Spatial mismatch between phytoplankton and zooplankton biomass at the Celtic Boundary Front

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Thermohaline fronts are present globally and have been identified as biodiversity hotspots, encouraging enhanced primary productivity and attracting dense aggregations of higher trophic level organisms. The Celtic Boundary Front (CBF) sits in an important zone of economic activity yet no contemporary studies describing the meso-zooplankton community exist for this region. High-frequency sampling during June 2009 revealed three distinct areas on the mixed (Irish Sea) and stratified (Celtic Sea; Celtic Deep) sides of the front, each exhibiting distinct physical and biological characteristics. Low zooplankton abundance was found above the Celtic Deep, despite apparent optimal phytoplankton conditions, conflicting with observations made at other frontal locations. Although zooplankton assemblages were generally distinct within areas, the copepod *Acartia clausii* was ubiquitous across all three areas and accounted for almost 60% of all counted individuals. The long-term variation of zooplankton during the seasonal front development was examined using samples from the Continuous Plankton Recorder. The results of this analysis suggest that low abundance is a recurring feature over the Celtic Deep. Possible explanations for the observed patterns may be top-down effects on zooplankton from pelagic fish; alternatively, these patterns may be a consequence of the strong density and stratification gradients in the Celtic Deep.

KEYWORDS: Celtic Sea; Irish Sea; thermohaline fronts; zooplankton; Continuous Plankton Recorder; mismatch

INTRODUCTION

Oceanographic fronts shape pelagic ecosystems and their importance is increasingly recognized for large marine predators (Belkin, 2009; Bost *et al*., 2009). Phytoplankton are entrained at the frontal convergence at distances ranging from < 1 to 20 km (Le Fevre, 1986; Franks, 1992; Simpson *et al*., 1977; Olsen *et al*., 1994). The enhanced productivity increases consumer abundance and attracts higher trophic
level organisms, creating biological hotspots in the pelagic ecosystem (Molinero et al., 2008; Munk et al., 2003). These areas are actively targeted by foragers such as seabirds and other predators that are often of major conservation concern (Queiroz et al., 2012; Sims and Quale, 1998; Vlietstra, 2005). Identifying these areas and understanding their persistence can lead to the establishment of marine protected areas and thereby help protect highly mobile species in good quality habitat with a minimal impact on marine industries (Game et al., 2009).

The Celtic Boundary Front (CBF) is located in St George’s Channel on the border of Britain and Ireland’s Exclusive Economic Zone. Much of our current understanding of the seasonal development and physical structure of the CBF is based on studies from the 1970s and 1980s (e.g. Hill and Simpson, 1989; Simpson and Hunter, 1974). This includes a seminal paper on thermohaline shelf fronts by Simpson and Hunter (Simpson and Hunter, 1974) which hypothesized that these fronts form through the interaction of tidally generated mixing and the heating by irradiation of surface waters. In the case of the CBF, a characteristic “S” shaped meander develops, which is thought to be due to the topographical constraints placed on the jet-like baroclinic flows in the area (Brown et al., 2003; Pingree et al., 1976). The front begins to develop in late April/early May, when the warming of the sea surface leads to thermal stratification on the Celtic Sea side, because the turbulent energy in this area is insufficient to maintain a fully mixed water column (Hill et al., 2008; Simpson, 1976). Beneath the thermocline, a dense pool of relatively saline cold water develops, which represents vestiges of the conditions from the previous winter (Hill et al., 2008; Horsburgh et al., 1998). On the Irish Sea side, in contrast, the water column remains vertically mixed year round, as tidally generated turbulent energy in this area remains high (Hill et al., 1997). Aside from this knowledge, little attention has been given to the CBF over the last 20 years and there are no contemporary studies describing the mesozooplankton community within the frontal boundary region. Because research at similar fronts (e.g. Ushant) has shown their conservation importance (Le Boyer et al., 2009; Le Fevre, 1986; Schultes et al., 2012), this is an obvious gap. For example, the area incorporating the Ushant front ultimately achieved marine protected area status (http://www.parc-marin-iroise.gouv.fr/).

Continuous underway logging data and the ready availability of remotely sensed data make frontal regions increasingly easy to identify and offer improved opportunities to understand their dynamics over time. Examples of this are investigations into the meso-scale dynamics of phytoplankton and zooplankton community structure along the Armorican and NW Iberian shelf in recent years (e.g. Albaina and Irigoien, 2007a; Gil et al., 2002; Fernandez de Puelles and Molinero, 2007). These have shown that it is possible to relate local hydrographic conditions to zooplankton species distributions using high-frequency sampling, i.e. distances between stations ranging between ~5 and 8 nmi (Albaina and Irigoien, 2007b; Gil et al., 2002). The Armorican front is a nearshore front which differs from the CBF because it is primarily driven by upwelling as the continental shelf narrows considerably in this area. It does, nevertheless, create a sharp environmental gradient along which distinct communities are formed over short distances (Albaina and Irigoien, 2007b).

The primary aim of this study was to characterize the zooplankton community structure on both sides of the CBF using a high-frequency sampling approach during June 2009. The linkages between zooplankton taxa and environmental variables were also investigated. The seasonal development of zooplankton communities at the CBF was further analysed using the wide spatio-temporal coverage of the Continuous Plankton Recorder (CPR). The results are discussed in the context of how important this area may be in terms of abundance produced and trophic linkages.

**METHOD**

**Study area**

The location of the CBF is at the southern margin of the Irish Sea (Fig. 1 and inset). The local bathymetry ranges between 70 and 110 m, with the deepest area corresponding to the Celtic Deep, which is a trough in the centre of St. George’s Channel. Samples were collected between the 14th and 19th June 2009 onboard the R.V. Celtic Voyager within a high-frequency Eulerian sampling grid of 44 stations, each separated by a distance of ~8 nmi. The CBF had already become established during the previous month, and was apparent from sea surface temperature (SST) data (see Supplementary data, Fig S1).

**Oceanographic data**

A sensor array (CTD; SBE 911) was used at each station to give a depth profile of the temperature, salinity, dissolved oxygen, fluorescence and density (expressed as sigma-t) at each station. The Potential Energy Anomaly (PEA; J m⁻³) was used as a measure of stratification intensity at each station and is defined as the energy required (per unit depth) to completely homogenize the water column. The equation for the PEA as defined by Simpson et al. (Simpson et al., 1977) is as follows:

\[
PEA = \frac{1}{D} \int_{-H}^{0} g \varepsilon (\bar{\rho} - \rho) dz
\]
where $g$ is the gravitational acceleration, $z$ is the vertical coordinate from $-H$ (deepest measurement) up to the sea surface $n$ and $p(z)$ is the density profile in a water column of depth $D$. Surface and bottom temperatures were calculated by averaging values from the upper and lower 10 m of the water column, respectively.

A VHRR (Advanced Very High Resolution Radiometer) is a satellite-derived radiometer which provided SST data onboard at 1 km spatial resolution; this, along with the in situ temperature measurements, was used to track any changes in the front boundary and allow equal sampling on either side of the CBF during the cruise. Satellite-derived estimates of chl-$\alpha$ were obtained from the Level 3 MODIS (Moderate Resolution Imaging Spectroradiometer) database. Eight-day composites were used to explore the timing of the spring bloom around the CBF during 2009 using the threshold method that classifies the onset of the spring bloom when the biomass reaches 5% above the median (Henson et al., 2009; Siegel et al., 2002).

**Zooplankton data**

Zooplankton samples from the sampling grid were collected by means of a WP-2 zooplankton net with a mesh size of 200 $\mu$m (UNESCO, 1968). Net casts were towed vertically at a constant velocity of 0.5 ms$^{-1}$ from 10 m above the sea floor to the surface. Filtration efficiency was maintained following the methods described by Hernroth (Hernroth, 1987), where a ratio of filtering area:mouth area was $\sim 6:1$, which is below the recognized ratio of 10:1 to prevent clogging in coastal eutrophic environments (Ohman, 2013). Net samples were preserved immediately in 4% buffered formalin solution for subsequent enumeration. The preserved zooplankton samples were examined in the laboratory under a stereo microscope and enumerated to either the level of genus or species for the major holoplanktonic groups. The meroplanktonic forms were usually identified to family level or more general categories. *Calanus* spp. were separated by development stages, where ‘juveniles’ refers to the combined abundance of all *Calanus* spp. in the copepodite stages I–IV, while species were separated for stages V–VI. For each sample, a suitable number of subsamples were taken (i.e. until at least 300 individuals had been encountered) and the counts were scaled based on the volume of water sampled ($m^3$). Counts were also examined as areal abundance ($m^{-2}$) to check for trends caused by differences in total volume of water sampled across stations (due to varying bathymetric depth).

Net haul data (June, 2009) were stored in a matrix of species ($n$) and stations ($s$). The number of individuals for each species was log transformed $\log_{10}(x+1)$ to down-weight the higher values, which have a greater impact on the similarity between stations. The data were clustered by Ward’s linkage method using a Bray–Curtis similarity metric on the most dominant species abundances (i.e. those that contribute $\geq 1\%$ of the total across all stations—rarer taxa were omitted in order to reduce the double zero effect). A SIMPROF (Clarke et al., 2008) test
was used to determine whether there were any significant clusters present within the cluster dendogram ($\alpha = 0.05$). The difference in abundance between clusters was determined for the most abundant taxa using a single factor ANOVA followed by a Bonferroni pair-wise test when the model was significant ($P < 0.05$). Ratios of integrated fluorescence versus zooplankton abundance were calculated for each station across the CBE.

The amount of variance in the plankton community abundance that could be explained by the environmental variables (PEA, surface and bottom temperature and integrated values of salinity, dissolved oxygen and fluorescence) were examined using redundancy analysis (RDA). RDA is a constrained ordination procedure combining multiple regression and principal component analysis. A PERMANOVA on the RDA output tested whether the variance explained by the principal axes was significant (Oksanen, 2011).

### Seasonal variability between areas

The CPR is a long-term plankton data set which has been regularly sampling the near surface plankton ($\sim 10$ m) in the N Atlantic with relatively unchanged methods since 1958 for both zooplankton and phytoplankton taxa, including the Phytoplankton Colour Index (PCI) (Richardson et al., 2006). A number of CPR routes exist within the study area, which are sampled regularly during the year. The range of samples available over time (1960–2009) in the CBF for each month varied between 75 in January and 135 in August. The distribution of the CPR data throughout the study area is shown in Fig. 1.

The delineation of the CBF area boundaries used for extracting CPR data (Fig. 2a) was determined initially by visually examining the biological (total abundance m$^{-3}$ across the net sampling grid) and environmental characteristics, i.e. PEA and position of the CBF. The position of these boundaries was confirmed by clustering the stations of the net sampling grid based on their similarity in community composition (see above and Fig. 2b). Studies comparing the CPR data with net haul samples collected within the same vicinity have shown that while the CPR underestimates the total number of individuals in an area (Dippner and Krause, 2012) compared with net haul samples (Clark et al., 2001); the monthly and multi-annual patterns nevertheless correlate strongly (Kane, 2009; McGinty et al., 2012). To confirm this, we compared the rank abundance of taxa collected through WP-2 and CPR sampling in the CBF areas to check whether the relative abundance of zooplankton taxa during Summer 2009 were consistent with the mean abundance for the CBF during June between 1960 and 2009. The PCI was also extracted for each of these areas.

The PCI is an estimate of the quantity and density of phytoplankton in the water column and is assigned one of four rank order categories (0, 1, 2, 6.5) based on standard colour charts (Colebrook and Robinson, 1964). The PCI has been shown to represent chl-a biomass based on direct PCI-satellite matchups (Raitos et al., 2005).

The seasonal variability across the boundary region focused on the average seasonal variability of the most dominant members of the zooplankton communities. Species that comprised the greatest proportion of the total net haul sample (i.e. within the Eulerian sampling grid) were extracted from the CPR database for a seasonal analysis of the three CBF areas (1960–2009). Average monthly species abundance values log$_{10}(x+1)$ were determined within each area and were plotted. Kendall rank correlations were used to compare the rank abundance of species collected during the June 2009 cruise and with the average rank abundance of the same species collected by the CPR in June between 1960 and 2009. A non-metric multi-dimensional scaling (nMDS) analysis was used to explore the relationships in species abundance from different areas and months. The relatedness between months-areas was based on Bray–Curtis similarities of the zooplankton abundance data and viewed on a 2D plane. All analysis was performed using bespoke packages (e.g. — vegan) within the R programming environment.

### RESULTS

#### Vertical profiles of the water column: June 2009

High-resolution (1 km) satellite imagery of SSTs for the CBF between 14th and 21st June shows the mean position of the boundary front layer (See Supplementary data, Fig S1). The ‘S’ shaped meander (approximately at the 13°C isopleth) of the frontal boundary is readily apparent with a small western protrusion of water from the Irish Sea in the Celtic Sea and a larger, more stable tongue of Celtic Sea water extending northwards over the Celtic Deep (Fig. 1a).

The average vertical profiles of temperature, salinity, fluorescence and dissolved oxygen were taken from three areas within the sampling grid (Fig. 3). The profiles show a mixed water column within the Irish Sea with $<1^\circ$C difference between surface and bottom waters. The homogenized water column was reflected by the absence of a subsurface chlorophyll maximum (SCM), as demonstrated by the fluctuations in fluorescence throughout the water column. The Celtic Sea had intermediate levels of stratification with the appearance of a near surface thermocline ranging in depth of between 10 and 20 m. There was also a weakly developed SCM formed at

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Stations above the Celtic Deep displayed the greatest change between surface and bottom temperatures with a change of at least 5°C. The thermocline within this area was deeper than elsewhere in the sample grid (~20–40 m) with a more pronounced SCM than was found elsewhere in the Celtic Sea.

The PEA summarized the relatively high stratification intensity at stations above the Celtic Deep with a PEA of between 93 and 132 J m⁻³. In contrast, the PEA at stations within the Irish Sea was only one-tenth of that intensity (<10 J m⁻³), or less than half that intensity in the Celtic Sea (Fig. 4).

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**Fig. 2.** (a) The location of three areas on the sampling grid determined by visual inspection of zooplankton abundance patterns and environmental characteristics of the ocean during a June 2009 cruise. Symbols relate to clustered ‘areas’ defined using a cluster dendogram (Fig 2b). The stippled areas labelled CD, CS and IS are the broader areas from which CPR samples were extracted. Also shown is the frequency of CPR samples within the CBF (black dots). (b) The cluster dendogram of the 44 stations sampled in June 2009. Clustering was based on the zooplankton taxa contributing at least 1% of the total biomass. A SIMPROF analysis (α = 0.05) which characterized nine unique station clusters were broadly congruent with the three areas defined around the CBF: Irish Sea (circle), Celtic Sea (square) and Celtic Deep (triangle).
Chlorophyll-a and ocean colour

The 8-day composite of surface chl-a derived from MODIS (14th–19th June 2009) revealed that peak levels of chl-a at the CBF occurred at the boundary interface and within the Celtic Deep area (see Supplementary data, Fig. S1). The onset of the spring bloom differed between the CBF areas: the earliest blooms occurred at the coast but also above the Celtic Deep, where values ranged between Julian Day 55 and 101. In contrast, the onset of the spring bloom in the Celtic and Irish seas occurred ≏1 month later, varying between Julian Day 97 and 123 days (see Supplementary data, Fig. S1). Seasonal patterns of the PCI showed that peak values of ‘greenness’ occurred in the CS and CD areas during May, while in the IS, this occurred a month later (Fig. 5a). The patterns did not appear to differ significantly between the areas during these months; however, the PCI remained high in the CD area and was significantly higher there than in other areas during August. Ratios of in situ fluorescence:zooplankton abundance showed that maximum disparities between fluorescence and zooplankton occurred at certain stations within the CD cluster (Fig. 5b). These ratios within the CS cluster remained consistently <10 and ratios did not exceed 25 in the IS cluster; however, almost half of the stations belonging to the CD cluster had ratios greater than 25 with a maximum of 74 at station 32 in the CD.

Zooplankton community structure: June 2009

A comparison between the volumetric (m$^{-3}$) and areal (m$^{-2}$) abundance at each station revealed that the abundance patterns were not dependent on using values in m$^{-3}$ or m$^{-2}$. A regression analysis between both measures yielded a high $R^2$ (0.97) value. Therefore, we proceeded with using the abundance m$^{-3}$ to aid comparison with the literature. Zooplankton abundances varied across the sampling grid, displaying a spatial coherence corresponding to different areas of the CBF (Fig. 4). The highest abundance was found in the Celtic Sea in the SW corner of the grid where the mean abundance of all taxa was found to be 2631 m$^{-3}$. In contrast, the stations found across the Celtic Deep showed particularly low zooplankton abundances with a mean value of 260 m$^{-3}$ which were more similar to the mean abundance for the Irish Sea stations (675 m$^{-3}$).

Forty-eight taxa were found within the stations sampled using net hauls, with the first 36 of these making up 99% of the total count (see Supplementary data, Table ST1). Copepods tended to dominate the samples and these contributed almost 75% towards the total number of individuals sampled. The copepod Acartia clausii (AC) was particularly abundant and constituted over 60% of the individuals sampled. Many of the other high-abundance categories belonged to small copepod taxa (<2 mm in length). These included Centropages hamatus (CHA), Pseudocalanus elongatus (PE), Temora longicornis (TL) and the small copepod category (SM) (i.e. copepodite stages of Pseudocalanus, Paracalanus and Ctenocalanus and unidentified copepods <1.5 mm). Other members of the zooplankton community which were found in considerable numbers included the cladoceran Evadne spp. (EV) and members of the Appendicularia (AP).

Patterns in both the PEA and zooplankton abundance were spatially coherent and the frontal area could be defined by three congruent areas. These were the Irish Sea (IS; filled circle), a group of stations with intermediate zooplankton abundance within the tidally mixed area north of the CBF, the Celtic Sea (CS; filled square), group
of stations found in the stratified waters of the Celtic Sea with high levels of zooplankton biomass and a third group of stations above the Celtic Deep (CD; filled triangle) where zooplankton abundance was low, but the area was nevertheless strongly stratified (Fig. 2a).

The results of the SIMPROF analysis on the cluster dendrogram which examined species similarities across stations revealed nine distinct clusters. These were broadly consistent with the three areas defined by the environmental and biological characteristics (Fig. 2b). Unlike the other two areas, which were rather homogeneous, the stations in the CD grouping were more heterogeneous, with seven significant subgroups ranging from one to five stations in size (Fig. 2b). Nevertheless, much like the patterns in zooplankton biomass, the clustering of the stations was spatially coherent and clusters were separated approximately by the $13^\circ C$ isopleth (i.e. the mean position of the CBF).

AC was numerically dominant in all three areas accounting for $\sim 65\%$ of all individuals in the CS and as much as $85\%$ of individuals in the IS. Non-copepod members of the mero- and holoplankton community were found in the CS in relatively high numbers; including the cladoceran EV, the AP and echinoderm larvae (EC). This area also had the highest abundance of zooplankton. For example, the total number of individuals counted in the CS was almost six times greater than in the CD area and three times greater than the IS (see Supplementary data, Table ST1). The IS area was largely dominated by small copepod species with coastal or neritic associations such as T. longicornis and C. hamatus. The CD area appeared to be the most distinct of the three areas, as shown by the dendogram grouping pattern, and also in the zooplankton communities present there. Abundance levels for many of the taxa within the CD area were generally much lower than the other areas. A comparison of abundance across areas using an ANOVA showed that 14/17 taxa differed significantly in abundance between them (see Supplementary data, Table ST11; results cited are for the first 17 of the most abundant species). There were strong discontinuities across areas in the abundance of individual taxa found in the net hauls, particularly among the most numerically abundant taxa (see Supplementary data, Fig. S2). With the exception of P. elongatus and Calanus juveniles (CJ), differences in abundance between the two stratified areas of the CBF (CS and CD) were quite evident, with CD being significantly lower in the majority of cases (13/17).

Fig. 4. Potential energy anomalies (PEA, $J m^{-3}$) interpolated across the CBF with the total zooplankton abundance (individuals $m^{-3}$) counted at each station also shown. See online supplementary data for a colour version of this figure.
whereas copepod species, were associated with the CS cluster, spp., together with a number of numerically abundant associated with the CD clusters (Fig. 6a and b).

Variation (RDA1 with both axes explaining over 90% of the constrained axes were found to be significant at the 0.001 level). The ratio of integrated fluorescence: zooplankton biomass at each of the 44 stations from left to right within the sampling grid. Stations are coloured based on the location within the grid; Celtic Sea (black column), Celtic Deep (grey column); Irish Sea (white column).

Zooplankton relationship with environmental variables: June 2009

In June 2009, combinations of environmental variables explained 36% of the variation in the community data and the grouping of the stations agreed with the clustering defined by the zooplankton data (Fig. 6a). The three most important environmental variables in explaining the variability of the community data between station groupings were SST (14%), DO2 (21%) and the PEA (13%).

Ordinations of several species with respect to the areas tended to agree with the findings of the hierarchical clustering of stations. The copepod species T. longicornis and C. hamatus were associated with the IS cluster/area (Fig. 6a and b). The cladoceran groups Evadne and Podon spp., together with a number of numerically abundant copepod species, were associated with the CS cluster, whereas Metridia lucens (ML) was the only species associated with the CD clusters (Fig. 6a and b).

Seasonal variability between areas: CPR

Of the 48 taxa counted within the June 2009 sampling grid, 12 of the most abundant taxa were also counted within the CPR data set; together, these 12 taxa made up almost 96% of the total abundance found within the sampling grid (Table 1). CPR samples covering the years 1960–2009 were divided into those which fell into the IS, CS and CD areas as defined by the clustering of stations for June 2009 (Fig. 2a). A total of 1434 samples were collected within the three areas, with 530 samples (mean month$^{-1}$ = 44) collected in the IS, 331 samples (mean month$^{-1}$ = 28) were collected in the CS and 569 samples (mean month$^{-1}$ = 48) were collected in the CD area. Comparisons were made between the rank abundance of the taxa collected during the June 2009 cruise using WP-2 nets and the mean rank abundance of the taxa for the month of June between 1960 and 2009 (CPR). There were large differences between the two methods for some species, most notably for the EC and TL. However, the Acartia spp. and small copepod groups consistently appeared in the top 3 for both methods in all areas. Also the congeneric species CHa and C. typicus were typically found in the bottom 4 for both methods in all areas. High Kendall rank correlations in the abundance between the CPR and WP-2 methods were found for each area with the weakest correlation ($r = 0.80$) occurring in the CS and the highest ($r = 0.88$) occurring in the CD. In contrast, the rank correlations between areas for the same methods were consistently lower and varied between (0.51 > r < 0.71).

The seasonal trends in average monthly abundance for each of the 12 taxa (1960–2009) are shown in Fig. 7. Taxa such as C. helgolandicus and P elongatus showed early peaks in abundance during April/May, while other taxa such as Acartia spp. and C. typicus displayed a late August/September peak in abundance. Abundances were significantly higher in the CS area compared with both the CD and IS during several months between April and September for 9/12 of the taxa. Peak abundances were found in the CS area for between 3 and 7 months, depending on the taxon. Two taxa (C. hamatus and T. longicornis) showed abundances to be greatest in the IS area during August, albeit with a large standard error. ML displayed highest abundance in winter and was low in late summer, in contrast to the trends in other taxa. Overall, the CPR data showed higher abundance in the CD relative to IS than did the net hauls (Fig. 7). However, this analysis confirmed that species abundance at the CD was still consistently lower than the CS for most taxa on a recurring annual basis.

The nMDS plot revealed distinct patterns in the spatial/seasonal variation of zooplankton data from the
CPR (Fig. 8). The ordination for the months between November and March showed a close similarity between areas (i.e. January samples clustered for the three areas etc.). From April, the monthly samples began to differentiate into the individual areas with the IS separating initially from the other areas, which is likely due to the onset of stratification on the Celtic Sea side, followed by a split in the Celtic Sea areas in the following month (Fig. 8).

**DISCUSSION**

Particular focus was placed in the present study on identifying any differences in the zooplankton communities between areas either side of the CBF as this forms in late spring and dissipates in late autumn. In June 2009, the results of the community clustering clearly identified the existence of at least three different areas with distinct
community composition and environmental conditions. The environmental variables which described the structure of the water column around the CBF appeared to be significant drivers in defining the zooplankton communities at the CBF, explaining \(\approx 39\%\) of the variation in the zooplankton data.

### Biophysical coupling between hydrography and the zooplankton community

The Irish and Celtic Sea clusters were relatively similar to each other, whereas the Celtic Deep was rather different (although see CPR analysis below). Combined with measurements of current velocities parallel to the front, which were strongest around the Celtic Deep and weakened further west (Brown et al., 2003), we believe that the greatest amount of cross frontal mixing occurs in the south west of the grid. This appeared to generate a zooplankton assemblage within the Celtic Deep (i.e. to the east) that was more isolated from the surrounding communities. There was no evidence to suggest the presence of any transitional communities in the vicinity of the boundary front. Instead, we saw zooplankton assemblages divided by the frontal boundary producing a sharp ecotone between the communities.

Thermohaline fronts such as the CBF usually facilitate phytoplankton growth, which in turn gives rise to high zooplankton abundance that benefits from the rapid phytoplankton turnover (Cabal et al., 2008; Franks, 1992). Perhaps the most interesting feature observed for the region was a decrease in overall abundance in the stratified area above the Celtic Deep, which runs counter to what was expected from observations made at other frontal locations (e.g. Holligan et al., 1980; Munk et al., 2003; Molinero et al., 2008; Scrope-Howe and Jones, 1985). The hydrographic conditions within the Celtic Deep appeared ideal to promote enhanced zooplankton growth and abundance, as this should benefit from the strong thermocline and associated chlorophyll maximum. Subsurface chl-a showed the highest phytoplankton biomass above the Celtic Deep during the cruise and the PCI was high over a multi-annual period within this area. It is known that annual primary production over the Celtic Deep ranges towards the upper values for the wider Celtic Sea region (Hickman et al., 2012). However, what we observed for zooplankton in the net hauls and the summer CPR tows in this area was depleted abundance compared with the neighbouring Celtic Sea area.

One clear difference between frontal areas was the average strength of the PEA. The maximum values for the PEA, which are indicative of a stronger density gradient between the bottom and surface waters, were all found above the Celtic Deep. This may occur over prolonged
periods since the density gradients of the CBF reportedly show a negligible response to the spring-neap tide cycle at depth (Sharples, 2008). Earlier stratification above the Celtic Deep appears to result in a patchy distribution of the spring bloom timing in this area compared with other areas of the front. Along with the higher PEA found above the Celtic Deep, we also found evidence of an early onset of the bloom in the Celtic Deep by \(\approx 1\)–\(2\) months (as shown in the Supplementary data). Variations of 20–30 days have been observed in bloom timing due to eddy-driven stratification in the North Atlantic (Mahadevan et al., 2012) and similar reports have been made at an oligotrophic front in the NW Mediterranean (Radenac et al., 2013). Overall, we have a time lag of \(\approx 1\)–\(2\) months between the isolation of the surface layer and the SCM above the Celtic Deep compared with the Celtic Sea area.

As a result, we find that many of the taxa present in large numbers in the Celtic Sea were found at abundances that were \(\approx 1/10\)th of that level within the Celtic Deep (see Supplementary data, Fig. S2). The possibility that this reduction in abundance might be caused by missing dense aggregations within the area seems unlikely given that the distance between stations was well within the expected environmental variability at this scale (Irigoien et al., 2011).

There was a marked change in several conditions traversing the front between the Irish Sea (low surface temperature and salinity; weak density gradient) and the Celtic Sea (high surface temperature and salinity; strong density gradient). CHa and TL were two of the most dominant species in the Irish Sea which is expected due to their coastal/neritic associations (Halsband and Hirche, 2001; Williams et al., 1994). Many taxa were only

**Fig. 7.** Average monthly abundance \(\log(x+1) \pm \text{SE}\) of 12 of the most common taxa collected by the CPR in the Celtic Sea (CS; black line), Celtic Deep (CD; grey line) and the Irish Sea (IS; dashed line).
found in the Celtic Sea (AP, EV, EC). The only two species which were found in higher concentrations in the CD area compared with elsewhere were both oceanic species: ML and Parapontella brevicornis (Beaugrand, 2003). This could be associated with the fact that the cold saline pool of water found within the Celtic Deep has been identified as being of Atlantic origin, sweeping up from the Celtic Shelf break (Brown et al., 2003).

The copepod, AC, had a cosmopolitan distribution and was found to be the most abundant species in all CBF areas. On average, it contributed to at least half the abundance of each sample, and constituted as much as 85% of the abundance in some areas. Several other studies have found single species domination across frontal boundaries (Olsen et al., 1994). While not as important numerically, individuals of P. elongatus and CJ were also found evenly distributed between the three CBF areas. Zooplankton aggregations at frontal boundaries may arise due to active processes (as opposed to passive results of current flow). Behavioural strategies of the smaller constituents of the zooplankton (e.g. P. elongatus) include adopting positions high in the water column and not undertaking vertical migration. A possible outcome of inhabiting surface layers is that these species are particularly susceptible to the upper layer flushing effect. Wind-driven frontal mixing at the sea surface may provide a limited amount of cross-frontal exchange for surface-dwelling species (Wang et al., 1990), whereas species that undergo vertical migration may encounter strong density barriers in deeper waters due to the greater differences between water masses at depth. Accordingly, the behaviour of larger species such as C. helgolandicus, which undertake daily vertical migrations, may promote a greater level of retention within optimal areas (Emsley et al., 2005). AC and its congener A. tonsa are often found to be the most dominant component of the mesozooplankton communities in stratified and turbulent coastal seas and estuaries. These species are found to have large thermal and salinity tolerance ranges (Gaudy et al., 2000) and are also known to migrate vertically with response to tidal not diel cues which would greatly influence their ability to propagate across a structurally complex frontal region (Naylor, 2006). Other behaviours may also promote cross-frontal distribution, for example, foraging activity in A. clausii is higher and more successful in turbulent water than calmer waters, which may give this species a particular advantage in frontal areas (Saiz and Alcaraz, 1992).

**Spatio-temporal variation in the zooplankton communities**

The results of the spatio-temporal analysis at the CBF suggest that the observed abundance anomaly at the CD is an annually recurring feature at the front. Monthly averaged CPR abundances (1960–2009) showed that abundances in the CD area are generally significantly reduced compared with the CS during the months that the front occurs. It is noted that the CPR analysis showed that abundance in the CD was generally higher than the Irish Sea. As mentioned previously, direct comparisons between the CPR and net haul data can be difficult, particularly for...
certain groups. For example, the differences in the rank abundance of certain species such as echinoderms and several copepod species have been noted previously in direct comparisons of WP-2 net hauls versus CPR data sets (Clark et al., 2001; Pitois and Fox, 2006). While the CPR data have been aggregated into monthly estimates of abundance, which may smooth out the variability observed across frontal areas; the net hauls represent a snap-shot, to some extent. Notwithstanding this, the CPR did confirm that the levels of abundance for many important zooplankton taxa are significantly less in the Celtic Deep area compared with the Celtic Sea over a season, and that the patterns observed during the June 2009 cruise appear not to be a result of short-term variability, but rather these are present on average over the last 50 years.

The presence of a strong chlorophyll maximum in the CD area was not suggestive of negative bottom up effects and the abundance of phytoplankton appeared to be similar in both stratified areas. There is relatively weak evidence for bottom up regulation of higher trophic level populations in the Celtic Sea, in contrast with other areas, such as the North Sea (Lauria et al., 2013). An alternative explanation for the observed decrease in zooplankton abundance within the CD area could be increased predation by epipelagic fish species which may form dense aggregations at the CBF. The area above the Celtic Deep is known as a productive fishing location and is one of the most heavily fished locations within the Celtic Sea (Sharples et al., 2013); accordingly, the presence of high densities of fish could depress zooplankton populations in this area. Spatial mismatches in the peak abundances of zooplankton (euphausiids) and phytoplankton concentrations are thought to be caused by top-down control at a Californian front (Lara-Lopez et al., 2012). An alternative or co-occurring process is area isolation, where the strength of the boundaries along the horizontal (front) and vertical (thermocline) axes around the CD prevents a net influx of individuals (apart from the exceptions noted earlier). Without incursions from the surrounding areas, it would be more difficult to replace the rapidly overturning populations of zooplankton. In effect, the CD area may not achieve its potential through a lack of net transport into the area.

Through the use of complimentary data resources on zooplankton abundance at the CBF, we have highlighted several physical and biological characteristics of the area which may contribute to the differences observed between the areas. It would appear that the variation in abundance between the areas is initiated in early spring when the spring bloom of the surface waters occurs ~30 days earlier above the Celtic Deep signifying an earlier onset of water column stratification. This would of course benefit the zooplankton populations found there prompting rapid growth in the area. However, this will also cause the surface waters to become isolated much earlier than the surrounding areas restricting access to the large SCM which is present below the well-developed density gradient. As a result, we find that the abundance of almost all (see earlier, M. lucens and P. brevicornis) species are diminished by mid-June until the autumnal bloom when stratification breaks down once more. The relative abundance of the species in all three areas is similar (Table I), suggesting that the change in abundance occurs across the whole zooplankton community and is not driven by changes in one or two dominant species. We would expect that the abundance in the Celtic Sea area would eventually reach similar levels as the Celtic Deep, but they remain significantly higher for most species throughout the summer. The potential source of variation may come from further top-down regulation of zooplankton abundance where fish biomass is known to be much higher above the Celtic Deep compared with neighbouring areas. There is a noticeable difference in the community structure at the CBF compared with other frontal locations in European shelf seas. For example, a thermohaline front develops in the north of the Irish Sea, where the spring bloom in the stratified area starts 1–2 months earlier than the tidally mixed area, and the maximum abundance found in each area is similar (Gowen et al., 1998). To the south of the current study, the Ushant Front exhibits a transitional zone between the well-mixed coastal and stratified waters (Schultes et al., 2012); this contrasts with the sharp boundaries at the CBF. Future examination of this area could involve exploring the seasonal development of zooplankton abundance at the CBF by performing stratified net haul samples before, during and after the development of front. This could be supplemented with the use of coupled biogeochemical models that are currently in operation for this area of the North East Atlantic (Dabrowski et al., 2014), which have already been used to accurately model spatio-temporal variability in the growth of Mytilus edulis (Dabrowski et al., 2013).

SUPPLEMENTARY DATA
Supplementary data can be found online at http://plankt.oxfordjournals.org.

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