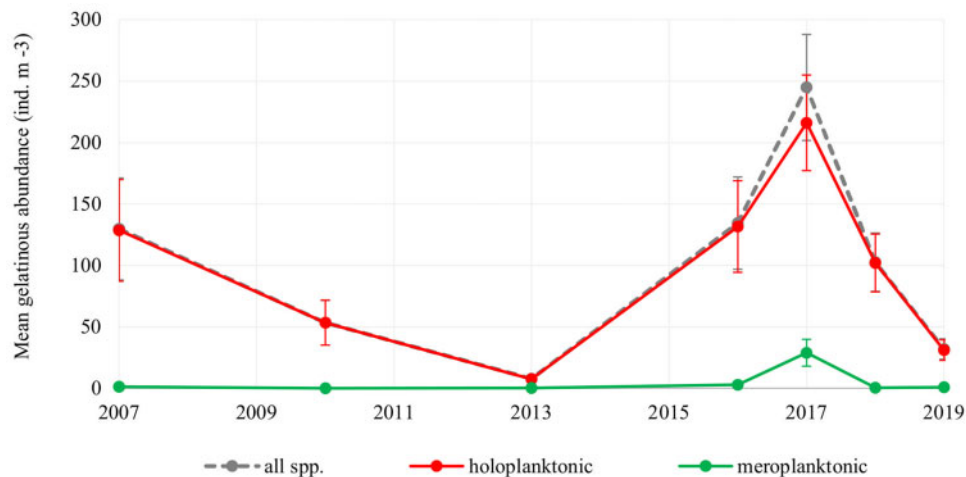
Figure 5. Interannual variability of gelatinous mesozooplankton abundance of all species combined (dashed grey line), holoplanktonic species abundance (red), and meroplanktonic species abundance (green). Holoplanktonic species abundance varied on a much larger magnitude compared to that of meroplanktonic species. Holoplanktonic species contributed to 93.27% of total gelatinous abundance on average over the study.
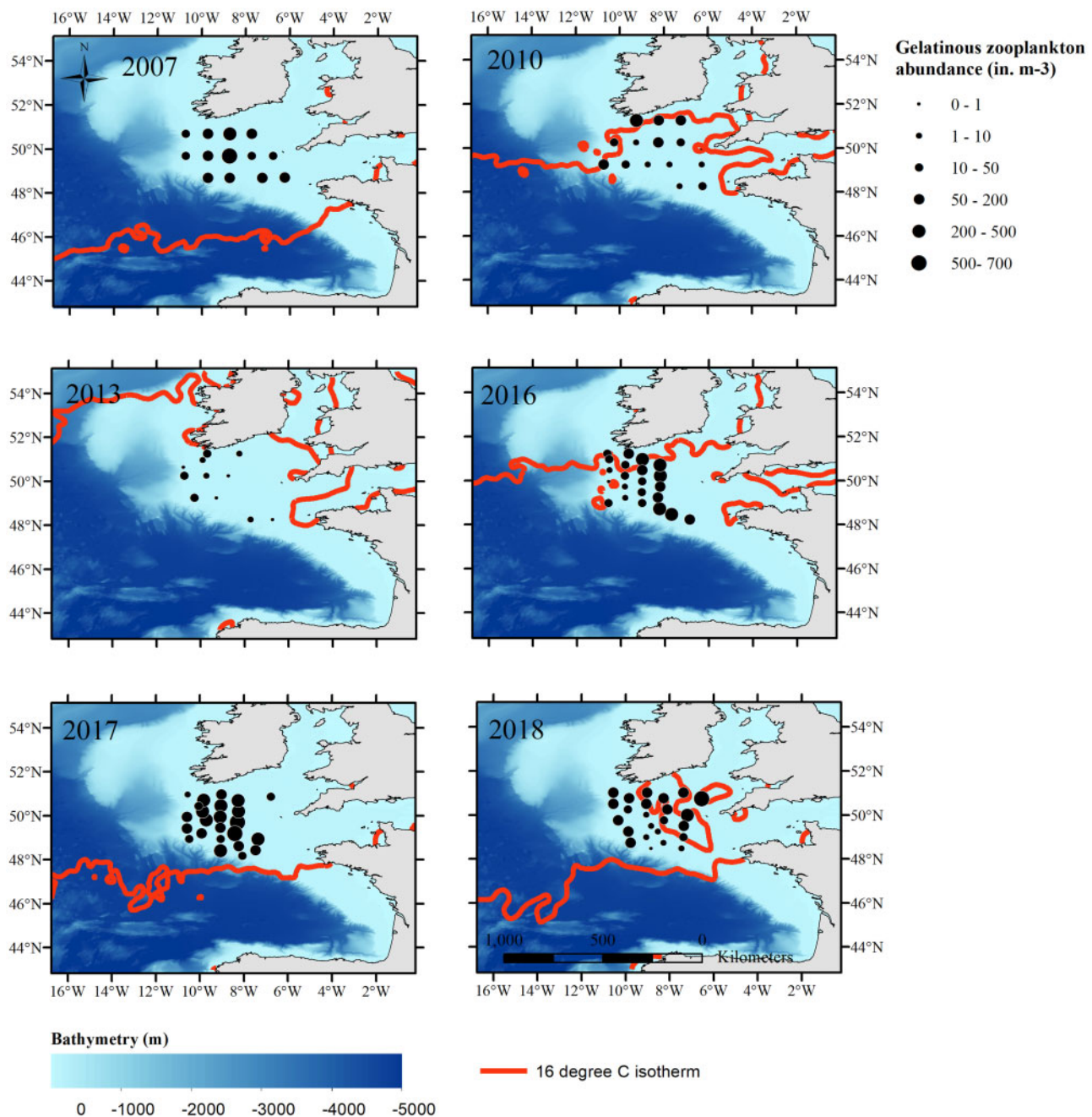
Figure 6. Distribution of the 16°C isotherm in July (red line) for surface waters in the Celtic Sea and neighbouring waterbodies over the study period. Black circles = Total gelatinous mesozooplankton abundance (individuals m^{-3}) per zooplankton sampling station. Total abundance was higher during summers when the 16°C isotherm was further south (e.g. in summers 2007 or 2017). In years when the 16°C isotherm was further north; total abundance was lower (e.g. in summers 2010 or 2013). Note: data for 2019 are not shown as the satellite product this year is not yet calibrated with the rest of the SST time series.

taxa. Reasons for this may be the limited time series used in this analysis (i.e. 7 data years collected over 13 years), which may not be sufficient to detect broader trends in gelatinous zooplankton abundance (Lavaniegos and Ohman, 2007). Furthermore, assessing the interannual trends as a single unit (i.e. total gelatinous abundance) may have masked distinct responses of certain gelatinous taxa due to differences in their biology.

While no linear trend was detected, it was noteworthy that the mean abundance varied from year to year by as much as a factor of 33 (mean gelatinous abundance: 7 ind. m^{-3} in 2013 vs. 245 ind. m^{-3} in 2017). This scale of variability in abundance is considerable, given that in the Western English Channel (a coastal region southeast of the Celtic Sea), the mean abundance of all zooplankton taxa varied each summer by a much smaller factor of 4 between 1988 and 2007 (Eloire *et al.*, 2010). Further south in the NW Mediterranean Sea, Guerrero *et al.* (2018) showed that the mean abundance of gelatinous zooplankton doubled from 7.23 ind. m^{-3} in June 1983, to 14.31 ind. m^{-3} in June 2018. The

abundance of gelatinous mesozooplankton in our study varied on a larger scale compared to the findings of Guerrero *et al.* (2018) over a much shorter time frame (13 years). This may have been a consequence of the intrinsically transitional nature of temperate shelf seas, which are known to contain different proportions of warm temperate and cold boreal taxa over decadal time scales in response to changes in environmental conditions (Southward *et al.*, 1995; Hátún *et al.*, 2009). The Celtic Sea may also support higher abundances of gelatinous mesozooplankton as it is highly productive (Schmidt *et al.*, 2020), while the Mediterranean Sea is typically oligotrophic (Conversi *et al.*, 2010).

The gelatinous mesozooplankton community also experienced compositional changes over time, especially among the five most abundant taxa on average over the study (Figure 4). A gradual decrease in the relative abundance of the calycophoran siphonophore *M. atlantica* and an increase in the abundance of the physonect siphonophore *A. elegans* may have had important ecological impacts. For example, *M. atlantica* feed primarily on small copepods, whereas *A. elegans* predate on larger zooplankton prey such as shrimp and larval fish (Purcell, 1981). As such, the change in abundance of these two siphonophore species represents an overall increase in the trophic position of the gelatinous mesozooplankton community, which may have benefitted small copepods (from decreased predation pressure) and reduced the abundance of larger crustacean zooplankton or ichthyoplankton in the Celtic Sea. Another important compositional change was an increase in *Aglantha digitale* abundance in the latter half of the study, which may have negatively affected certain copepod species (Williams and Conway, 1981; Pagès *et al.*, 1996). In Norwegian fjords, adult *A. digitale* medusae can consume 8.7% of the daily abundance of the copepod *Temora longicornis* (Pagès *et al.*, 1996). The increase in *A. digitale* abundance may have also benefitted some commercial fish such as Atlantic mackerel (*Scomber scombrus*), as they are known to feed on *A. digitale* both in situ (Lamb *et al.*, 2019) and in mesocosms (Runge *et al.*, 1987). But perhaps the most ecologically significant change was the abundance of Appendicularia, which varied between 15 and 80% of total gelatinous abundance over time, in line with changes in the temperature regime. As filter feeders, appendicularians play a major role in the biological pump by selectively capturing and consuming particulate organic carbon (Katija *et al.*, 2017) and they sequester carbon by frequently shedding mucosal tests and producing faecal pellets (Conley *et al.*, 2018). Some larval flatfish also rely heavily on the consumption of appendicularians for optimal development (Last, 1978). Therefore, the high interannual variability of appendicularian abundance detected in the Celtic Sea represents substantial changes in the rate of carbon recycling in the epipelagic zone, the rate of carbon transfer from the microbial loop to the animal food chain, and the rate at which biogenic carbon is sequestered (Holland, 2016). The negative relationship between appendicularian abundance and SST detected in this study is also evidence that appendicularians are a strong bioindicator of changes in the thermal regime (i.e. the physical structure) of the Celtic Sea. Analysing gelatinous mesozooplankton at a high taxonomic resolution can therefore provide a valuable way of tracking environmental changes in the Celtic Sea, and may offer an alternative perspective than crustacean centric methods.

By grouping the gelatinous taxa abundance data based on their life history, we revealed that holoplanktonic and meroplanktonic gelatinous taxa followed different trends in abundance over time in response to different environmental factors. Mixed-effects

modelling indicated that the interannual variability of holoplanktonic gelatinous taxa abundance was largely influenced by the combined effects of the spring EAP index and summer SST (represented by the latitude of the 16°C isotherm in July). This is similar to findings from other shelf seas where zooplankton communities have exhibited regionally specific responses to changes in oceanographic conditions (SST, wind, and/or thermal stratification) and natural oscillations of atmospheric pressure systems (Beaugrand and Reid, 2003; Lavaniegos and Ohman, 2007; Eloire *et al.*, 2010). In the NW Mediterranean Sea, Guerrero *et al.* (2018) found that the gelatinous mesozooplankton community there responded to a 30-year increase in summer SST, with a pronounced increase in the abundance of two holoplanktonic hydrozoans (*Muggiaea kochii* and *Aglaura hemistoma*). The holoplanktonic gelatinous taxa in our study had a negative relationship with summer SST (represented by the position of the 16°C isotherm in July; Figure 6), possibly due to the higher proportion of cold temperate gelatinous taxa in the Celtic Sea, which are indicative of milder temperatures (Southward *et al.*, 1995). The EAP index documents the oscillatory movement of atmospheric pressure centres between the central North Atlantic and the Western European continent. Such changes in the atmosphere can affect sea-level pressure, wind (Zubiate *et al.*, 2017), and heat exchange processes, which together influence the multi-decadal variability of SST in the Celtic Sea (Cannaby and Hüsrevoğlu, 2009). The fact that the EAP index has displayed an increasingly positive trend over the last 50 years with anthropogenically induced climate change (Cannaby and Hüsrevoğlu, 2009) means that Celtic Sea SST will likely increase in the future. A continued increase in SST may favour lower abundances of holoplanktonic gelatinous mesozooplankton through a direct physiological response to temperature (i.e. cessation of growth or reduction of gametogenesis; Beaugrand and Kirby 2018). Furthermore, an increase in temperature could prolong seasonal periods of thermal stratification, which may favour small-celled picophytoplankton blooms (Schmidt *et al.* 2020) and smaller, less abundant crustacean zooplankton (Beaugrand *et al.* 2009; Bedford *et al.* 2020). This could reduce the availability of food for some gelatinous mesozooplankton (especially those that are predators) and may further reduce their abundance as a result. Prolonged periods of thermal stratification could also incur phenological shifts in plankton communities, which could cause mismatches among gelatinous zooplankton predators, other mesozooplankton, and phytoplankton blooms (Southward *et al.* 1995; Edwards and Richardson 2004; Boero *et al.* 2016).

The abundance of meroplanktonic gelatinous zooplankton varied on a smaller scale and contributed to <7% of total gelatinous abundance on average. This is an important result, which suggests that during the summer, the Celtic Sea does not support high abundances of meroplanktonic gelatinous mesozooplankton relative to that of holoplanktonic gelatinous mesozooplankton. Naturally, meroplanktonic medusae are more abundant in coastal waters compared to offshore shelf waters due to the increased availability of food and suitable substrata for benthic life stages to settle on in coastal waters (Russell, 1953; Hays *et al.*, 2005). It is possible that the physical structure of the Celtic Sea may also play a role in preventing the advection of meroplanktonic medusae further offshore. During the summer, the Celtic Sea becomes vertically stratified due to solar heating, while coastal waters remain mixed. The density gradient between these two water masses forms a baroclinic coastal current that may act as physical barrier

that could help retain meroplanktonic medusae in coastal waters, or at least reduce their chances of being advected towards the Celtic Sea to the south (Fernand *et al.*, 2006; Haberlin *et al.*, 2019). However, it must also be noted that the annual occurrence of the sexual free-living stage of most gelatinous meroplankton (the medusa) is often short lived (weeks to a few months; Russell, 1953) and the seasonal timing of their peak abundance can vary each year by several months (Russell, 1953; Edwards, 1965; Schuchert, 2010). For the rest of the year, gelatinous meroplankton populations are maintained as benthic life stages (hydroids), which occupy a range of benthic substrata including bedrock, sediment (Schuchert, 2010), or attached to other organisms (mollusc shells; Edwards, 1965; marine sponges; Schuchert, 2019; kelp fronds; Ronowicz *et al.*, 2008). These additional factors may explain some of the variability of the meroplanktonic taxa abundance data. Despite their low contribution to total abundance, the interannual variability of meroplanktonic taxa abundance was affected by a combination of parameters, including the SST in the preceding spring (from satellite data; largest effect) and the latitude of zooplankton stations each year (smallest effect). Changes in SST in the preceding spring may have directly affected the interannual abundance of meroplanktonic taxa as this coincides with a seasonal event where medusae are produced asexually from benthic hydroids (via lateral budding) and are released into the plankton (Purcell *et al.*, 2009). Although several young medusae may bud from each hydroid for several months thereafter, a change in spring temperature may affect the rate of lateral budding, the mortality rate of hydroids or the mortality rate of young medusae (Lynam *et al.*, 2011). The interannual variability of spring SST could also indirectly affect the abundance of meroplanktonic gelatinous taxa via the availability of food for young medusae in the water column (i.e. phytoplankton and copepods) and the availability of food for benthic hydroids as particulate organic matter transported from the epipelagic zone to depth (Lynam *et al.*, 2011; D'Ambrosio *et al.*, 2016; Guerrero *et al.*, 2018).

Despite an attempt to ensure that zooplankton samples from each survey represented a similar spatial extent of the Celtic Sea, mixed-effects modelling indicated that the interannual variability of station latitude was an additional source of variation in holoplanktonic and meroplanktonic taxa abundance (detailed description of GLMM outputs in Results section). Mean station latitude was slightly higher in 2013 compared to the survey mean (2013 = 49.986°N, overall mean station latitude = 49.803°N), although the difference in station latitude among surveys was not significant ($H = 1.098$, df = 6, $p = 0.982$). Nonetheless, any potential variability caused by station latitude each year was incorporated into our mixed-effects models. The fact that sampling date (day of year) reduced the goodness of fit of mixed-effects models also suggested that differences in sampling dates among sample years were not an important source of variability. It is also likely that several biological interactions would have also played distinct roles in modulating the variability of gelatinous mesozooplankton abundance, which were not incorporated in the study. Such interactions include the predation of or competition with other zooplankton like copepods, the abundance of phytoplankton, or the abundance of pelagic fish (Lynam *et al.*, 2011). Future incorporation of these additional biological data would provide a more comprehensive description of the factors that affect the abundance and diversity of gelatinous mesozooplankton.

To conclude, here we describe distinct interannual trends in the abundance of different gelatinous mesozooplankton taxa that may have had substantial ecological impacts on the Celtic Sea ecosystem. If gelatinous mesozooplankton were monitored as a broad taxonomic group, we would not have detected these distinct and important compositional changes. The detection of a negative relationship between the abundance of holoplanktonic gelatinous mesozooplankton and the thermal regime of the Celtic Sea suggests that this particular taxonomic grouping may be a useful bioindicator of structural changes in the Celtic Sea (Southward *et al.*, 1995). Given the projected increase in the average temperature of the Celtic Sea and intensification of vertical stratification during the summer (Cannaby and Hüsrevoğlu, 2009; Schmidt *et al.*, 2020), the abundance of holoplanktonic gelatinous mesozooplankton will likely decrease in the future.

Supplementary data
Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions
Conceptualization: APL and TKD. Data curation: APL, DH, BO, and CO. Formal analysis: APL, DH, OL, RGS, and DB. Funding acquisition: TKD and CL. Visualization: APL, DH, and RGS. Writing—original draft: APL, TKD, and DH. Writing—review and editing: APL, TKD, DH, RGS, CL, OL, BO, CO, and DB.

Data availability
The data underlying this article will be shared on reasonable request to the corresponding author.

References
Aubert, A., Antajan, E., Lynam, C., Pitois, S., Pliru, A., Vaz, S., and Thibault, D. 2018. No more reason for ignoring gelatinous zooplankton in ecosystem assessment and marine management: concrete cost-effective methodology during routine fishery trawl surveys. Marine Policy, 89: 100–108.

Autret, E., Paul, F., and Piolle, J. F. 2019. Quality information document for level 4 Odyssea reprocessed SST product over the European North West Shelf/Iberia Biscay Irish Seas SST_ATL_SST_L4_REP_OBSERVATIONS_010_026. Copernicus, Marine Environment Monitoring Service.

Autret, E., Paul, F., and Piolle, J. F. 2019. Product user manual for level 4 Odyssea reprocessed SST product over the European

North West Shelf/Iberia/Biscay Irish Sea. Copernicus, Marine Environment Monitoring Service.

Bates, D., Maechler, M., Bolker, B., Walker, S., Christensen, R. H. B., Singmann, H., Dai, B. et al. 2020. lme4: linear mixed-effects models using 'Eigen' and S4. R Package Version, 1: 1–23.

Baxter, E. J., Walne, A. W., Purcell, J. E., McAllen, R., and Doyle, T. K. 2010. Identification of jellyfish from Continuous Plankton Recorder samples. Hydrobiologia, 645: 193–201.

Beare, D. J., Gislason, A., Astthorsson, O. S., and Mckenzie, E. 2000. Assessing long-term changes in early summer zooplankton communities around Iceland. ICES Journal of Marine Science, 57: 1545–1561.

Beaugrand, G., Ibañez, F., and Reid, P. C. 2000. Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. Marine Ecology Progress Series, 200: 93–102.

Beaugrand, G., and Reid, P. C. 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. Global Change Biology, 9: 801–817.

Beaugrand, G., Luczak, C., and Edwards, M. 2009. Rapid biogeographical plankton shifts in the North Atlantic Ocean. Global Change Biology, 15: 1790–1803.

Beaugrand, G., and Kirby, R. R. 2018. How do marine pelagic species respond to climate change? Theories and observations. Annual Review of Marine Science, 10: 169–119.

Bedford, J., Ostle, C., Johns, D. G., Atkinson, A., Best, M., Bresnan, E., Machairopoulou, M. et al. 2020. Lifeform indicators reveal large-scale shifts in plankton across the North-West European shelf. Global Change Biology, 26: 3482–3497.

Boero, F., Brotz, L., Gibbons, M. J., Piranio, S., and Zampardi, S. 2016. Impacts and effects of ocean warming on jellyfish. In Explaining Ocean Warming: Causes, Scale, Effects and Consequences, Gland, Switzerland. https://portals.iucn.org/library/sites/library/files/documents/2016-046_0.pdf (last accessed 20 September 2020).

Bone, Q. 1998. The Biology of Pelagic Tunicates. Oxford University Press, Oxford. 340 pp.

Brodeur, R. D., Link, J. S., Smith, B. E., Ford, M. D., Kobayashi, D. R., and Jones, T. T. 2016. Ecological and economic consequences of ignoring jellyfish: a plea for increased monitoring of ecosystems. Fisheries, 41: 630–637.

Cannaby, H., and Hüsrevoğlu, Y. S. 2009. The influence of low-frequency variability and long-term trends in north Atlantic sea surface temperature on Irish waters. ICES Journal of Marine Science, 66: 1480–1489.

Conley, K. R., Lombard, F., and Sutherland, K. R. 2018. Mammoth grazers on the ocean's minuteness: a review of selective feeding using mucous meshes. Proceedings of the Royal Society B, 285: 20180056.

Conversi, A., Umani, S. F., Peluso, T., Molinero, J. C., Santojanni, A., and Edwards, M. 2010. The Mediterranean Sea regime shift at the end of the 1980s, and intriguing parallelisms with other European basins. PLoS One, 5: e10633.

Conway, D. V. P. 2012. Marine zooplankton of southern Britain. In Part 1: Radiolaria, Heliozoa, Foraminifera, Ciliophora, Cnidaria, Ctenophora, Platyhelminthes, Nemertea, Rotifera and Mollusca. Ed. by A.W.G. John. Occasional Publications. Marine Biological Association of the United Kingdom, Plymouth, UK. 138 pp.

Conway, D. V. P. 2015. Marine zooplankton of southern Britain. In Part 3: Ostracoda, Stomatopoda, Nebaliacea, Mysida, Amphipoda, Isopoda, Cumacea, Euphausiacea, Decapoda, Annelida, Tardigrada, Nematoda, Phoronida, Bryozoa, Entoprocta, Brachiopoda, Echinodermata, Chaetognatha, Hemichordata and Chordata. Ed. by A.W.G. John. Occasional Publications. Marine Biological Association of the United Kingdom, Plymouth, UK. 271 pp.

D'Ambrosio, M., Molinero, J. C., Azeiteiro, U. M., Pardal, M. A., Primo, A. L., Nyitrai, D., and Marques, S. C. 2016. Interannual abundance changes of gelatinous carnivore zooplankton unveil climate-driven hydrographic variations in the Iberian Peninsula, Portugal. Marine Environmental Research, 120: 103–110.

Delignetter-Muller, M., Dutang, C., Pouillot, R., Denis, J., and Siberchicot, A. 2019. fitdistrplus: help to fit of a parametric distribution to non-censored or censored data. R Package Version 1.1-1 https://cran.r-project.org/package=fitdistrplus (last accessed 20 August 2020).

Doyle, T. K., Hays, G. C., Harrod, C., and Houghton, J. D. R. 2014. Ecological and societal benefits of jellyfish. In Jellyfish Blooms, pp. 105–127. Ed. by K. A. Pitt and C. H. Lucas. © Springer Science+Business Media, Dordrecht.

Edwards, C. 1965. The hydroid and the medusa Neoturris pileata. Journal of the Marine Biological Association of the United Kingdom, 45: 443–468.

Edwards, M., and Richardson, A. J. 2004. Impact of climate change on marine pelagic phenology and trophic mismatch. Nature, 430: 881–884.

Eloire, D., Somerfield, P. J., Conway, D. V. P., Halsband-Lenk, C., Harris, R., and Bonnet, D. 2010. Temporal variability and community composition of zooplankton at station L4 in the Western Channel: 20 years of sampling. Journal of Plankton Research, 32: 657–679.

Ershova, E. A., Hopcroft, R. R., Kosobokova, K. N., Matsuno, K., Nelson, R. J., Yamaguchi, A., and Eisner, L. B. 2015. Long-term changes in summer zooplankton communities of the Western Chukchi Sea, 1945–2012. Oceanography, 28: 100–115.

Fernand, L., Nolan, G. D., Raine, R., Chambers, C. E., Dye, S. R., White, M., and Brown, J. 2006. The Irish coastal current: a seasonal jet-like circulation. Continental Shelf Research, 26: 1775–1793.

Fraser, J. H. 1955. The plankton of the waters approaching the British Isles in 1953. Marine Research, 1: 1–12.

Gibbons, M. J., and Richardson, A. J. 2009. Patterns of jellyfish abundance in the North Atlantic. Hydrobiologia, 616: 51–65.

Giering, S. L. C., Wells, S. R., Mayers, K. M. J., Schuster, H., Cornwell, L., Fileman, E. S., Atkinson, A. et al. 2019. Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: a stable isotope and biovolume spectrum approach. Progress in Oceanography, 177: 101943.

Guerrero, E., Gili, J. M., Grinyó, J., Raya, V., and Sabatés, A. 2018. Long-term changes in the planktonic cnidarian community in a mesoscale area of the NW Mediterranean. PLoS One, 13: e0196431.

Haberlin, D., Raine, R., McAllen, R., and Doyle, T. K. 2019. Distinct gelatinous zooplankton communities across a dynamic shelf sea. Limnology and Oceanography, 64: 1802–1817.

Hátún, H., Payne, M. R., Beaugrand, G., Reid, P. C., Sandø, A. B., Drange, H., Hansen, B. et al. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. Progress in Oceanography, 80: 149–162.

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

Hays, G. C., Doyle, T. K., and Houghton, J. D. R. 2018. A paradigm shift in the trophic importance of jellyfish? Trends in Ecology and Evolution, 33: 874–884.

Holland, L. Z. 2016. Tunicates. Current Biology, 26: R146–R152.

Hosia, A., Falkenhaug, T., Baxter, E. J., and Pagès, F. 2017. Abundance, distribution and diversity of gelatinous predators along the northern Mid-Atlantic Ridge: a comparison of different sampling methodologies. PLoS One, 12: e0187491–18.

ICES. 2019. Manual for mackerel and horse mackerel egg surveys, sampling at sea. Series of ICES Survey Protocols SISP 6. 82 pp. 10.17895/ices.pub.5140.

Katija, K., Sherlock, R. E., Sherman, A. D., and Robison, B. H. 2017. New technology reveals the role of giant larvaceans in oceanic carbon cycling. Science Advances, 3: e1602374.

Kelly, D., Richards, C., and Layton, C. 2020. oce: analysis of oceanographic data. R package version 1.2-0 https://cran.r-project.org/package=oce (last accessed 24 July 2020).

Lamb, P. D., Hunter, E., Pinnegar, J. K., van der Kooij, J., Creer, S., and Taylor, M. I. 2019. Cryptic diets of forage fish: jellyfish consumption observed in the Celtic Sea and western English Channel. Journal of Fish Biology, 94: 1026–1032.

Last, J. M. 1978. The food of four species of pleuronectiform larvae in the eastern English Channel and southern North Sea. Marine Biology, 45: 359–368.

Lauria, V., Attrill, M. J., Pinnegar, J. K., Brown, A., Edwards, M., and Votier, S. C. 2012. Influence of climate change and trophic coupling across four trophic levels in the Celtic Sea. PLoS One, 7: e47408.

Lavaniegos, B. E., and Ohman, M. D. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. Progress in Oceanography, 75: 42–69.

Lebrato, M., Pitt, K. A., Sweetman, A. K., Jones, D. O. B., Cartes, J. E., Oschlies, A., Condon, R. H., et al. 2012. Jelly-falls historic and recent observations: a review to drive future research directions. Hydrobiologia, 690: 227–245.

Licandro, P., Blackett, M., Fischer, A., Hosia, A., Kennedy, J., Kirby, R. R., Raab, K. et al. 2015. Biogeography of jellyfish in the North Atlantic, by traditional and genomic methods. Earth System Science Data, 7: 173–191.

Long, A. P., O'Donnell, C., Haberlin, D., Lawton, C., and Doyle, T. K. 2020. A novel platform for monitoring gelatinous mesozooplankton: the high-speed Gulf VII sampler quantifies gelatinous mesozooplankton similar to a ring net. Limnology and Oceanography: Methods, 18: 696–706.

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

Mayer, A. G. 1912. Ctenophores of the Atlantic coast of North America. Carnegie Institute Washington, Washington DC. 130 pp.

Mills, C. E. 1998. Phylum Ctenophora: list of all valid species names. Electronic internet document. http://faculty.washington.edu/cemills/Ctenolist.html (last accessed 12 June 2017).

Napp, J. M., Baier, C. T., Brodeur, R. D., Coyle, K. O., Shiga, N., and Mier, K. 2002. Interannual and decadal variability in zooplankton communities of the southeast Bering Sea shelf. Deep-Sea Research Part II: Topical Studies in Oceanography, 49: 5991–6008.

O'Donnell, C., O'Malley, M., Lynch, D., Mullins, E., Connaughton, P., Power, J., and Long, A. 2019. Western European Shelf Pelagic Acoustic Survey (WESPAS) 13 June – 24 July, 2019. FEAS Survey Series: 2019/03. Marine Institute. https://oar.marine.ie/handle/10793/1462 (last accessed 9 September 2020).

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L. et al. 2014. vegan: Community Ecology Package, R Package Version 2.2-0 https://cran.r-project.org/package=vegan (last accessed 20 July 2020).

Pagès, F., González, H. E., and González, S. R. 1996. Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by Aglantha digitale (Trachymedusae). Marine Ecology Progress Series, 139: 69–77.

Pauly, D., Graham, W., Libralato, S., Morissette, L., and Deng Palomares, M. L. 2009. Jellyfish in ecosystems, online databases, and ecosystem models. Hydrobiologia, 616: 67–85.

Pershing, A. J., Head, E. H. J., Greene, C. H., and Jossi, J. W. 2010. Pattern and scale of variability among Northwest Atlantic Shelf plankton communities. Journal of Plankton Research, 32: 1661–1674.

Pinnegar, J. K., Jennings, S., O'Brien, C. M., and Polunin, N. V. C. 2002. Long-term changes in the trophic level of the Celtic Sea fish community and fish market price distribution. Journal of Applied Ecology, 39: 377–390.

Pitois, S. G., and Fox, C. J. 2006. Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. ICES Journal of Marine Science, 63: 785–798.

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

Purcell, J. E. 1991. A review of cnidarians and ctenophores feeding on competitors in the plankton. Hydrobiologia, 216–217: 335–342.

Purcell, J. E., Hoover, R. A., and Schwarck, N. T. 2009. Interannual variation of strobilation by the scyphozoan Amelia labiata in relation to polyp density, temperature, salinity, and light conditions in situ. Marine Ecology Progress Series, 375: 139–149.

R Core Team 2016. R: A Language and Environment for Statistical Computing. R foundation for statistical computing, Vienna, Austria. https://www.R-project.org/ (last accessed 10 January 2020).

Ronowicz, M., Wlodarska-Kowalczuk, M., and Kuklinski, P. 2008. Factors influencing hydroids (Cnidaria: Hydrozoa) biodiversity and distribution in Arctic kelp forest. Journal of the Marine Biological Association of the United Kingdom, 88: 1567–1575.

Runge, J. A., Pepin, P., and Silvert, W. 1987. Feeding behaviour of the Atlantic mackerel Scomber scombrus on the hydromedusa Aglantha digitale. Marine Biology, 94: 329–333.

Russell, F. S. 1953. The Medusae of the British Isles I. Cambridge University Press, Cambridge.

Russell, F. S. 1970. The Medusae of the British Isles II. Cambridge University Press, Cambridge.

Sabatés, A., Pagès, F., Atienza, D., Fuentes, V., Purcell, J. E., and Gili, J. M. 2010. Planktonic cnidarian distribution and feeding of Pelagia noctiluca in the NW Mediterranean Sea. Hydrobiologia, 645: 153–165.

Schmidt, K., Birchill, A. J., Atkinson, A., Brewin, R. J. W., Clark, J. R., Hickman, A. E., and Johns, D. G. 2020. Increasing picocyanobacteria success in shelf waters contributes to long-term food web degradation. Global Change Biology, 26: 1–14.

Schuchert, P. 2010. The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 2. Revue Suisse de Zoologie, 117: 337–555.

Schuchert, P. 2019. The hydroid of the medusa Lizzia blondina Forbes, 1848. Marine Biodiversity, 49: 1683–1693.

Southward, A. J., Hawkins, S. J., and Burrows, M. T. 1995. Seventy 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.

Totton, A. K. 1965. A Synopsis of the Siphonophora. Trustees of the British Museum (Natural History), London.

Williams, R. 1985. Vertical distribution of Calanus finmarchicus and C. helgolandicus in relation to the development of the seasonal thermocline in the Celtic Sea. Marine Biology, 86: 145–149.

Williams, R., and Conway, D. V. P. 1981. Vertical distribution and seasonal abundance of Aglantha digitale (O. F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean. Journal of Plankton Research, 3: 633–643.

Williams, R., Conway, D. V. P., and Hunt, H. G. 1994. The role of copepods in the planktonic ecosystems of mixed and stratified waters of the European shelf seas. Hydrobiologia, 292–293: 521–530.

Winslow, R., Read, J., Woolway, R., Brentrup, J., Leach, T., Zwart, J., Albers, S., *et al.* 2019. rLakeAnalyzer: lake physics tools. R Package Version 1.11.4.1 (last accessed 17 August 2020).

Zubiate, L., McDermott, F., Sweeney, C., and O'Malley, M. 2017. Spatial variability in winter NAO–wind speed relationships in western Europe linked to concomitant states of the East Atlantic and Scandinavian patterns. Quarterly Journal of the Royal Meteorological Society, 143: 552–562.

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