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# Distinct gelatinous zooplankton communities across a dynamic shelf sea

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## *Abstract*

Understanding how gelatinous zooplankton communities are structured by local hydrography and physical forcing has important implications for fisheries and higher trophic predators. Although a large body of research has described how fronts, hydrographic boundaries, and different water masses (e.g., mixed vs. stratified) influence phytoplankton and zooplankton communities, comparatively few studies have investigated their influence on gelatinous zooplankton communities. In July 2015, 49 plankton samples were collected from 50 m depth to the surface, across five transects in the Celtic Sea, of which, four crossed the Celtic Sea Front. Two distinct gelatinous communities were found in this dynamic shelf sea: a cold water community in the cooler mixed water that mainly contained neritic taxa and a warm water community in the warmer stratified water that contained a mixture of neritic and oceanic taxa. The gelatinous biomass was 40% greater in the warm water community ($\sim$ 2 mg C $m^{-3}$) compared with the cold water community ($\sim$ 1.3 mg C $m^{-3}$). The warm water community was dominated by *Aglantha digitale, Lizzia blondina*, and *Nanomia bijuga*, whereas the cold water community was dominated by *Clytia hemisphaerica* and ctenophores. Physonect siphonophores contributed > 36% to the gelatinous biomass in the warm water community, and their widespread distribution suggests they are ecologically more important than previously thought. A distinct oceanic influence was also recorded in the wider warm water zooplankton community, accounting for a $\sim$ 20 mg C $m^{-3}$ increase in biomass in that region.

Research into the ecology of gelatinous zooplankton has advanced considerably in recent years, creating a more nuanced understanding of a diverse and widespread group of animals that occupy different trophic guilds (Mackie et al. 1987; Haddock 2004; Robison 2004; Hays et al. 2018). Some of the recent work has been prompted by the negative interactions between "nuisance" species (e.g., *Pelagia noctiluca*) and human activities like fisheries, aquaculture, and tourism (CIESM 2001; Purcell et al. 2007; Doyle et al. 2008; Lucas et al. 2014), however, it has generally been restricted geographically. Studies covering larger geographic regions have relied heavily on fisheries bycatch data that can capture large scyphozoan species (Lynam et al. 2009; Uye and Brodeur 2017) but do not adequately capture smaller gelatinous taxa, e.g., hydrozoans and ctenophores. This has meant a lack of community analysis over broader scales in many neritic regions and a lack of data with which to connect those focused, but geographically disparate, studies. Many neritic shelf regions are physically dynamic with seasonally variable oceanographic processes, and support some of the richest ecosystems in the pelagic domain. Understanding how the gelatinous zooplankton community is structured by these processes is important in order to predict potential ecosystem changes and be able to sustainably exploit these ecosystems.

The majority of gelatinous zooplankton are predators with a broad zooplanktivorous diet (Purcell 1991; Purcell 1997; Arai 2012), with the exception of the tunicates that consume autotrophs and microplankton (Anderson 1998; Holland 2016). They can exert substantial top-down pressure on prey species, and on occasion, intense blooms of particular species can cause a trophic cascade, transforming an entire ecosystem into a less desirable state, at least from a human perspective (Greve 1994; Kideys and Romanova 2001; Kideys 2002). Just as important is the role of gelatinous zooplankton as competitors, whereby their rapid growth potentially allows them to outcompete planktivorous fish species (Brodeur et al. 2008; Ruzicka et al. 2016). It is also increasingly apparent that gelatinous zooplankton are consumed by a substantial number of marine predators (Hays et al. 2018), including a large number of important commercial fish species (Arai 1988; Purcell and

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Arai 2001; Lamb et al. 2017). There are also substantial trophic interactions between gelatinous taxa, i.e., within the "jelly web" (Robison 2004), which can reduce the vertical flow of biomass through pelagic foodwebs by retaining that biomass within mesotrophic levels for long periods. Furthermore, gelatinous zooplankton creates large quantities of mucus that potentially diverts biomass into the microbial and phytoplankton communities and away from higher trophic levels (Pitt et al. 2009; Condon et al. 2011; Pitt et al. 2013). Gelatinous zooplankton also connects the pelagic and benthic habitats, as dying populations/blooms deliver large quantities of biomass to benthic and demersal fauna (Lebrato et al. 2012; Ates 2017; Hays et al. 2018).

Although the aforementioned biological interactions will determine the structure of a gelatinous zooplankton community to a large degree, at the individual organism scale (Folt and Burns 1999; Kiørboe 2008), it is clear that physical processes beyond the scale of a single zooplankter are equally important. This is perhaps most clearly demonstrated by the dramatic change in community structure and composition that can occur between adjacent water masses (Pagès and Gili 1992; Pages et al. 1996; Graham et al. 2001; Guerrero et al. 2016). The community transition can be abrupt and is usually coherent with the physical discontinuity or "front" that partitions the water masses (Le Fèvre 1987; Graham et al. 2001; Acha et al. 2015). Scyphozoan species are clearly partitioned by seasonal fronts between distinct water masses in northwest Europe (Doyle et al. 2007), and the majority of work on gelatinous zooplankton would suggest that most fronts are barriers with negligible community exchange (Pagès and Gili 1992; Pages et al. 1996; Graham et al. 2001; Guerrero et al. 2016). However, there are some studies that demonstrate no barrier effect but rather a gradual change in the zooplankton community structure (Schultes et al. 2013; Luo et al. 2014) and, in fact, Acha et al. (2015) suggested that most fronts are "leaky boundaries." Some work suggests that the enhanced primary productivity at fronts (Le Fèvre 1987; McGillicuddy 2016) can directly enhance gelatinous biomass through bottom-up effects (Mianzan and Guerrero 2000; Luo et al. 2014); however, it is not clear how these studies distinguish between potential bottom-up effects and physical aggregative processes. Much of the literature seems to suggest that it is the hydrographic conditions within the distinct water masses rather than frontal dynamics that influence the gelatinous community (Hutchings et al. 1986; Pages et al. 1996; Luo et al. 2014; Guerrero et al. 2016). Considering that distinct water masses and fronts exist on every continental shelf region (Hill et al. 2008; Belkin et al. 2009; Raine 2014; Acha et al. 2015), there remains a strong imperitive to understand their influence over gelatinous zooplankton.

With this in mind, this study aimed to investigate the gelatinous zooplankton community across a dynamic continental shelf region with variable hydrography. The variation in gelatinous community structure and the standing biomass is examined in relation to the physical environment and within the context of the greater zooplankton community.

## Materials and methods

### Study site

The study site was located in the Celtic Sea, off the southeast coast of Ireland. This region is situated on the broad northwest European continental shelf and has a strong oceanic influence, experiencing profound seasonal changes. The depth ranges from $\sim$ 40 to 110 m, with the deepest region lying approximately southwest of St. George's Channel, which marks the geographic boundary between the Celtic and Irish Seas (Fig. 1A). In the spring/summer, a combination of tidal and density driven processes produce a dynamic front between the Celtic Sea and the Irish Sea, which is referred to as the Celtic Sea Front (CSF) (Pingree and Griffiths 1978; Le Fèvre 1987). The front is a serpentine feature, with a large meander that can pull Irish Sea water into the Celtic Sea (Fig. 1B), and its position does shift interannually in response to climatic variation and also intra-annually in response to spring tides and weather (Le Fèvre 1987; Brown et al. 2003). Most of the Celtic Sea becomes thermally stratified in spring and summer because of solar heating (Cooper 1967; Brown et al. 2003; Raine 2014), with a residual cold saline dome of water remaining beneath the warming less saline water above. This dome of water is situated in the Celtic Deep (Fig. 1), and the density gradient across these two water masses creates an anticlockwise baroclinic flow (Brown et al. 2003; Fernand et al. 2006; Hill et al. 2008). Powerful tidal forces overcome stratification in the shallower coastal areas, creating a tidal front between the stratified and tidally mixed water masses. Indeed, both the CSF and the similar thermohaline Ushant Front, that separates the Western English Channel and the Celtic Sea, drive a peripheral current around the entire Celtic Sea, advecting Atlantic water and plankton around the Celtic Sea (Brown et al. 2003; Fernand et al. 2006; Hill et al. 2008; Raine 2014).

The research cruise was undertaken aboard the R.V. *Prince Madog*, between the 13 and 17 July 2015, at which time the CSF front had become well-established (Fig. 1B). Zooplankton sampling was carried out along five transects within the study area, with Transect 1 (T1) being a predominantly coastal transect 50 km long, T2 being the longest transect running 150 km south east from Ireland. Transect 3 (T3) began near the Welsh coast moving directly east over the Celtic Deep and ending on the central axis of St. George's Channel. From this point, Transect 4 (T4) proceeded north into the Irish Sea, ending approximately 6 km north of the CSF. From this point, Transect 5 (T5) started, proceeding southwest through the Irish Sea and crossing back into the Celtic Sea.

### Zooplankton analysis

In total, 49 zooplankton samples were collected, every 6 km, using a 1-m diameter, 270 $\mu$m mesh plankton net with a flowmeter. At each station, the plankton net was towed vertically from

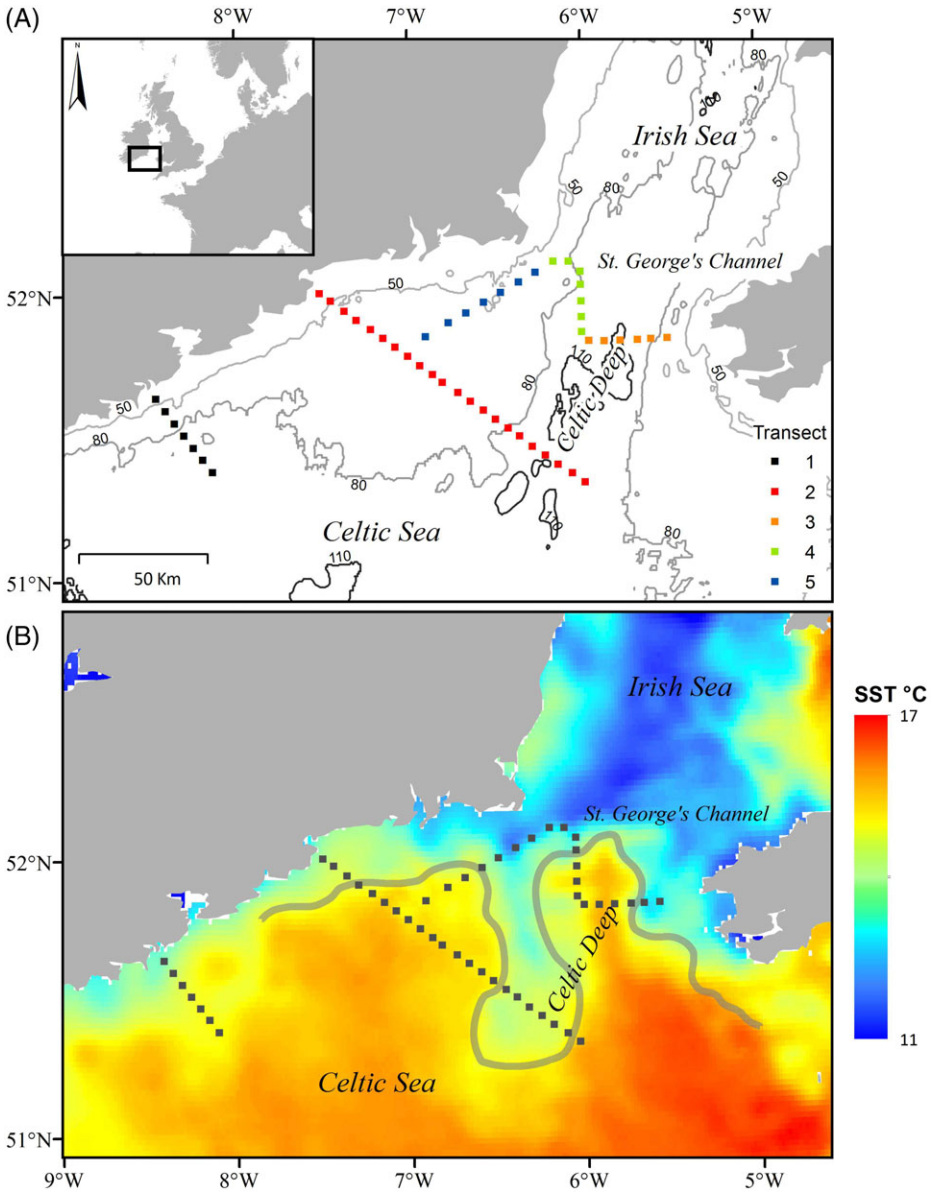



**Fig. 1.** (**A**) Study site in the north eastern Celtic Sea with the five transects and topographic features, and (**B**) mean SST in mid-July (8th–16th) 2015 with the CSF marked by the gray line.

50 m depth to the surface at a velocity of $\sim$ 1 m $s^{-1}$. Two teams sampled continuously, day ($N$ = 38) and night ($N$ = 11), with breaks in the regime while steaming between some transects. The short period between sunset and sunrise at this time of year, at this latitude, resulted in the majority of stations falling within daylight hours. The cod end was emptied into a small glass tank in order to count ctenophores, particularly *Bolinopsis infundibulum* O. F. Müller 1776 that does not preserve well. Upon completing the ctenophore count, the sample was immediately fixed in 4% formalin and filtered (50 $\mu$m) seawater solution. Samples were analyzed in the lab using a dark-field stereomicroscope, quantifying the dominant taxa and identifying all gelatinous zooplankton and fish to the lowest taxonomic level. All copepods were grouped as a single taxon. Quantitative data were determined from subsamples using a Folsom splitter, and the entire samples were analyzed for larger taxa (individuals > 2 cm), for example, the larger hydromedusae like *Leuckartiara octona* Fleming 1823. Biomass data and biometric conversions for dry weight (DW) and carbon content (C) were sourced from existing literature (Supporting Information Table S1). Where possible, biometric equations for the specific species were used and applied to the mean sizes found. Where this was not possible, relationships for closely related or morphologically similar species were used: equations for *Clytia hemisphaerica* Linnaeus 1767 were used to determine *Laodicea undulata* Forbes and Goodsir 1853 biomass. For *Agalma elegans* Sars 1846 ($N$ = 11) and *Nanomia bijuga* Delle Chiaje 1844 ($N$ = 1), samples collected by hand (snorkeling) during the summer 2015/2016 were used to

get the biovolume per colony and then converted in the same way as the above. Despite the availability of only a single *N. bijuga* specimen, it nonetheless represented a better estimate of individual biomass than using a similar species, which would have essentially meant using *A. elegans*, resulting in an overestimate of *N. bijuga* biomass. A comparison of the hand and net collected colonies is difficult considering the fragmented colonies that are recovered from the nets. However, the hand collected colonies were captured at approximately the same time of year in the Celtic Sea and were of a size that was consistent with previous years (Baxter et al. 2012: Haberlin et al. 2016) and consistent with what is considered a mean size in the taxonomic literature (Totton 1965; Kirkpatrick and Pugh 1984). On this basis, the biomass of the hand-collected colonies were adjudged to represent a reasonable estimate of the physonect species over the study area.

**Temperature and salinity analysis**

A conductivity-temperature-depth (CTD; Seabird, SBE 911) profile was taken at each station ($N = 98$) every 3 km, profiling from the surface to approximately 10 m above the seabed. The parameters recorded were density (kg $m^{-3}$), salinity (PSU), temperature (°C), and chlorophyll *a* fluorescence ($\mu$g $L^{-1}$; hereafter referred to as Chl *a*). Each profile was analyzed using the "Oce" package (Kelley and Richards 2017) for oceanographic data analysis implemented in R (R Core Team 2017). Each profile was trimmed, retaining only the downcast, and interpolated to 1 m intervals. The processed profiles were then analyzed to extract the depth of maximum cline intensity according to the methods used by Reygondeau and Beaugrand (2010). This method defines the depth of the cline as the depth of the maximum gradient over a 5 m rolling mean values. The calculated depths were checked against the raw CTD profiles and there was good agreement between the calculated cline and the raw profile. Data for the top and bottom 5 m of each CTD cast were averaged and used as the top/bottom parameter for subsequent analysis. This had little impact on bottom values but would smooth out any diel variation at the surface. The vertical change for each parameter was calculated, which was effectively the difference between the maximum and the minimum value of each parameter, with the exception of Chl *a* values that did not change linearly with depth. Finally, a measure of water column stability, the Brunt–Väisälä frequency or buoyancy frequency, was calculated for each cast.

**Statistical analysis**

The gelatinous zooplankton abundance (individuals $m^{-3}$), DW (mg $m^{-3}$), and carbon content (mg C $m^{-3}$) were compiled into station by species matrices. The matrices were double square root transformed to down weight the dominant taxa and then transformed again into (nonparametric) Bray–Curtiss dissimilarity matrices (Clarke and Warwick 2001). Rare species were retained in the analysis, as the calculation of the Bray–Curtiss coefficients reduces the contribution of these rare species to the final dissimilarity matrix (Clarke and Warwick 2001). Moreover, this makes no assumptions about the importance of species where there is large variability between stations, as there was here, and allows the nonmetric multidimensional scaled ordination (NMDS) algorithm to find a final ordination without imposing arbitrary rules (Poos and Jackson 2012). From these matrices, NMDS and cluster analysis were used to identify distinct communities. The three different NMDS ordinations (abundance, dry mass, and carbon biomass) were compared using Procrustes analysis, which rotates 1 ordination to achieve maximum similarity with a second ordination, by minimizing the sum of squared differences. The ENVFIT (Oksanen et al. 2017) and BIO-ENV (Clarke and Ainsworth 1993) functions were used to investigate which environmental parameters were most influential. ENVFIT fits environmental parameters onto a community ordination, and BIO-ENV finds the best subset of environmental parameters, so that the Euclidean distances of scaled environmental parameters have the maximum (rank) correlation with community dissimilarities. Analysis of Similarities (ANOSIM) (Clarke 1993) was used to determine whether the clusters were significantly different. Permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) implemented using the ADONIS function was used to determine which environmental variables were most significant in explaining the clusters. The SIMPER function (Clarke 1993) was used to investigate which taxa contributed to the between cluster differences. All community and multivariate analysis was carried out using the "Vegan" package (Oksanen et al. 2017) in R. Differences between taxa and individual species, with respect to clustering, were tested using Mann Whitney or Kruskal Wallis tests, as the residuals for almost all the data was non-normally distributed. Potential relationships between individual environmental variables and individual taxa were investigated using Pearson's correlation. All mean values are presented with standard deviation unless stated otherwise.

**CSF detection**

The CSF front was defined using remotely sensed satellite sea surface temperature (SST) data and the open source package, Marine Geospatial Ecology Tools (Roberts et al. 2010). This software was used to implement a single-image edge detection algorithm (Cayula and Cornillon 1992), which can detect the SST fronts in raster images. The raster image was an 8-d mean SST raster, for the period 08–15 July, created from ODYSSEA North West Shelf Sea Surface Temperature data and downloaded from the Copernicus data portal (www.copernicus.eu.org). This is processed gap-free data set on a $0.02° \times 0.02°$ resolution grid, created by the group for high-resolution SST using combined satellite and in situ observations. The detected edge was turned into a georeferenced object, which allowed the calculation of the distance between each station and the surface front. All analysis was carried out using ArcGIS.

## Results

### Oceanographic data

The CTD profiles clearly indicated the changing vertical structure of the water column, particularly along T2, T3, and T4, where parts of the Celtic Deep were sampled (Fig. 2; Supporting Information Figs. S1–S3). The water column over the Celtic Deep was intensely stratified with the strongest physical gradients recorded along T2 and T3 (Fig. 2). The shallow stations during T1 and T3 highlight the relatively narrow corridor (~ 10 km) of tidally mixed water, characteristic of coastal water in the region (Brown et al. 2003). T1 and T2 both start within ~ 4 km of the coastline, and T1 is mixed within 10–15 km of the coastline and weakly stratified thereafter. In contrast, T2 appears to retain a pycnocline approaching the near-coast stations. The cooler water that is present at the surface in the CSF meander (Fig. 1B) is also evident below the surface with a weakening of the pycnocline between 90 and 110 km along T2 (at 80 m contour) and thereafter the water column stratifies toward the eastern margin of the CSF meander (Fig. 2). The final 10 km of T4 and the first 30 km of T5 indicate a homogeneous vertical structure (Fig. 2) and cooler water (Supporting Information Fig. S1), which suggest that these stations are in water contiguous with the Irish Sea, despite being geographically in the Celtic Sea. Plots of temperature, salinity, and Chl *a* conform to the same general pattern (Supporting Information Figs. S1–S3). The highest Chl *a* values were recorded along T1 and T2 (Celtic Sea) at ~ 30 m depth (Supporting Information Fig. S3), and the depth of the subsurface chlorophyll maximum was positively correlated with the pycnocline ($r = 0.97$, $p < 0.001$). The highest surface Chl *a* was recorded at stations in T1, T3, T4, and T5 (east of the SST front), the lowest values were all recorded during T2 and remained low within the mixed water evident between the 90 and 110 km mark (Supporting Information Figs. S1, S3). Bottom density fronts were evident along Transects T2–T5, indicative of along front flows (Fig. 2).

### Gelatinous zooplankton community

In total, 21 gelatinous taxa were identified from the 49 samples, including 17 hydromedusae, 3 ctenophores, and 1 scyphozoan species. Several hydrozoans were relatively common across the survey area, with *Aglantha digitale, C. hemisphaerica*, *A. elegans*, *N. bijuga*, *Lizzia blondina,* and *L. octona* all recorded at > 60% of stations (Fig. 3). *A. digitale* and *L. blondina* were, by an order of magnitude, the dominant hydromedusae throughout the survey area reaching a mean of 200 ± 247 and 88 ± 159 $m^{-3}$, respectively, and present at 80% and 75% of stations, respectively. Of the ctenophores, *Pleurobrachia pileus* was the most widespread, present at 94% of stations, with a mean abundance of 0.25 ± 0.23 $m^{-3}$.

Analysis of the gelatinous zooplankton using hierarchical clustering and NMDS ordination indicated that there were two distinct and significantly different communities (ANOSIM, $r = 0.72$, $p < 0.001$) across the survey area (Fig. 4). The first community included stations in the warmer stratified water of the Celtic Sea lying to the west of the CSF meander. The second community included all the stations in the cooler mixed water within the meander and contiguous with the Irish Sea and the stations over the warm stratified Celtic Deep region (Fig. 4A). Hereafter, for simplicity, these will be referred to as the warm water gelatinous and cold water gelatinous communities, respectively.

SIMPER analysis of the abundance matrix (individuals $m^{-3}$) showed that dissimilarity between the communities was dominated by *A. digitale* (65%) and *L. blondina* (31%), which together accounted for 96%, with no other species accounting for greater than 1% of the dissimilarity. The same analysis of the biomass matrix (mg C $m^{-3}$) indicated that the dissimilarity between the communities was dominated by *A. digitale* (24%), *N. bijuga* (23%), *B. infundibulum* (16%), *L. blondina* (8%), and *C. hemisphaerica* (5%) (Table 1) and all were indicated as significant ($p < 0.05$) except for *B. infundibulum* (Table 1). Six species made a negligible contribution to community dissimilarities, most likely because they were rare and only present in one community, e.g., *Hydractinia borealis* and *Euphysa aurata* were both present at only two stations, respectively. Both the abundance and carbon biomass NDMS ordinations were highly correlated ($r = 0.85$, $p < 0.001$), and although there was some rotation of points, only two stations switched between communities. One station was in the center of the Celtic Deep, and the second was very close to the CSF. Therefore, the remaining analysis was carried out using the community biomass, with the geographic communities as indicated in Fig. 3.

### Gelatinous zooplankton biomass

Total gelatinous biomass was significantly higher in the warm water gelatinous community (2.08 ± 1.72 mg C $m^{-3}$) compared with the cold water community (1.33 ± 1.19 mg C $m^{-3}$; Table 1). Of the 21 gelatinous zooplankton species recorded, only 6 had a greater biomass in the cold water gelatinous community (Table 1), of which 4 (*Muggiaea atlantica*, *P. pileus, C. hemisphaerica,* and *Mitrocomella polydiademata*) were significantly greater. Gelatinous zooplankton biomass as a percentage of the total zooplankton biomass ranged from 0.005% to 16.8%; the mean percentage in the warm water gelatinous community (6% ± 4%) was higher than the mean percentage in the cold water gelatinous community (4% ± 4.3%; Mann Whitney, $U = 407$, $p = 0.047$). The contribution of individual species to the gelatinous biomass at each station varied substantially (Fig. 3). The mean contribution of *A. digitale* in the warm water gelatinous community was 33% ± 23% (max 96%) and then declined to 1.1% ± 4.9% (max 24%) in the cold water gelatinous community. Siphonophore biomass was substantial in both the warm water and cold water gelatinous communities (Fig. 3), with a mean contribution of 36.4% ± 20% (max 78%) and 26.8% ± 21% (max of 63%), respectively, nonetheless, some stations in both communities had no siphonophores present. The siphonophore biomass was dominated by *N. bijuga* with a mean contribution of 30.1% ± 19.7% (max 73%) and 9.5% ± 16.3% (max 58%) in

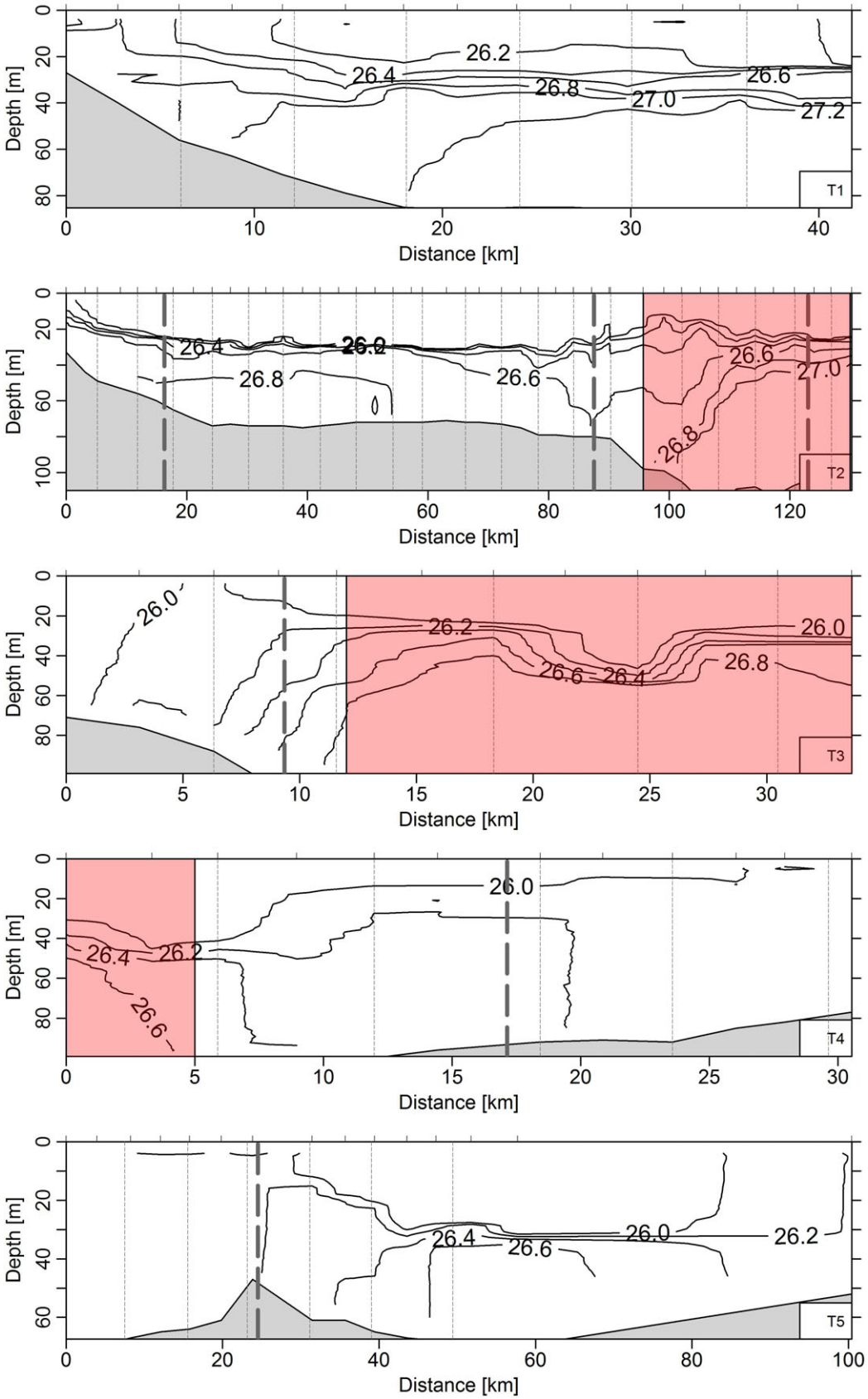



**Fig. 2.** Legend on next page.

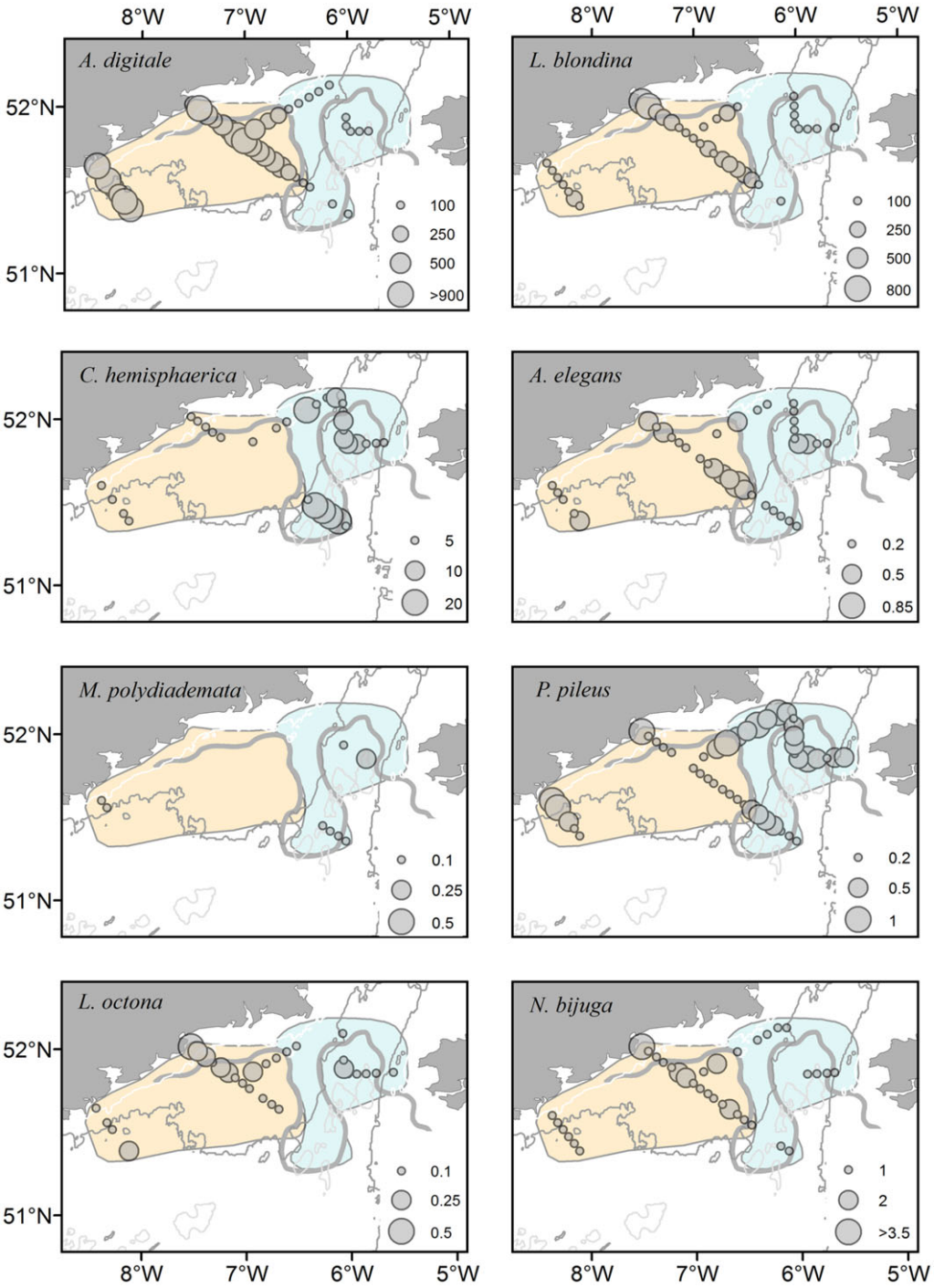



**Fig. 3.** Abundance (individuals $m^{-3}$) and distribution of the dominant gelatinous species across the study area, which contributed to the two distinct gelatinous communities; a warm water gelatinous community (orange) and a cold water gelatinous community (blue). Note, the scale for each species is difference, and the shaded polygons are simply a visual aid to identify the extent of the two gelatinous communities.

**Fig. 2.** Density (kg $m^{-3}$) contour for the five transects, T1–T5. CTD stations (ca. every 3 km) are marked along the top *x* axis, and zooplankton sample stations (ca. every 6 km) are indicated by vertical dotted lines. Distance on the *x* axis is calculated from the first station of each transect. The heavy dashed line represents the position of the CSF, taken from Fig. 1B. Note, plots are scaled differently. The red shading marks the Celtic deep boundary.

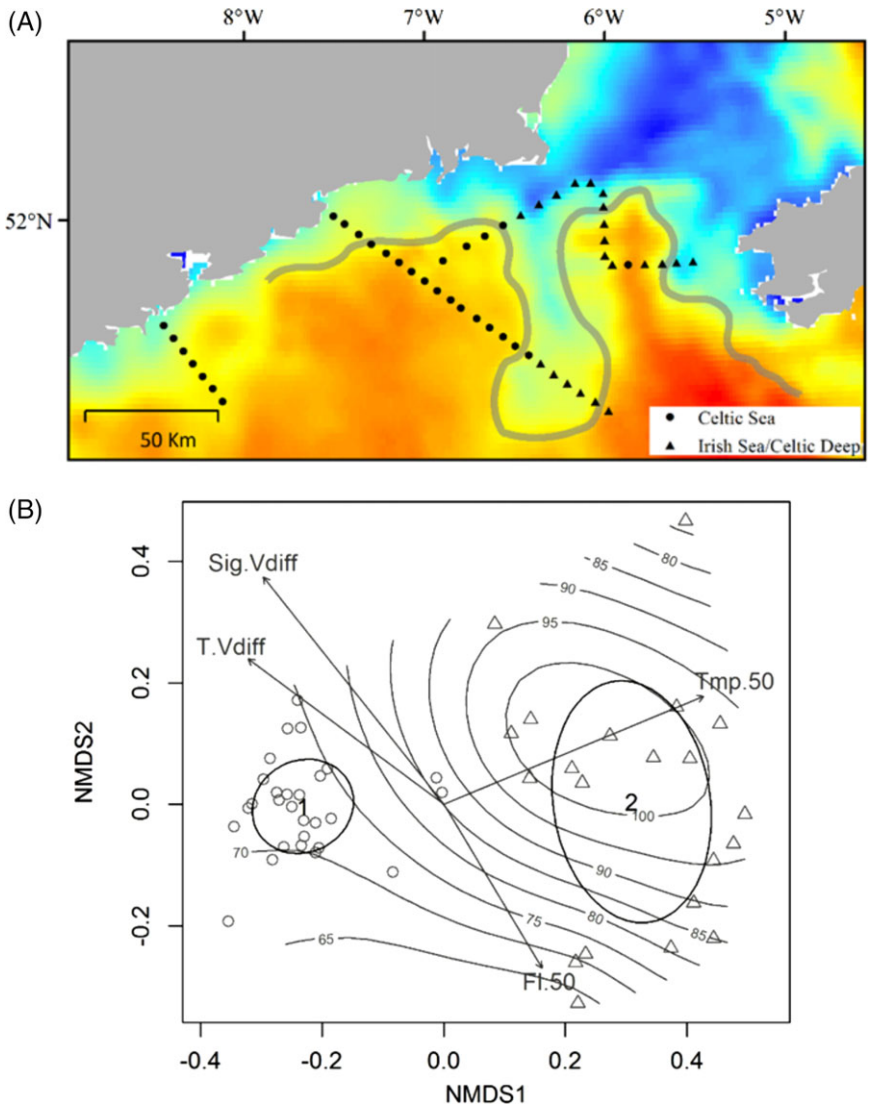



**Fig. 4.** (**A**) Map of the survey stations coded by the hierarchical clustering, and (**B**) the NDMS ordination (stress = 0.1) of the gelatinous zooplankton abundance (individuals $m^{-3}$) matrix, with stations symbolized according to hierarchical clustering; ○, warm water gelatinous community; Δ, cold water gelatinous community. Influential environmental parameters are indicated by fitted contours for bathymetry and vectors; T.Vdiff, vertical temperature difference; Sig.Vdiff, vertical density difference; Tmp.50, bottom temperature at 50 m; and Fl.50, Chl *a* at 50 m depth.

the warm water and cold water gelatinous communities, respectively. The contribution of *A. elegans* did not change significantly across the survey region (Fig. 3), reaching a maximum of 42%; however, the mean contribution was generally low at 5.9% ± 8.8%.

The ENVFIT function indicated that thermocline intensity ($r^2$ = 0.35, $p$ = 0.001), bathymetry ($r^2$ = 0.33, $p$ = 0.001), bottom salinity ($r^2$ = 0.18, $p$ = 0.013), bottom density ($r^2$ = 0.24, $p$ = 0.003), bottom temperature ($r^2$ = 0.24, $p$ = 0.004), and pycnocline intensity ($r^2$ = 0.24, $p$ = 0.002) were significantly correlated with the gelatinous biomass ordination. There was a significant, though weak, correlation between the ordination and distance to the front ($r^2$ = 0.14, $p$ = 0.027); however, none of the environmental parameters measured at the surface, i.e., temperature, salinity, and Chl *a*, has a strong or significant correlation with the biomass ordination. The BIOENV analysis indicated that the best correlation between the environmental parameters and the community matrix was achieved with only depth and the temperature at 50 m depth (Mantel, $r$ = 0.53, $p$ < 0.001). However, retaining fluorescence at 50 m, the vertical temperature difference and the vertical density difference made little difference to the $r$ value and would suggest that these are also influential (Fig. 4B).

To investigate whether there was any evidence of enhanced biomass of gelatinous zooplankton at the front, the biomass was modeled against distance to the front while excluding T1 stations that were ∼ 40 km from the SST front. There was a significant positive relationship between biomass and distance

**Table 1.** Mean biomass ± standard deviation (mg C $m^{-3}$) of the gelatinous species that drove the dissimilarity between the warm water and cold water gelatinous communities according to the SIMPER analysis, ordered from most to least influential, and including a Mann Whitney test statistic.

| Species | Warm water | Cold water | Mann Whitney test |
|---|---|---|---|
| *A. digitale* | 0.59 ± 0.36 | 0.012 ± 0.052 | $U$=589, $p < 0.001$ |
| *N. bijuga* | 0.77 ± 1.27 | 0.11 ± 0.23 | $U$=516, $p < 0.001$ |
| *B. infundibulum* | 0.15 ± 0.56 | 0.57 ± 0.96 | $U$=241, $p > 0.1$ |
| *L. blondina* | 0.24 ± 0.30 | 0.02 ± 0.05 | $U$=533, $p < 0.001$ |
| *P. pileus* | 0.14 ± 0.17 | 0.23 ± 0.15 | $U$=159, $p < 0.005$ |
| *Beroe* sp. | 0.06 ± 0.14 | 0.15 ± 0.32 | $U$=241, $p > 0.1$ |
| *C. hemisphaerica* | 0.017 ± 0.005 | 0.12 ± 0.11 | $U$=25, $p < 0.001$ |
| *A. elegans* | 0.12 ± 0.15 | 0.05 ± 0.07 | $U$=391, $p > 0.05$ |
| *Obelia* sp. | 0.004 ± 0.008 | 0.001 ± 0.004 | $U$=356, $p > 0.2$ |
| *M. polydiademata* | 0.0001 ± 0.0004 | 0.002 ± 0.006 | $U$=227, $p < 0.05$ |
| *L. octona* | 0.0005 ± 0.0007 | 0.0005 ± 0.0002 | $U$=398, $p > 0.05$ |
| *L. undulata* | 0.0004 ± 0.0007 | 0.0001 ± 0.0002 | $U$=304, $p > 0.8$ |
| *Euglena gracilis* | 0.0001 ± 0.0003 | 0.00005 ± 0.00014 | $U$=317, $p > 0.58$ |
| *M. atlantica* | 0.0002 ± 1.0 | 0.10 ± 0.19 | $U$=96, $p < 0.001$ |
| Total biomass | 2.085 ± 1.718 | 1.328 ± 1.189 | $U$=411, $p < 0.005$ |

($r^2 = 0.16$, $p = 0.007$; Fig. 5A); however, a separate analysis of each community indicated a negligible trend in the warm water community, whereas there was an increasing trend in the cold water community ($r^2 = 0.38$, $p = 0.002$; Fig. 5A). Investigation of the raw data suggested that the large bodied ctenophores had a disproportionate impact at some stations and removing the ctenophores resulted in similar linear trends across both communities (Fig. 5B), with the linear relationship in the cold water gelatinous community becoming insignificant ($r^2 = 0.12$, $p = 0.11$).

**Total zooplankton community**

In an effort to investigate spatial overlap and possible associations between the gelatinous zooplankton and the wider zooplankton community, the 49 samples collected were analyzed further to identify and enumerate the wider zooplankton community. Furthermore, 53 taxa were identified, with only the larval fish identified to species level, and merged with the gelatinous data set. The zooplankton community was dominated by copepods, Limacinidae molluscs, decapod larvae, appendicularians, and polychaete larvae from the families Poecilochaetidae, Magelonidae, Polynoidae, and Sabellariidae (Fig. 6). Decapod larvae including both megalopal and zoeal stages were most abundant in northernmost cold mixed water, in contrast, oceanic species like *Tomopteris* sp., *Clione* sp. molluscs, and *Sagitta elegans*, though widespread, were more abundant in the warm stratified water lying to the west of the CSF meander (Fig. 6). Twenty-five species of fish larvae were identified in total. *Arnoglossus laterna, Callionymus* sp., *Sardina pilchardus, Scomber scombrus*, and *Gobidae* were the most numerous, recorded at ~ 30% of stations. Gobidae larvae were the most widespread, recorded at 63% of stations. The highest abundance of fish larvae was found within the shallow (< 80 m) warm stratified water along T2, and they were largely absent from the deeper stations (Fig. 6). Phytoplankton (*Ceratium* spp.) was abundant at stations near the southern coastline, reaching > 83,000 cells $m^{-3}$ during T1. Its occurrence appeared to be largely restricted to colder mixed water, and it was absent from deeper stratified water. The presence of *Ceratium* spp. was considered noteworthy; however, it was not included in any subsequent analysis.

Hierarchical clustering and NMDS analysis of total zooplankton matrix (individuals $m^{-3}$) identified three distinct and significantly different communities (ANOSIM, $r = 0.86$, $p < 0.001$; Figs. 6, 7). The first community included the same stations that were previously identified as the warm water gelatinous community (Fig. 4). The second community included most of the stations previously identified as the cold water gelatinous community (Fig. 4), with the exception of six stations over the Celtic Deep that were identified as a third community. Hereafter, these will be referred to as the warm water zooplankton, the cold water zooplankton, and the deep water zooplankton communities, respectively (Fig. 6).

The NMDS ordination shows that cold water zooplankton and deep-water zooplankton stations were loosely clustered (Fig. 7B), nonetheless, analysis of similarities, excluding the warm water zooplankton stations indicated a significant difference between these two communities (ANOSIM, $r = 0.29$, $p < 0.01$). Interestingly, analysis of the zooplankton biomass (mg C $m^{-3}$) produced a slightly different clustering. The warm water zooplankton community remained unchanged (Fig. 7); however, the six southern-most stations in the CSF meander were all placed with the deep-water zooplankton community. A procrustes comparison of the abundance and biomass ordinations

demonstrated a positive and significant correlation ($r = 0.96$, $p < 0.001$), suggesting that the minor rotation of these stations was enough to switch between communities. Therefore, as before, the remaining analysis was carried out using the community biomass, with the communities as indicated in Fig. 6.

**Total zooplankton biomass**

Analysis of dissimilarities between the communities (SIMPER) showed that the change in community structure was dominated by copepods, decapod larvae, *Clione* sp., *Tomopteris*, and *S. elegans*. The dissimilarity between the warm water zooplankton and cold water zooplankton communities was dominated by copepods (68%), *Clione* sp. (8%), decapod larvae (8%), and *Tomopteris* (5%); however, only decapod larvae, *A. digitale* (0.02%), and *Limacina* sp. (< 0.001%) were indicated as significant ($p < 0.001$). The dissimilarity between warm water zooplankton and deep-water zooplankton communities was also dominated by copepods (72%), *Clione* sp. (7%), *Tomopteris* (5%), and decapod larvae (5%). Of those taxa, *Clione* sp. and *Tomopteris* were significant ($p < 0.001$), as were *S. elegans, B. infundibulum, A. digitale, Beroe* sp., *M. atlantica, C. hemisphaerica,* polychaete larvae, and *Limacina* sp. (Figs. 3 and 6). The dissimilarity between the cold water zooplankton and deep-water zooplankton communities was dominated by copepods (82%) and decapod larvae (10%), of which, only decapod larvae were significant (Fig. 6). In addition, *M. atlantica, C. hemisphaerica,* polychaete larvae, ichthyoplankton, *Sagitta setosa,* and *Lepeophtheirus* sp. were significant. The mean biomass in the warm water zooplankton community (~ 64 mg C $m^{-3}$) was greater than the mean biomass in the deep-water zooplankton community (~ 45 mg C $m^{-3}$) and the cold water zooplankton community (~ 41 mg C $m^{-3}$), but the differences were not significant (Table 2). This increase in the warm water zooplankton community was largely attributable to *Limacina* sp., *Clione* sp., *S. elegans*, and *Tomopteris* sp., which were far less prevalent in the cold water zooplankton and deep-water zooplankton communities.

The ENVFIT function indicated that all of the environmental parameters had a significant relationship with the NMDS ordination ($p < 0.05$), except for halocline depth, halocline intensity, surface Chl *a*, max Chl *a*, and the vertical change in Chl *a*. Many of these parameters were collinear and had a clear relationship with bathymetry. The BIOENV analysis indicated that the best correlation between the environmental parameters and the community matrix was achieved with only bathymetry and the temperature at 50 m depth (Mantel, $r = 0.53$, $p < 0.001$). However, and as before, retaining the halocline depth, the surface salinity, and buoyancy made little impact on the *r* value and probably represent a more realistic combination of parameters (Fig. 7B).

To explore potential predator–prey associations between the gelatinous taxa and other zooplankton taxa, potential prey was regressed against the gelatinous biomass ordination using the ENVFIT analysis. *S. elegans* ($r^2 = 0.31$, $p = 0.001$), *Tomopteris* ($r^2 = 0.24$, $p = 0.002$), polychaete larvae ($r^2 = 0.19$, $p = 0.01$), and ichthyoplankton ($r^2 = 0.17$, $p = 0.015$) were all significant. However, no potential prey taxa were retained by the BIOENV function, the best correlation was achieved by retaining only bottom temperature and bathymetry as before (Mantel, $r = 0.53$, $p < 0.001$). Using the gelatinous matrix in a PERMANOVA analysis with community clustering as a factor suggested that both thermocline gradient ($r^2 = 0.04$, $p = 0.03$) and the distance to the CSF front ($r^2 = 0.03$, $p = 0.01$) have some small influence over the community; however, once again, the bathymetry ($r^2 = 0.15$, $p = 0.001$) and bottom temperature ($r^2 = 0.16$, $p = 0.002$) demonstrated the strongest relationship with the gelatinous community.

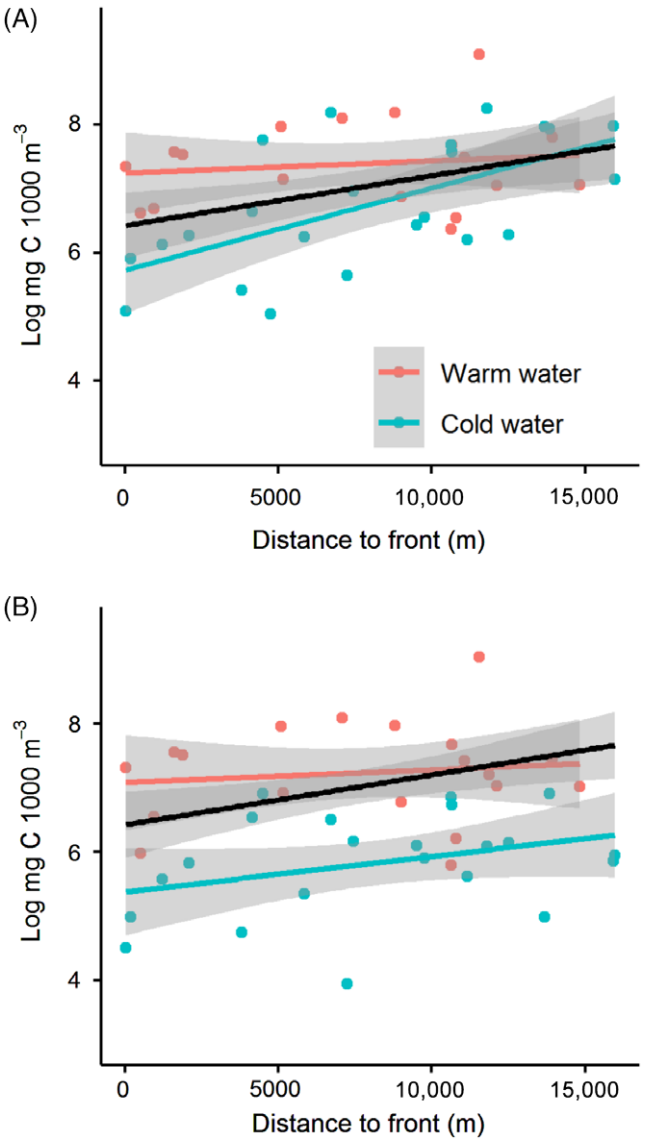



**Fig. 5.** Relationship between the distance to the CSF and (**A**) gelatinous zooplankton biomass (log mg C 1000 $m^{-3}$) and (**B**) gelatinous zooplankton biomass excluding ctenophores. The black line is the linear trend for all data points and the red and blue lines are the trends for the two distinct gelatinous communities.

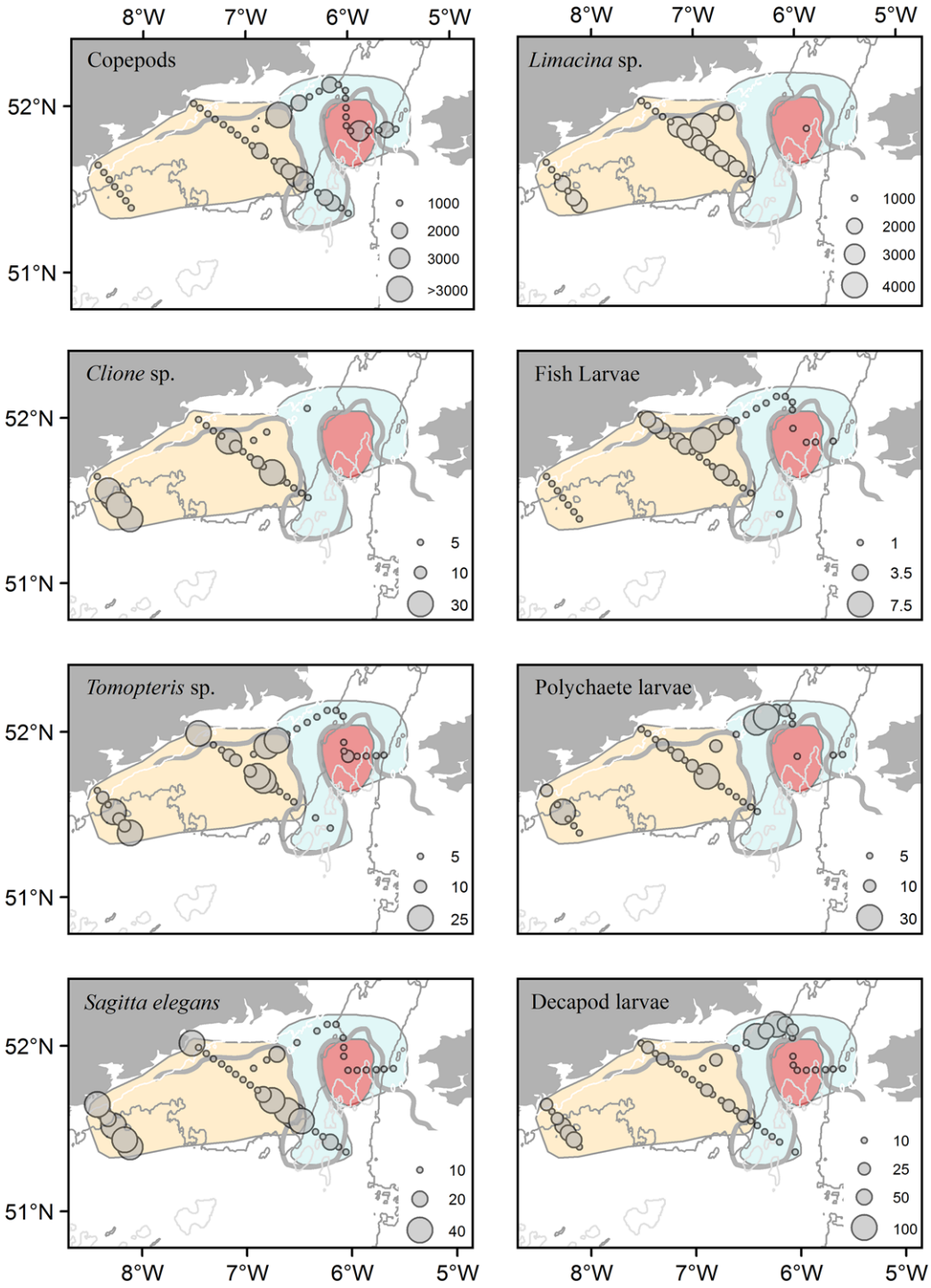



**Fig. 6.** Abundance (individuals $m^{-3}$) and distribution of the dominant nongelatinous taxa across the study area. Analysis of the gelatinous and nongelatinous taxa combined indicated three distinct zooplankton communities; a warm water zooplankton community (orange), a cold water zooplankton community (blue), and a deep-water zooplankton community (red). Note, the scale for each species is different and displayed in the legend. The shaded polygons are simply a visual aid to identify the extent of the distinct zooplankton communities.

## *Discussion*

The results of this study suggest that there are two distinct gelatinous zooplankton communities within the study area: (1) a warm stratified water community within the Celtic Sea, west of the CSF, and (2) a cooler mixed water community contiguous with the Irish Sea. These two communities were

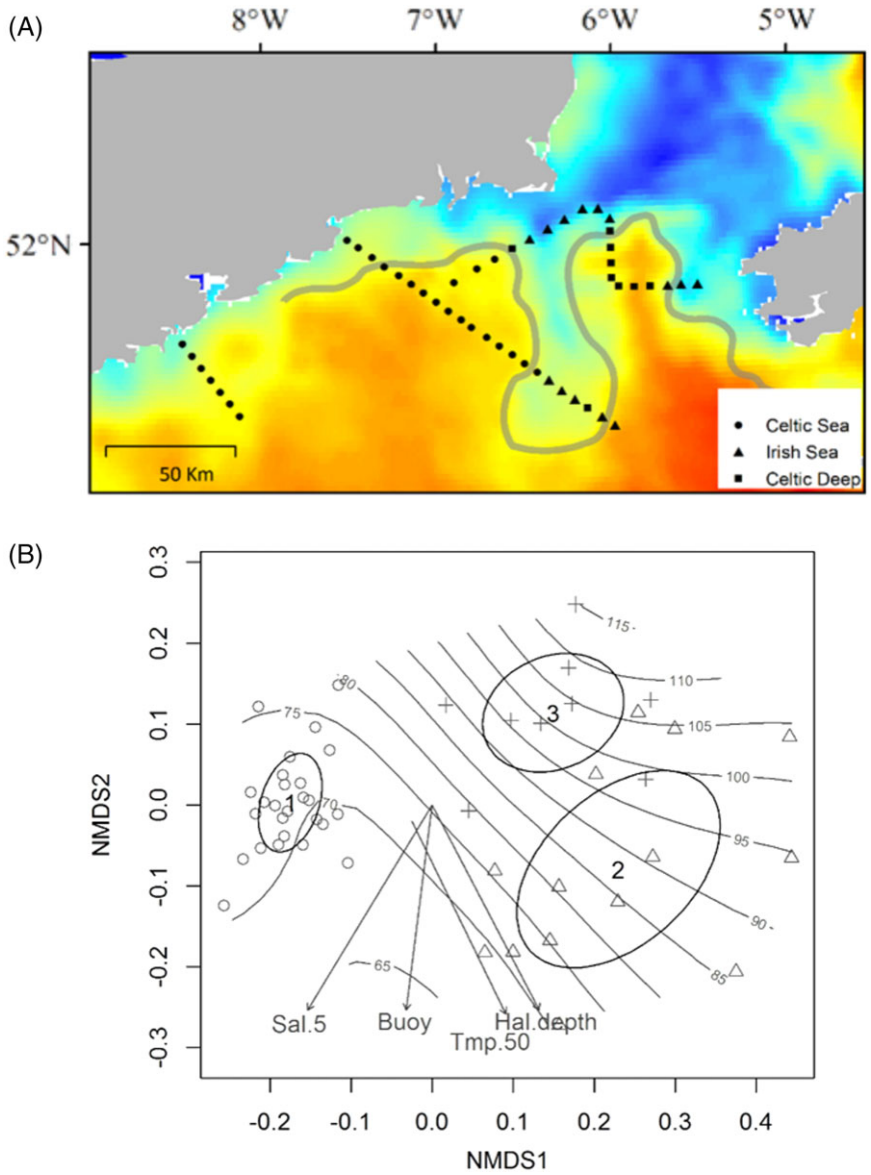



**Fig. 7.** (**A**) Map of survey stations coded by the hierarchical clustering, i.e., as in the NMDS plot. (**B**) NDMS ordination (stress = 0.13) of zooplankton abundance (individual $m^{-3}$), with stations symbolized according to hierarchical clustering; ○, warm water zooplankton community; Δ, cold water zooplankton community; and +, deep-water zooplankton community. Influential environmental parameters are indicated by fitted contours for bathymetry and vectors; Hal.depth, halocline depth; Tmp.50, bottom temperature at 50 m; Sal.5, surface salinity at 5 m.

broadly partitioned by the seasonal CSF, except over the Celtic Deep region where there was evidence of mixing. The warm water gelatinous community was dominated by holoplanktonic species such as *A. digitale* and *A. elegans*, whereas the cold water gelatinous community was dominated by the meroplanktonic *C. hemisphaerica* but also had higher numbers of ctenophores (*B. infundibulum* and *P. pileus*). Perhaps of greater importance than the differences in species composition was the significant differences in gelatinous biomass between the two distinct communities. The warm water gelatinous community typically had ~ 40% greater gelatinous biomass than the cold water gelatinous community (2.08 compared with 1.33 mg C $m^{-3}$, respectively), and also the decreased variation across the warm stratified water indicated a more consistent gelatinous biomass. The broader relevance of these findings is that the warm water gelatinous community contained a greater abundance of gelatinous zooplankton predators and this has important ecological implications. Indeed, studies using new technologies are indicating that many more taxa are routinely consuming gelatinous zooplankton, including commercially important fish species such as herring and whiting that are abundant in the Celtic Sea (Lamb et al. 2017; Hays et al. 2018). The corollary of a higher abundance of gelatinous zooplankton in the warm water gelatinous community is a potentially greater

**Table 2.** Mean carbon biomass ± standard deviation (mg C $m^{-3}$) of the taxa that drove the dissimilarity among the warm water, cold water, and deep-water zooplankton communities according to SIMPER analysis, and the results of individual Kruskal Wallis tests for these influential taxa.

| Taxa | Warm water | Deep water | Cold water | Chi$^2$ statistic |
|---|---|---|---|---|
| Copepoda | 44.76 ± 47.20 | 39.51 ± 51.62 | 40.91 ± 26.53 | $\chi^2$=1.123, $p > 0.5$ |
| Decapoda | 1.66 ± 1.30 | 0.05 ± 0.08 | 2.47 ± 4.34 | $\chi^2$=12.78, $p < 0.005$ |
| *Limacina* sp. | 10.11 ± 7.20 | 0.10 ± 0.19 | 0.03 ± 0.04 | $\chi^2$=36.41, $p < 0.001$ |
| *Clione* sp. | 2.49 ± 3.31 | 0 ± 0 | 0.01 ± 0.02 | $\chi^2$=31.78, $p < 0.001$ |
| *Tomopteris* sp. | 2.17 ± 1.87 | 0.51 ± 0.75 | 0.22 ± 0.31 | $\chi^2$=18.62, $p < 0.001$ |
| Larval fish | 0.07 ± 0.08 | 0.001 ± 0.002 | 0.02 ± 0.03 | $\chi^2$=21.65, $p < 0.001$ |
| Polychaete larvae | 0.12 ± 0.08 | 0.002 ± 0.003 | 0.045 ± 0.052 | $\chi^2$=24.49, $p < 0.001$ |
| *S. elegans* | 1.20 ± 0.93 | 0.14 ± 0.19 | 0.13 ± 0.23 | $\chi^2$=25.44, $p < 0.001$ |
| *Beroe* sp. | 0.06 ± 0.14 | 0.30 ± 0.45 | 0.09 ± 0.23 | $\chi^2$=3.25, $p > 0.1$ |
| *A. digitale* | 0.60 ± 0.35 | 0.004 ± 0.008 | 0.0002 ± 0.0003 | $\chi^2$=36.38, $p < 0.001$ |
| *C. hemisphaerica* | 0.0008 ± 0.0020 | 0.09 ± 0.06 | 0.13 ± 0.12 | $\chi^2$=32.27, $p < 0.001$ |
| *M. atlantica* | 0.002 ± 0.001 | 0.28 ± 0.28 | 0.03 ± 0.06 | $\chi^2$=31.15, $p < 0.001$ |
| *M. polydiademata* | 0.0001 ± 0.0004 | 0.005 ± 0.010 | 0.0006 ± 0.0010 | $\chi^2$=6.06, $p < 0.05$ |
| Total biomass | 64.85 ± 45.18 | 41.89 ± 52.75 | 45.16 ± 28.36 | $\chi^2$=3.84, $p > 0.1$ |

top-down effect on the zooplankton prey and increased competition with other zooplanktivorous species.

With top-down effects in mind, one of the most important findings of this study was that despite the substantial changes in gelatinous zooplankton communities, there was a largely unchanging copepod abundance/biomass across the study area (Fig. 6; Table 2). So rather than the gelatinous zooplankton exerting a top-down impact on the zooplankton, our findings suggest a weak link between the gelatinous predators and potential prey. For example, the numerically dominant *A. digitale* population in the warm water gelatinous community was largely composed of immature hydromedusae < 2.5 mm in height that are too small to prey on the copepods present (Williams and Conway 1981). Likewise, the *L. blondina* were minute in size (~ 1 mm diameter) and also possibly unable to consume the copepods present. A notable finding of the study was the substantial contribution of physonect siphonophores to the gelatinous biomass (Table 2), contributing > 36% in the warm water gelatinous community. An inshore survey in 2009 found *N. bijuga* at ~ 50% of stations along the south and southwest coasts, with *A. elegans* at a single station (Baxter et al. 2012), whereas here both species were found at > 60% of stations. Historically, surveys that identify and enumerate physonects in shelf regions are sparse and it is difficult to determine the importance of these observations against a poor baseline. The data here would indicate that these species are ecologically more important in the Celtic Sea than previously thought. Physonect siphonophores consume a variety of prey including chaetognaths, decapod larvae, copepods, and larval fish (Purcell 1981; Mills 1995; Purcell 1997), and their widespread abundance here might impact the larvae of important commercial species. In fact, the predation of physonect siphonophores is potentially greater than other hydrozoan taxa because of the large volume of water occupied by a "fishing" physonect with its siphosome and tentilla extended (Mackie et al. 1987).

In terms of biomass, copepods were by far the dominant taxa across the study area, and while their biomass did increase in the warm water zooplankton community, the mean total biomass increase of ~ 20 mg C $m^{-3}$ was largely driven by semigelatinous taxa, e.g., *Tomopteris* sp. and the pelagic molluscs, combined (Table 2). In contrast, the increase in gelatinous biomass from ~ 1.3 to ~ 2 mg C $m^{-3}$ in this context seems modest and might suggest that the hydrozoans and ctenophores are of minor ecological importance. However, both groups turn over large quantities of carbon and ammonia which can alter trophic structures in less direct ways (Biggs 1977; Pitt et al. 2013). They acquire excess carbon that is not needed because of an extremely low metabolic demand and the excess is shed as dissolved organic matter (DOM) and mucus (Pitt et al. 2013). The discarded nutrients become available to microbes and phytoplankton; therefore, a substantial proportion of the nutrients consumed by gelatinous taxa are shunted away from higher trophic levels (Biggs 1977; Condon et al. 2011). Increased nutrient levels in the presence of cnidarians, allied to predations on copepods, have been shown to enhance heterotrophic dinoflagellate abundance in mesocosm experiments (Pitt et al. 2007). Therefore, an increase in gelatinous zooplankton may favor harmful algal blooms that are known to originate in the Celtic Sea (Raine and McMahon 1998; O'Boyle and Raine 2007; Raine 2014). *Limacina* sp. alone contributed approximately half of the biomass increase (~ 10 mg C $m^{-3}$) in the warm water zooplankton community. Its feeding mechanism, which involves producing a mucus web, would also create substantial DOM, shunting biomass away from higher trophic levels (Condon et al. 2011), and creating larger rapidly sinking particles that increase biomass flow to the benthos (Noji et al. 1997).

As bathymetry, temperature, and salinity explained most of the variability in the BIOENV and PERMANOVA analysis, our results suggest that ultimately it is the underlying topography of the study area that is the primary driver of the two observed gelatinous communities. The residual cold water that remains in the Celtic Deep as the surface heats up during spring, allied with powerful tides over the shallow coastal regions create a dynamic front between two distinct water masses (Horsburgh et al. 1998; Brown et al. 2003; Hill et al. 2008) and their respective gelatinous communities. Previous work has indicated that large scyphozoan species are similarly restricted by seasonal hydrographic boundaries around Britain and Ireland (Hay et al. 1990; Doyle et al. 2007) and is consistent with the results of this study. These studies used methods suited only to sample the larger scyphozoans, such as trawl bycatch and visual survey methods, and were therefore unable to investigate the wider gelatinous assemblage. Where the wider gelatinous assemblage has been sampled, much of the literature reports fronts acting as a barrier between distinct gelatinous communities (Hutchings et al. 1986; Pagès and Gili 1992; Mianzan and Guerrero 2000; Graham et al. 2001; Guerrero et al. 2016). In regions where the front separates a warm offshore region from a tidally mixed or an upwelling inshore region, there seems to be greater gelatinous diversity and biomass in the offshore region (Pagès et al. 1992). This is consistent with the results here, where there was a slight increase in gelatinous biomass moving away from the front, and an obvious increase in diversity in the warm water gelatinous community. Gelatinous biomass does not always increase in the offshore regions, as demonstrated by the increased hydrozoan abundance on the shoreward side of the Catalan front (Guerrero et al. 2016). However, an increase in diversity with the oceanic influence is well-reported (Mackie et al. 1987; Pagès and Gili 1992; Mianzan and Guerrero 2000; Graham et al. 2001), and Pagès et al. (1992) suggested that the warm stable conditions in stratified water provided a favorable environment for gelatinous taxa.

The increase in diversity in the warm water gelatinous community was also evident in the warm water zooplankton community (Fig. 6) and indicated a substantial oceanic influence over that warm stratified region of the Celtic Sea. Indeed, this shift between a neritic and oceanic zooplankton assemblage is a consistent feature of the long-term monitoring in the Western English Channel (Russell 1953; Southward 1980). The prevalence of the pelagic molluscs *Clione* sp. and *Limacina* sp., the polychaete *Tomopteris*, the hydromedusa *A. digitale*, and chaetognath *S. elegans* in the Western English Channel are generally indicative of a western Atlantic influence (Russell 1935; Southward et al. 1995). In contrast, the prevalence of neritic taxa like *C. hemisphaerica, M. atlantica*, and *Sagitta setosa* are indicative of a south western Atlantic, "Lusitanian," influence (Russell 1935; Southward et al. 1995). The Western English Channel is also separated from the Celtic Sea by the seasonal front called the Ushant Front (Le Fèvre et al. 1983), and therefore, analogous zooplankton changes are very likely to occur near the CSF. Although Southward et al. (1995) did not invoke the formation or breaking up of the Ushant Front as an explanation of this pattern, our understanding of the fronts has advanced considerably since the mid-1990s (Hill et al. 2008). Therefore, it seems reasonable to suggest that the alternation between these communities is linked to the fronts in the Celtic Sea as they have a profound seasonal impact (Horsburgh et al. 1998; Hill et al. 2008; Raine 2014) and as both the Ushant Front and the CSF are a fundamental driver of circulation around the Celtic Sea (Hill et al. 2008).

It must be acknowledged that the inferences in this discussion regarding trophic associations are tentative. Identifying copepods to species level was beyond the scope of the current study, and this is potentially a problem for our interpretation. However, as the point above is based on the respective size of both predator and prey, simply identifying copepods to species is unlikely to alter the inference that there is poor alignment between gelatinous predators and their potential prey. Perhaps of greater concern is the integrated vertical sampling and the 270 $\mu$m mesh size. The coarse sampling could certainly obscure vertical associations between taxa, and the mesh size (270 $\mu$m) would probably have undersampled the small early copepod stages and crustacean nauplii. It is difficult to speculate on whether this "additional" biomass would alter the results of this study; however, these particular zooplankters were not conspicuous in samples and it is unlikely they would have substantially change the patterns reported here. Interesting questions arise as to how these biological and oceanographic fluctuations discussed here might impact the neritic community, and future studies should include stratified vertical sampling in order to address the shortcomings identified here. Novel methods using aerial surveys, ship surveys, and acoustic and video surveys have addressed many shortcomings in scyphozoan research (Uye and Brodeur 2017); however, of these, only video is applicable to small hydrozoans and ctenophores. Video profilers have been used to good effect elsewhere, providing good quantitative data and high spatial resolution that can reveal potential trophic associations (McClatchie et al. 2012; Luo et al. 2014).

## Conclusion

This study significantly advances our understanding of the gelatinous zooplankton community in the Celtic Sea, a large productive shelf sea that supports important fisheries (Pinnegar et al. 2002). Prior to this study, there has been few recent studies that specifically targeted the smaller gelatinous zooplankton fraction, such as siphonophores and hydromedusae, yet understanding their ecology may have important implications for fisheries and the wider ecosystem. Our results identified two distinct gelatinous communities that were partially separated by the CSF, which support previous work on other taxa, e.g., large scyphozoans (Doyle et al. 2007) and zooplankton (Williams et al. 1994; McGinty et al. 2014). This research suggests that the ultimate drivers of these two gelatinous communities is the interaction among the underlying

topography, tidal forcing, and surface heating that creates a dynamic front between two distinct water masses. Finally, this research has identified physonect siphonophores as a significant component of the gelatinous community in the warm stratified water of the Celtic Sea and merits further attention.

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## Conflict of Interest

None declared

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