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Abstract

The patchy distribution of planktonic organisms has been known for over 100 years and ever since then attempts have been made to model this variability over a hierarchy of scales. Forcing mechanisms that act on plankton distributions are scale dependent and without consideration to the scale in question the model results become meaningless from being without reference. I attempted to address this issue by establishing a procedure to divide the Irish coastal and offshore waters in an ecologically meaningful way. In Chapter 2 eco regions (which are at scales below that of the Longhurst biomes or Large Marine Ecosystems) were defined using *chl-a* data derived from satellite observations. *Chl-a*, acting as a proxy for phytoplankton production, were used as “passive tracers” for defining ecosystem boundaries. K means clustering revealed 10 cohesive regions which agreed with the known hydrodynamics of the area. Data from the Continuous Plankton Recorder were extracted for three trophically important species (*Calanus helgolandicus*, *C. finmarchicus* and *Parapseudocalanus spp.*) and their phenology (seasonal timing) and interannual variability was modelled and compared against sea surface temperature. The phenology of each species in almost all regions was found to correlate with SST however the responses varied considerably interannually which is thought to be due to broad scale climatic forcing interacting with the local environment. In Chapter 3 the regional comparison was extended to include trophic communities to see whether the variability is species specific or representative of the whole community. Using control charts (which is an intuitive way of measuring whether an ecosystem is in a state of control) as a novel method for assessing ecosystem stability, similar inter regional and trophic variability was found to occur particular those regions at the shelf interface. In Chapter 4 the local-regional dependencies of conspecific zooplankton species in a coastal inlet and the adjoining waters were examined for Galway Bay. Bays and estuaries are treated as an insular system but a large degree of variability usually remains unexplained which may be due to external effects (population connections). Strong interannual relationships were found for most species with adjoining eco regions with the majority of species related to the Celtic Stratified region. All eco regions were examined against Galway Bay populations revealing only one dominant relationship for all species. Finally an examination on one of the regional boundaries (Celtic-Irish Sea) using a high frequency sampling grid in order to examine the structure of zooplankton assemblages at these boundary points. Distinct assemblages occurred on either side of the front with no transitional group found. SIMPER analysis revealed all assemblages to be equally stable suggesting that clusters were persistent during summer months. *Acartia clausii* dominated the communities averaging ~50% of total biomass. It's believed that this is not an opportunistic response but an active response where species behaviour facilitates retention and transport across the front.

Chapter 1

General Introduction

Introduction

Many areas of ecology have properties that are scale-dependent. This means that the perceived influence of different processes will change with the spatial extent or length of a study. One example, found in both the marine and terrestrial environments, is a hierarchy of scales where the influence of biological interactions on organism abundance is felt to be superseded by large scale climatic events at large spatial and temporal scales increasing scales (Edwards et al., 2010). With many ecological variables, such as population size, the spectrum of variability is thought to be 'red-shifted' such that the largest variations are only apparent once the system is examined over a sufficient length of time.

Perhaps one of the best ways to visualise spatio-temporal variability in marine ecological processes is through the use of Stommell diagrams (Stommell, 1963). These diagrams were developed as a way to plot the spectral distribution of oceanographic processes on a logarithmic scale of both time and space. Initially developed to highlight the spatial and temporal scale of oceanographic processes and the concerns in developing adequate sampling strategies to detect the spectral variability of those processes, it has since been adopted to highlight similar problems in plankton ecology. The first attempt to develop a conceptual model for space-time variability in biological oceanography was realised by Haury et al. (1978) and reproduced here in Fig 1. Although not strictly a spectral graph in the traditional sense due to many of the assumptions of spectral analysis not met, it does succeed in highlighting the relative importance of the different spatial scale processes in the distribution of biomass in the world's oceans. Placing the level of spatio/temporal scale addressed by each of the chapters we see that the work covers processes ranging from the decadal (50 years) and regional (~100-1000 km) scales as is the case with the eco regions on our study area Fig 2, to the weekly / local (10 km) scale of the boundary front Fig 2.

Longhurst's defined two different biogeographical zonation techniques for the world's oceans. Biogeochemical provinces groups the entire ocean into distinct province based on properties including mixed layer depth, mixed layer temperature, phytoplankton production characteristics (Longhurst, 2001). These regions were largely defined using remote sensing techniques. This extends the reach of the ocean classification from the prior method of Large Marine Ecosystems, which is restricted to the seas adjacent to continental land masses and largely based on topographical features (Longhurst, 1998). In Fig 2 we see that our study area (red box) crosses two principal biogeographical provinces and one LME. Part of the concern with these fixed regions is that oceanographic studies do not benefit from having pre defined boundaries that are considered as part of a global mosaic. Our aim is to

develop a procedure for selecting regions that have a certain level of plasticity, can be used to define regions over a hierarchy of scales and can be tuned to suit the particular hypothesis that is in question. There are some general differences in the scaling processes observed in terrestrial and marine environments. Terrestrial changes at a regional (~100-1000km) scale may take several millennia before the flora and fauna for that area become distinct from the preceding assemblage (Willis and Whittaker, 2002), however within the marine environment, particularly in pelagic ecosystems, such changes have been observed within the last 60 years (Beaugrand et al., 2009). The speed of broad scale oceanic change may reflect the relatively weak environmental heterogeneity compared to terrestrial systems and the intermittency or leakiness of marine boundaries such as fronts, upwelling zones or current systems..

The possible role of biological and environmental heterogeneity in the response of a system to large scale forcing suggests a requirement for characterising the grain and extent of patches within that system. Haeckel (1891) displaced the idea that plankton were uniformly distributed, leading to the view that pelagic organisms are patchy in their distribution with dense local accumulations and often with distinct boundaries. The literature relating to plankton patchiness is quite extensive but some examples of significant developments in quantifying plankton patchiness have been through work by (Hardy, 1935; Wiebe, 1970; Mackas et al., 1985; Levin, 1992; Martin, 2003). Wiebe (1970) found patch sizes varied between night and day tows and that plankton densities within these patches were 2-5 times background densities while Martin (2003) reviewed a number of possible mechanisms involved in generating patchiness and suggested new lines of approach that could stimulate further research in this area.

Descriptions of patchiness in marine plankton are meaningless without an explicit link to scale. Aggregations of plankton patchiness can occur over a range of centimetres (Seuront, 2001) to hundreds of kilometres (Rombouts et al., 2010) and the physical and biological constraints differ depending on the scale in question. Smaller scale aggregations are related to predator prey relationships and local hydrographic processes including the relationship between accumulation through growth and loss through diffusion (the KISS theory) (Kirsthead, 1953), and aggregation at features such as sub surface chlorophyll maxima (McManus et al., 2005; Menden-Deuer and Fredrickson, 2010). As the spatial scale increases towards the ocean basin scale, biological interactions become less important and instead the oceanic and atmospheric climate become the dominant factor in explaining the variation in plankton distribution (Helouet and Beaugrand, 2007). Dense aggregations of plankton in

certain areas can create food sources for higher trophic level organisms creating biodiversity hotspots in an otherwise relatively low productivity environment. For example large phytoplankton blooms are regularly seen by satellite imagery along continental shelf regions in the summer months with patches in excess of a 1000 km² (e.g.- Garcia Sota and Pingree, 2009) associated with increased vertical mixing along the shelf break.

Scale concepts in plankton dynamics are a central theme of this thesis. The scale concept relates both to the understanding of how plankton abundance and distribution vary and to the implications of scale for management, particularly with reference to the EU Marine Strategy Framework Directive. It is not feasible to consider entire ocean basins or shelf seas for management but rather divide the ocean into regions which are ecologically meaningful and not arbitrary divisions based on political boundaries. Determining suitable regional ecosystems is important for the developing of an Ecosystem Based Fisheries Management (EBFM) (Garcia et al., 2002) as well and this work will hopefully serve as a valuable resource to its development.

The Continuous Plankton Recorder (CPR): The cornerstone of plankton research

A universal point of reference for any work on plankton in coastal and oceanic waters is the CPR. The CPR time series and spatial extent enable questions of scale to be addressed from the basin scale down wards and encompassing temporal change over decades. The data that form the CPR survey are generated using a self-contained plankton sampler that captures zooplankton and phytoplankton on a 250 µm silk mesh, calibrated to move so that a sample cast corresponds to a distance of 15 km. The plankton recorder is low volume, (3 m⁻³), collecting samples at a fixed depth of ~10 m behind merchant ships (Warner and Hays, 1994). Regular plankton tows have been made across the North Sea since 1939, which have since been expanded with a programme to cover to cover much of the North Atlantic complemented by several sister surveys in other oceans (e.g. - Batten and Freeland, 2007). The CPR is currently the largest on-going plankton survey, spanning over 50 years and including identification of up to 450 taxa.

The initial goals set out by the CPR survey at its inception were to create an atlas of plankton distributions for the North Sea and wider Atlantic region for specific usage for the fisheries industry. Analyses for many other purposes have been developed. Since the mid 1990's the CPR dataset has been central to investigations of long term change in the oceans, with many investigations of the link between the pelagic ecosystem and climate.

Some of the interpretations of change in pelagic systems are disputed, possibly reflecting the different scales at which analyses and conclusions have been drawn. Phytoplankton is believed to be tightly coupled to environmental and climatic change due to rapid turnover rates and short generation times. Significant changes in the Phytoplankton Colour Index (PCI), a semi-quantitative measure of chlorophyll concentration derived from CPR silk colour, have been found in areas across the N. Atlantic and linked to the rising sea surface temperatures (SST; Reid et al., 1998; Edwards et al.; 2001, Leterme et al.; 2005). Areas north of 60° N have shown a negative relationship with SST while south of 60° N there has been a strong positive relationship with SST (Reid et al., 1998). In addition to anthropogenic warming, long term changes in SST reflect the Atlantic Multidecadal Oscillation (AMO) () and may be linked to the North Atlantic Oscillation (NAO): the most dominant mode of atmospheric variation in the N. Atlantic (Hurrell, 1995). Attempts to associate phytoplankton abundance directly with the NAO have produced mixed results (Edwards et al., 2001; Barton et al., 2003). Attempts to distinguish between the two primary functional groups in the CPR phytoplankton (Dinoflagellates and Diatoms) by Leterme et al. (2005) found evidence of a Dinoflagellate increase/Diatom decrease across the N. Atlantic thought to be linked to SST. This change in phytoplankton composition can be interpreted as a reflection of increased stratification in warmer seas, benefitting motile dinoflagellates able to access nutrients in deeper waters and also able to maintain position in the water column in contrast to passively sinking diatoms. It may also be responsible for restricting the upwelling of important nutrients necessary for a diatom dominated community (e.g. – silicates) (Egge and Asknes, 1992). Recently Boyce et al. (2010) reported a decrease in the global median of phytoplankton concentrations at a rate of 1% year⁻¹. However subsequent rebuttals (Mackas, 2011; McQuatters Gallop et al., 2011; Rykaczewski and Dunne, 2011) questioned the Boyce et al. (2010) methodology, attributing the perceived change as a bias between the datasets used and a consensus that time series (often collated in different ways) have shown consistent increases in phytoplankton in the last 50 years.

In most cases attempts to derive estimates of phytoplankton biomass for an area involve using univariate measures, either a concentration (pigment or some other currency such as carbon) in mg l⁻¹ or a summed cell count of all species. In chapter 3, biomass estimates are derived for the most abundant phytoplankton taxa per area and develop a multivariate index of phytoplankton change. This provides a more detailed representation of the long and short term

trends for phytoplankton abundance in the N. Atlantic than is possible on the basis of a univariate measure.

Zooplankton species, in particular the Calanoid copepods, have also been found to be closely linked to changes in both phytoplankton (Beaugrand and Reid, 2003) and climate, potentially with a lagged response (Hays et al., 2005). While phytoplankton biomass signals are equivocal with respect to links to atmospheric teleconnection patterns, the two *Calanus* species *C. helgolandicus* and *C. finmarchicus* have been found to be strongly correlated with the NAO, with opposing species-specific signals (positive and negative respectively; (Fromentin and Planque, 1996). While further attempts to predict *C. finmarchicus* abundance based on the NAO failed (Planque and Reid, 1998), the presence of an NAO signal has been found in many measures of diversity and abundance used on CPR data (Beaugrand and Reid, 2003). Despite these potential links to the NAO, and hence storm tracks and other elements of the weather ‘package’ represented by the NAO (Stenseth and Mysterud, 2005), the variability of both phytoplankton and zooplankton generally also associate with changes in SST (e.g. - Richardson and Schoeman, 2004) where positive correlations between primary producers and grazers imply bottom-up regulation of the zooplankton community.

Perhaps one the most novel uses of the copepod taxa within the CPR dataset was to generate multiple assemblages across the N. Atlantic with known hydrodynamic associations (Beaugrand, 2004) which saw a move from the traditional method of using individual species as climate indicators. These species assemblages have been used quite successfully to highlight the extreme poleward movement of groups in response to the rapidly rising SSTs (Beaugrand et al., 2002; Beaugrand and Ibanez, 2004; Beaugrand, 2005). The time series was extended to include all copepod taxa up until 2005 and found that the northward shift is in the order of 23.16km year⁻¹ (Beaugrand et al., 2009). Similarly there have been changes to the timing of their seasonal maxima (phenology) and these changes to the species life history are also attributed to the changing SST and environmental conditions (Edwards and Richardson, 2004; Edwards et al, 2006). The changes in the timing vary between the different zooplankton taxa but on average copepods peak 10 days earlier compared to the 1960’s, while several meroplankton taxa peak almost a month earlier.

Many of the processes affecting plankton, such as feeding rates, loss rates and reproduction are non-linear and as a result the pelagic system can change rather abruptly once across an environmental threshold (Beaugrand et al., 2008) leading to a “regime shift”: a change from

one stable ecosystem community to another (Reid et al., 2001; Beaugrand, 2004; Alheit et al., 2005). There is still debate on whether the CPR data and the available techniques are capable of detecting accurately such shifts in community structure (Burrows et al., 2009; Mieszkowska et al., 2011) but broad scale summaries tend to emphasize that quite large changes in pelagic ecosystems occur on the N. Atlantic and other ocean basins once sufficiently large temporal scales are used (e.g. McGowan et al., 2003).

While the CPR dataset has been used successfully to further the scientific understanding of the large scale spatial and temporal dynamics of plankton in the oceans there are many alternative analyses that can be made. These relate to the scales chosen for analyses, the dependent variable or variables and the reference points for comparison. A number of potential goals from further research on the CPR goals are set out by Mackas and Beaugrand, (2010) and several of these are taken up in this thesis and are elaborated upon below.

Broad scale oceanography of the N. E. Atlantic

Transporting up to 20 Sv of water, the North Atlantic Current (NAC) represents the north-eastern extension of the Gulf Stream and is the primary source in which warm waters are transported into the higher latitudes (Bower and von Appen, 2007). Once across the Mid Atlantic Ridge it forms two main branches, one which travels northwards towards the Nordic seas, while the other forms a large counter clockwise rotating body of cold/saline sub arctic water known as the Sub Polar Gyre (SPG) (Hatun et al., 2005). The SPG forms strong boundary currents and is important for the wider ocean circulation as the deep ocean convection cells (~2500 m) formed there means that it contributes greatly to the origins of the North Atlantic Deep water (NADW) (Hakkinen and Rhines, 2004). The strength of the SPG can greatly influence the direction of the NAC and the flow of the East North Atlantic Waters (ENAW) north (Harvey, 1982). The ENAW originates from the sub tropical gyre and allows the penetration of warmer and more saline waters north (Hatun et al., 2005). Studies of the SPG have revealed that there is a strong coupling between the atmospheric forcing and the ocean currents as reflected by the NAO (Hakkinen and Rhines, 2004; Boning et al., 2006). Over the last 40 years the transport flow of the NAC weakens during negative NAO phases (e.g. 1960's) but has gradually intensified up until the early 1990's in concordance with relatively high NAO conditions (Curry and McCartney, 2001). Since then we have seen a progressive weakening of the SPG which has been attributed again to the negative NAO forcing (Hakkinen and Rhines, 2004) which has allowed an increase in volume transport of

the ENAW to penetrate as far as the Nordic Seas in 2002 (Hakkinen and Rhines, 2009). The interface between the SPG/ENAW is more commonly known as the Modified North Atlantic Water (Hansen and Osterhaus, 2000) and is situated to the N.W of Ireland. Subsurface currents off shelf may hold an equal importance in facilitating plankton transport and distribution particularly for those species with deep sea resting stages. The Subarctic intermediate water (SAIW) strongly influences intermediate waters north of 51° N, near the entrance to the Rockall Channel. The SAIW undergoes strong seasonal variation and during periods of strong SAIW influence Mohn et al., (2007) has shown that it can inhibit the northward progression of Mediterranean water (MW). This highly dynamic region lies within our study area and is considered a major underlying factor that effects the distribution of planktonic organisms in this region.

The Shelf Edge Current (SEC) is a polewards moving near seafloor current that is driven by an along-shelf pressure gradient from the Iberian margin to the Norwegian Sea (Hutchnace and Gould, 1989). Mean northward velocities increase as it progresses into higher latitudes although there is a periodic reversal of flow caused by the presence of slope waves west of the Porcupine Bank (Thorpe et al., 1991). The SEC is responsible for transporting a large proportion of the warmer, saline waters of the ENAW northwards into the higher latitudes (Mohn et al., 2007). The SEC is also pivotal in its role in the physical exchange processes at the continental shelf edge (White and Bowyer, 1997). The interannual to decadal variability of these currents has important implications for the plankton communities within our study area. In fact, we allude to these large scale ocean dynamics as possible mechanisms for explaining the interannual variability of plankton abundance in the offshore regions in Chapter 2.

Much of the recent observational evidence for the circulation patterns within the Celtic Sea allude to the importance of the dense bottom water baroclinic flows which are isolated from the upper reaches of the water column after the summer stratification (Brown et al., 2003; Hill et al., 2008). Much of the transport in the currents within the Celtic Sea can be explained by a means of a density driven process. These density gradients form fast flowing jet currents which travel in counter clockwise and subsequently move northward around the west coast of Ireland (Fernand et al., 2006). Within much of the Irish Sea the level of tidal mixing means that the water column fails to stabilise and remains permanently mixed year round. However a small baroclinic circulation does form (known as the Western Irish Sea gyre) through a similar process seen in the Celtic Sea (Hill et al., 1998). The resulting thermally stratified

front formed across the Celtic Deep creates a strong barrier where we see little in the way of cross frontal exchange (Brown et al., 2003). The implications for much of the seasonal variation in the continental shelf circulation are also elaborated upon in the next research chapters. With this section and the associated figure it is hoped that readers will be able to return to this section as an aid in following how the changes in plankton dynamics may have been brought about through oceanographic variation.

Research aims

In keeping with the management aims of the Marine Strategy Framework Directive and the Ecosystem Approach to Fisheries (an element of which is concerned with ensuring that management has an appropriate spatial scale), this thesis seeks to define regional scales and to examine the interrelationships within and between regions. The regional scale is smaller than the ocean basin scale of many existing studies and may not reflect the existing biogeographical and administrative boundaries (e.g., ICES statistical areas). Spatial variability for calanoid copepods in the N.E. Atlantic can be found at small scales < 400km (Beaugrand and Ibanez, 2002), below the level of Longhurst's biogeographic provinces or Large Marine Ecosystems (LME's; Longhurst, 1998). Without careful consideration of potential regional limits, time series may aggregate species abundances across important boundaries potentially losing important dynamic signals. In chapter 2 the issue of identifying regional boundaries follows the logic of Longhurst (1998) in using the best available spatially resolved data: satellite-derived chlorophyll estimates. By grouping regions showing similar evolution through time, important boundaries in the offshore and shelf regions were potentially identified. The work will look to resolve an area of ocean below the scale of the LME to investigate climatic forcing on plankton communities at finer scales and at spatial resolution that better matches the spatial variability in this area. The box outlined in Fig 2 represents the study area for much of the research in this thesis and within it we will look to divide the ocean in an ecologically meaningful way. The two *Calanus spp.* of *Calanus helgolandicus* and *Calanus finmarchicus* and the small copepods primarily of the *Pseudocalanus* and *Paracalanus* genera were used to assess the differences between regions and the differential responses of species or genera to climatic forcing in separate regions of the North Atlantic. These taxa were used, in this thesis and by other researchers, as model organisms due to ubiquity in temperate oceans and important roles in the trophic ecology of these areas (Napp et al., 2005; Bonnet et al., 2005).

As mentioned earlier, single species analyses have tended to dominate in the literature, potentially confounding changes at the assemblage level. These are addressed in Chapter 3, along with an alternative approach to looking at the potential state of the community (as suggested under proposed regime shifts). Specifically, the regional patterns observed within the *Calanus spp.* and the *Pseudocalanus/Paracalanus* group may be species-specific or may manifest at the community level. A trophic approach was taken, using the literature in order to divide species or taxa into three trophic groups (Phytoplankton, Herbivorous copepods or Carnivorous zooplankton) and to also compare the stability of different trophic groups over the last 50 years. Ecosystem stability follows the definition of “the ability for an ecosystem to remain within or return to a dynamic equilibrium when an external force is applied to that system” (Connel and Sousa, 1982). The number of times a community deviates significantly from a baseline which is set *a priori* determines the level of long term stability for a particular community.

While the initial two research chapters will have dealt with community differences of zooplankton in the N.E. Atlantic at a regional level, chapter 4 attempts to relate populations of several important copepod taxa in a relatively small coastal setting with their populations at broader scales. This chapter involves assembling a time series from archive material for Galway Bay on the west coast of Ireland (between 1973 and 1987). Freshwater influx from the Corrib river leads to a salinity gradient through the Bay from ~24 (Inner Bay) to ~35 (Outer Bay). Galway Bay lies within a sampling shadow of the CPR and so the construction of a time series represents a direct addition to data gaps in the CPR. Use of Galway Bay samples required some modelling of abundances to allow interpolation. Reconstructed time series were modelled using CPR derived time series as predictors in order to find possible connections with or advection routes for zooplankton into the Galway Bay area.

The early chapters of the thesis are concerned with the process and implications of defining regions in the North East Atlantic. Regions are, by necessity, separated by a boundary, which may also be a hydrographic feature. Chapter 5 is a closer examination of the nature of a boundary: the zooplankton distribution across the front which separates the seasonally stratified Celtic Sea from the mixed water column of the Irish Sea. Of interest is the pattern of change in the pelagic assemblage: do two distinct assemblages meet at the front, is the zone of contact a sharp boundary or a gradual diffusion of one assemblage to the next, alternatively, does an intermediate community arise at the boundary, distinct from wider region. To test these alternatives, samples were collected in June 2009 along a high frequency sampling grid

across the frontal boundary. This work complements previous research. Although there have been over 40 years of research into the physical development of the Celtic Boundary Front (CBF; Hill et al., 2008) and the nutrient and chlorophyll fluxes across it (Pingree et al., 1976; Savidge, 1976), there have been few descriptions of the mesozooplankton community within the frontal zone. This contrasts with the study of zooplankton communities across many of the other prominent fronts along the European Continental Shelf.

Each of these chapters develops patterns of contrasting spatial extents: ranging from (1000km⁺: Ocean Basin), regional (100-1000km: eco regions) and local (100km: Galway Bay and CBF). Novel ways in which to analyse a well-established plankton dataset (CPR) are developed in addition to a new time series for zooplankton populations in Galway Bay.

The context and significance of the findings made in Chapters 2-5 are discussed in a general discussion in Chapter 6. This includes the impact of a multiscale approach to the understanding of plankton dynamics and the implications for a regional approach to marine environmental monitoring.

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Figures

Figure 1

A Stommel diagram (adapted from Haury et al., 1978) which displays the principal biological oceanographic processes on a log scale for both space and time. The spectral peaks of each biological process relate to the change in the biomass variability of planktonic organisms at these scales. Overlaid on this graph are the approximate spatio-temporal scales that each research chapter addresses.

Figure 2

A map of the N.E. Atlantic displaying the major biogeochemical provinces and Large Marine Ecosystems in which our study area is contained within (Red box). The two provinces are the North Atlantic Drift province (NADR) and the North East Atlantic Continental Shelf Province (NECS) while the Celtic Sea Biscay Shelf LME is also shown (Hatched)

Figure 3

The major upper layer oceanic water bodies and the principal shelf sea currents that exist in the N.E. Atlantic. Shown here are the Sub Polar Gyre (SPG) in blue, The Modified North Atlantic Water (MNAW) in Yellow and the East North Atlantic Water (ENAW). The bottom layer Shelf Edge Current (SEC) is shown moving northward along the continental shelf edge. The main research area used in this thesis is found within the red box.

Figure 1.

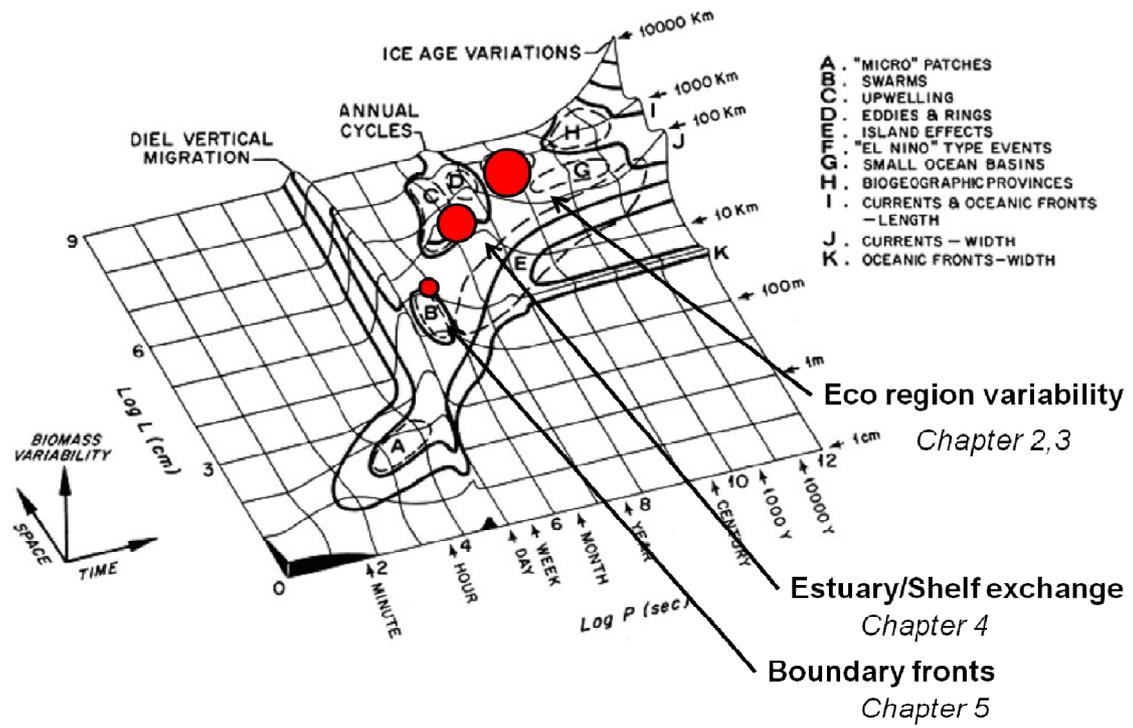


Figure 2.

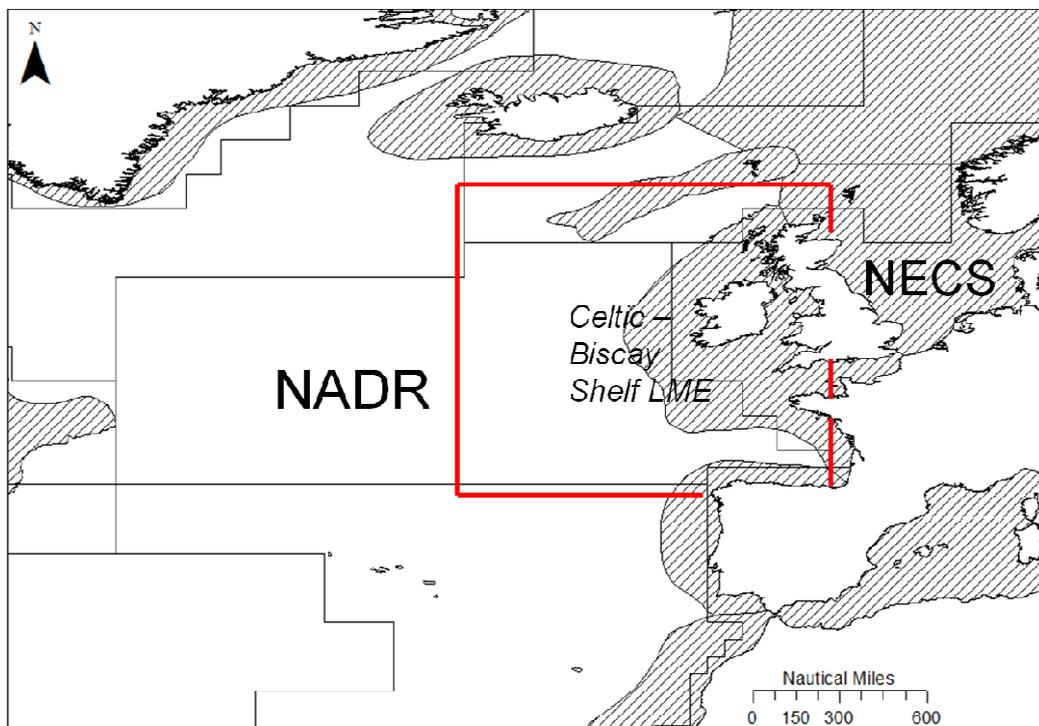
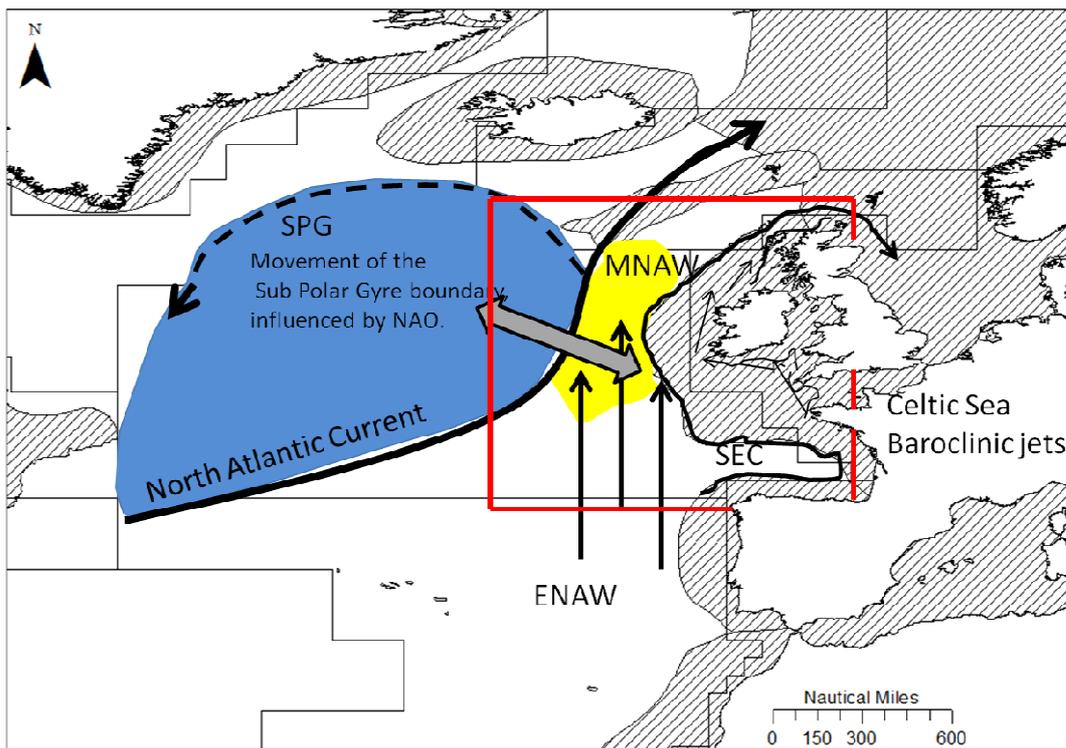


Figure 3.



Chapter 2

Variation among northeast Atlantic regions in the responses of zooplankton to climate change: not all areas follow the same path

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Abstract

Broad scale climate forcing can interact with local environmental processes to affect the observed ecological phenomena. This causes potential problems of over-extrapolation for results from a limited number of sites or the averaging out of region-specific responses if data from too wide an area are combined. In this study, an area similar in extent to the Celtic Biscay Large Marine Ecosystem, but including off-shelf areas, was partitioned using clustering of satellite chlorophyll (*chl-a*) measurements. The resulting clusters were used to define areas over which to combine copepod data from the Continuous Plankton Recorder. Following filtering due to data limitations, nine regions were defined with sufficient records for analysis. These regions were consistent with known oceanographic structure in the study area. Off-shelf regions showed a progressively later timing in the seasonal peak of *chl-a* measurements moving northwards. Generalized additive models were used to estimate seasonal and multiannual signals in the adult and juvenile stages of *Calanus finmarchicus*, *C. helgolandicus* and the *Paracalanus-Pseudocalanus* group. Associations between variables (sea surface temperature (SST), phenology and annual abundance) differed among taxonomic groups, but even within taxonomic groups, relationships were not consistent across regions. For example, in the deep waters off Spain and Portugal the annual abundance of *Calanus finmarchicus* has a weak positive association with SST, in contrast to the pattern in most other regions. The regions defined in this study provide an objective basis for investigations into the long term dynamics of plankton populations and suggest suitable sub regions for deriving pelagic system indicators.

Keywords: *Calanus*, phenology, ecosystem management, sea surface temperature, clustering, Continuous Plankton Recorder

1. Introduction

Climate change interacts with processes at different scales to affect ecosystem function and the distribution and abundance of individual species (Overland et al., 2010). The interactions between processes at different scales can produce divergent results in the same response variable. For example, large-scale declines in the northern species *Calanus finmarchicus* (Gunnerus) (e.g., Planque and Fromentin, 1996) exist alongside divergent abundance falls and increases in adjoining areas (Beare et al., 2002a, Beare et al., 2002b). Specifying the scale (both geographical extent and resolution) can help clarify the key processes in a study system. Terrestrial ecosystems have been defined based on a hierarchical scale domain ranging from the global >10,000 km down to micro <10 m scales (Willis and Whittaker, 2002). These scale domains have analogues in ocean systems where continental scales (2000-10000 km) correspond to the extent of ocean basins while regional scales (200-2000 km) correspond to the different water masses within ocean basins. Little work addressing regional scale zooplankton dynamics has been done so far in the offshore waters and continental shelf areas around Ireland; despite these setting the scene for interpretation of ecosystem changes documented in inshore areas e.g. in the English Channel (Southward et al., 1995; Hawkins et al., 2003), North Sea (Clarke et al., 2003) and German Bight (Wiltshire et al., 2010). The present study aims to define appropriate regional scales at which to study zooplankton dynamics in the offshore waters and shelf areas around Ireland. Our approach is to use Chlorophyll a (*chl-a*), expressed as mg m^{-3} , as a proxy for autotrophic activity, to define coherent regions that will form the basis of our analysis.

The significance of regional variability in ecosystem structure and response has been recognised in environmental policy. For example, a fundamental component of the Ecosystem Approach to Fisheries, which forms a policy objective of international commitments to the Convention on Biological Diversity, is the need for scientific descriptions of ecosystem scales to guide appropriate management scales (Garcia et al., 2003). Two major descriptions of ecosystem scale are available for the North East Atlantic. Longhurst (1998) defined a Northeast Atlantic Shelves Province (NECS) ranging from northern Spain to the edge of the Faroe Shetland channel in the North and as far East as the Baltic Sea. This area is approximately the same as is delineated by the three Large Marine Ecosystems (LMEs) of the Baltic Sea, North Sea and Celtic-Biscay Shelf (<http://www.lme.noaa.gov/>). Longhurst (1998) recognised that subdivisions based on oceanographic criteria (primarily the positions of

fronts) may be appropriate in certain circumstances. The current study examines the evidence for such coherent regions at levels below the Province and LME extent, given that the CPR analysis of Beare et al. (2002b) suggests divergence among areas as small as 3 degrees latitude by 8.75 degrees longitude. This is in stark contrast to the spatial extent of the LMEs in this area which stretch to >15 degrees latitude by >25 degrees longitude.

A number of decisions are required when partitioning data within spatially extensive datasets such as the Continuous Plankton Recorder (CPR) database (Beare et al., 2003). Attempts to impose a standard grain size have included using standardized statistical areas (Colebrook, 1960, 1975; Robinson, 1970), whereby data were first aggregated into 1 x 0.5 degree squares. The size and position of these areas ensured that enough samples were available for subsequent statistical analyses. Interpolation methods using inverse distance weighting (Beaugrand et al., 2001) and kriging (Planque and Fromentin, 1996) have produced regularly-spaced sample pixels of 1 x 1 degree latitude and longitude for the North Atlantic. Interpolated data were subsequently used to document pronounced changes in zooplankton community structure of the North Atlantic during recent decades, such as large poleward shifts of warm-water assemblages (Beaugrand et al., 2002a). However, interpolation from the CPR may not be an appropriate way to define regions. For example, in the standardized area C3 (Irish Sea), there are approximately 5.2 samples month⁻¹ over an area ~60,000 km². Interpolation schemes have included the use of six neighbours with a search radius of 250 nm (Beaugrand et al., 2002b), which would make it necessary to select samples across prominent fronts such as the Celtic Deep Front (Pingree et al., 1982). This approach is problematic for planktonic organisms because in the process of sampling across strong physical barriers one could move from areas of high to low biological productivity within only a few km (Molinero et al., 2008). Zooplankton assemblages including Chaetognaths (Pierrot-Bults, 2008), salps and krill larvae (Molinero et al., 2008) and copepods (Berasategui et al., 2006) may be strongly influenced by frontal structures. Interpolating data across such features can mean that the particular characteristics of a distinct hydrographical boundary could be lost through smoothing.

Phytoplankton data represent, through satellite measurements, the only biological data available across wide regions with a fine grain size (Longhurst 1998). These data integrate many of the signals relevant to the definition of regions but avoid the relative sparseness of CPR data for regions below that of LMEs. We developed a method to select, *a priori*, the

regions (200-2000 km) from which to sample CPR by using satellite-derived ocean colour from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). This dataset offers accessible high-resolution data of calibrated *chl-a* across 12 years (Vantrepotte and Melin, 2009). *Chl-a* is the principal photosynthetic pigment found in phytoplankton (Ryther and Yentsch, 1957) and this satellite remote sensed measure of *chl-a* can describe much of the variance in phytoplankton abundance such as the timing of the spring bloom and changes in overall biomass (Harding Jr. et al., 2005 ; Raitsos et al., 2005). *Chl-a* can therefore be thought of as a proxy for variability in primary production, facilitating the clustering of regions that have similar temporal patterns (Longhurst 1998). The close temporal relationship between phytoplankton and copepod zooplankton (Richardson and Schoeman, 2004) implies that *chl-a* is also an appropriate measure to define relevant regions for zooplankton.

Once a series of regions was defined within an extensive study area, time series of the abundance of selected zooplankton were examined for each region, namely the copepod taxa *C. finmarchicus*, *C. helgolandicus* (Claus) and a group which includes *Paracalanus* and *Pseudocalanus*. These species are numerically important in the CPR data, are implicated as having important trophic links to fisheries (Heath and Lough, 2007) and provide useful benchmarks for comparison with CPR analyses made at different scales. Changes in phenology and average annual abundance were compared with changes in SST, to examine the effects of physical forcings, as well as to examine whether the relationships were similar or different among regions. The definition of regions and subsequent inter-regional comparisons add a different perspective to the current understanding of the links between climate and plankton dynamics, particularly as multi-regional comparisons are far less common to date than within-region analyses of zooplankton time series (Mackas and Beaugrand, 2010).

2. Materials and methods

2.1 Defining the ecosystem regions

The study area included the area of the Celtic-Biscay LME with slight overlaps into the North Sea, Iberian Coastal and Faroe Plateau LMEs. In contrast to the LMEs, waters off the shelf edge were included. ICES have also proposed eco-regions for the implementation of the ecosystem approach and Marine Strategy Framework Directive in European waters (ICES, 2004). The Celtic Seas eco-region, as defined by ICES, is contained within the study area.

Satellite-derived ocean colour data acquired from the SeaWiFS data set (assimilated *chl-a*, www.oceancolor.gsfc.nasa.gov) were used to partition the study area into regions with coherent phytoplankton dynamics. Due to resuspended sediments and terrestrially-derived materials, shallower coastal regions (so-called ‘Case 2 waters’ e.g. Alvain, 2005; Lee and Hu, 2006) return inflated and incorrect *chl-a* values (Harding Jr. et al., 2005) in comparison to oceanic ‘Case 1 waters’ (Lee and Hu, 2006). While these considerations may confound absolute estimates of phytoplankton density, influences of estuarine outflow and suspended sediments on plankton communities are well known (Tian et al., 2009). We therefore consider that the presence of yellow substance and suspended solids is information about the coastal ecosystem which will in fact add to the definition of regions.

Data for all months between 1998 and 2008 were extracted as level 3 monthly composite images (pixels of 9km x 9km resolution) of *chl-a* (O’Reilly et al., 1998, 2000), expressed as per unit volume (mg m^{-3}) and the data were $\ln(x + 1)$ transformed. It became apparent that coverage within the study area decreased to <10% in the months between November and February in all years so these months were omitted from subsequent analysis. The maps were organised into a matrix where the pixels from each map were unrolled to form a column corresponding to a particular year-month, with each row consisting of values for the same pixel through time. A second filtering process was necessary on the temporal dimension, such that all rows that contained more than ten months of missing values were removed (see Beaugrand et al., 2002b for an example of a similar matrix design).

Pixel vectors (point location, separate values for each date) with similar chlorophyll patterns over time were clustered using a K-means method. This method aims to cluster n objects into K clusters in a p -dimensional space, selecting the optimum clustering by reducing the error

sum of squares (E^2_K). The error sum of squares summarizes the distance of each object to the centroid of the cluster to which it has been assigned. The amount of variation explained for each choice of K can be estimated using a sum of squares comparison analogous to ANOVA to generate an r^2 value (Legendre and Legendre, 1998). The total sum of squares for this calculation is calculated using the distance of each object from the global mean when $K = 1$. The most parsimonious number of clusters can be defined using the asymptote of r^2 values with respect to increasing values of K . Determination of the asymptote was based on the point at which the change in r^2 between different values of K fell below 5%.

K-means clustering is unsupervised, meaning that clusters can be of any size. Cluster definition based on *chl-a* was subsequently refined to ensure sufficiently large numbers of CPR samples were found within each region. The first step was to repeat the r^2 -based definition of optimum K using only those clusters with over 2000 pixels. This means that small clusters, unlikely to contain sufficient CPR samples to define a time series, were excluded from the count of defined clusters. A further filter was based on the threshold of at least five samples per month, recommended by Beaugrand (2004) for investigating long term monthly changes in CPR. Assuming regular monthly tows per region, an approximate minimum requirement is 3060 CPR samples per region (5 samples x 12 months x 51 years). Relatively large regions in terms of number of pixels could potentially contain too few CPR samples. A threshold similarity was therefore applied to test whether it was reasonable to combine regions with too few CPR samples. The test for suitability of combination was based on bootstrapped similarity values. Support for each node in a dendrogram of regions was calculated using the *pvclust* package (Suzuki and Shimaidora, 2004) for R statistical language (R Development Core Team, 2008). Regions that grouped with >95% similarity within the dendrogram were amalgamated. This processing of the original clusters reduced the number of regions by either rejecting regions due to insufficient CPR data or by amalgamating similar regions to improve CPR coverage.

2.2 Zooplankton data

CPR data are collected by towing a continuous plankton recorder behind ships of opportunity at a depth of approximately 10 m and a speed of 20 km h⁻¹ (see Warner and Hays, 1994, Richardson et al., 2006). The machine is calibrated so that each section of the silk roll that captures plankton corresponds to a length of 10 m and 3 m⁻³ of water filtered. Over 450 taxa

of both phytoplankton and zooplankton have been identified in CPR samples since 1946, although some taxa have not been counted over the entire period (Warner and Hays, 1994).

The copepods *Calanus finmarchicus* and *C. helgolandicus* occupy different thermal niches (Beaugrand and Helaouet, 2008) and reach peak abundances at different times of the year (Planque and Fromentin, 1996). *C. finmarchicus* is a sub-polar species whose presence in an area indicates a cold water influence while its congener, *C. helgolandicus* is seen as a more temperate oceanic species (Helaouët and Beaugrand, 2007). We have therefore decided to use these two species to test the inter-regional variation in the study area. Only the adult stages (CV-CVI) are differentiated to species level while the early copepodite stages *Calanus* CI-CIV contain individuals from both (and potentially other *Calanus* species). Because the mean size of calanoid copepods has decreased in the N.E. Atlantic over the last 50 years (Beaugrand et al., 2010), the relatively abundant ‘*Para/Pseudo*’ group was also selected as an indicator of small copepods in this area. This includes *Paracalanus* spp., adults of *Pseudocalanus* spp. (the latter identifiable to genus but not species) and any unidentifiable small copepods (<2 mm). The temporal range covers the period between 1958 and 2008, where methodologies have remained constant during this time (Warner and Hays, 1994).

2.3 Estimates of regional population dynamics

CPR data for separate taxa are recorded in 12 abundance categories and therefore represent ordinal response variables. These abundance estimates can be treated in various ways, but this study follows the reasoning of Beare and McKenzie (1999). Resolving uneven sample densities requires an interpolation based on fitting a model to the data. For each point in time, the model provides a regional estimate of the probability distribution (P ; $r = 0, 1, 2 \dots 12$) where P is the probability that the date yields a recorded value r (P_r). Numerical abundance can be estimated using the accepted number per sample A_r (see Beare and McKenzie, 1999). Accepted number per sample in this case will be abundance 3 m^{-3} due to the nature of CPR sampling mechanism. Given the probability distribution across abundance classes, the estimated average abundance per sample is calculated as:

$$\text{Estimated abundance} = \sum_{r=0}^{r=12} A_r P_r \quad (1)$$

Seasonal and long term trends were estimated using a generalized additive model (GAM). GAMs fit a smoothing spline to the data, allowing flexibility in the representation of pattern and with no *a priori* model shape. Each species by region combination was modelled using two temporal patterns representing the long term and the seasonal trend. For the seasonal predictor, each month m was given a value between 1 and 12 (Jan = 1, Feb = 2...) and repeated for each of the 51 years (1958-2008). The long term trend predictor t used values of between 1 and 612 (51 years x 12 months). GAMs require a method for representing the smooth functions and deciding how smooth they should be. The smooth functions were represented by thin plate regression splines because these have the advantages of being computationally stable, avoiding the problem of knot placement and being suitable for any number of predictor variables (Wood, 2006a). Once the spline was set, estimations of the model's smoothness were solved by penalized iteratively re-weighted least squares (P-IRLS) and the smoothing parameters were estimated using cross validation or related criteria (Wood, 2006b). Analyses used the *gam* procedure within the *mgcv* package developed by Wood (2004) for the R statistical language (R Development Core Team, 2008). The smoothing parameter estimation was carried out by a minimization of the Unbiased Risk Estimator (UBRE), which can be viewed as an approximation to an Akaike's information criterion (AIC), for many GAMs (Craven and Wahba, 1979). The GAM produces fitted values of the response variable at each sampling period (m, t) using a logit link function g .

Two alternative GAM models were compared for each time series. Equation (2) describes constant seasonality over time. In contrast, equation (3) estimates the interaction between month of year and month since start of the time series so that changes in seasonality are described.

$$\text{Model 1: } g(P_{r,t}) = Y + f_1(m_i) + f_2(t_i) + \varepsilon_i \quad (2)$$

$$\text{Model 2: } g(P_{r,t}) = Y + f(m_i, t_i) + \varepsilon_i \quad (3)$$

Where $P_{r,t}$ is the monthly probability distribution for zooplankton abundance classes in the time series and f are smooth functions of the covariates m and t . Y is the model intercept and ε_i the error term.

The negative binomial (NB) distribution was used to address the issue of over dispersion in the data (Beare and McKenzie, 1999). The NB distribution has two free parameters such that the mean and variance are independent. The dispersion parameter k was found using “outer iteration” during model selection and values of k yielding the lowest UBRE/AIC value were selected for each model (Zuur et al., 2009). The optimum model (interactive or main effects only with respect to month and long term trend) was selected based on the lowest UBRE/AIC score as well as the amount of deviance explained according to a pseudo F statistic for each model. Regression fits were examined using plots of residuals against fitted values. These confirmed that a negative binomial error model was appropriate, with no systematic lack of fit.

2.5 Phenology estimates

Changes in phenology are implied when there is a significant month by time interaction. The centre-of-gravity date for seasonal zooplankton abundance was used as a measure of the timing of the seasonal peak (Edwards and Richardson, 2004). The centre-of-gravity (also known as the central tendency) T , is sensitive to monthly changes in abundance and can be viewed as a measure of the phenological change in the species annual cycle over time. T is estimated in decimal month units as:

$$T = \frac{\sum_{m=1}^{12} m \cdot x_m}{\sum_{m=1}^{12} x_m} \quad (4)$$

Where x_m is the mean for month m (Jan=1, Feb=2...Dec=12.). Where the annual abundance pattern in a year is bimodal (typically a spring and autumn peak), the centre of gravity approach can be misleading. The annual cycle for each species in a particular region was classified as unimodal or bimodal by examination of abundance fluctuations. A species was considered bimodal if, after the initial spring bloom, abundances clearly declined before a secondary peak in autumn. The central tendency for bimodal years was calculated for the first six months and the last six months separately whereas for unimodal years the central tendency was calculated over the whole twelve months (Richardson et al., 2006).

2.7 Temperature data

Changes in sea surface temperature (SST) represent a strong environmental proxy for measuring climate related changes as this variable affects zooplankton at both the macro-ecological and the physiological level; this variable is also well-represented within the sample area. SST data came from the HadISST1 dataset, provided by the Hadley Centre for Climate Prediction and Research, Meteorological Office, London, UK (Rayner et al., 2003). These were mean monthly values of SST on a 1 x 1 degree latitude-longitude grid between 1958 and 2008. SSTs were standardized to remove the average seasonal signal in each region, leaving anomalies that indicate months warmer or cooler than the overall time series mean. Each monthly temperature was subtracted from the overall time series mean for the same month and divided by its respective standard deviation value.

2.8 Comparisons among regions

Following the *chl-a* based clustering, the long term SST pattern was compared among regions. The long term trend in SST was estimated from the slope of a linear regression of standardized SST against year. Variations in the link between SST and the dominant modes for the overall study area Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP), and the North Atlantic Oscillation (NAO) index; Cannaby and Husrevoglu, 2009) were examined using best fit regressions. Teleconnection time series were obtained from www.cpc.noaa.gov for the EAP, with winter NAO values from www.cru.uea.ac.uk/~timo/datapages/naoi.htm and AMO values from www.-esrl.-noaa.-gov/-psd/-data/-climateindices/-list/. The similarities between different regional SST time series were visualized using PCA.

Variations of the influence of SST on phenology and average annual abundance were estimated using Pearson correlations. Serial autocorrelation in time series can cause spurious correlations as non-independence of nearby points in time reduces the effective degrees of freedom for tests. There are a number of ways of dealing with this issue, including techniques for lowering the effective degrees of freedom based on the degree of autocorrelation (Pyper and Peterman, 1998). The focus of interregional comparisons presented here was on the relative magnitude of correlation coefficients rather than judgements over the threshold level of significance. In this respect the calculated correlation coefficients are unbiased estimates of the association between variables, but the precision of the estimate is lower than would be the case if no autocorrelation existed.

3. Results

3.1 Defining the ecosystem regions

The analysis of variance explained by K-means clustering suggested 14 clusters as an appropriate level of aggregation for chlorophyll time series (Fig. 1). Change in r^2 values beyond this point were below the preset threshold. 57.5 % of the variance in the SeaWiFS *chl-a* was explained by a 14 cluster partition. When only those clusters > 2000 pixels were counted, the maximum number of large clusters also seemed to be defined at a 14 cluster partition. Bootstrap analysis of the cluster dendrogram identified one instance of similarity at the 95% significance level for two neighbouring clusters located within the North East of the study region. These clusters were subsequently merged into the RT region (see below). Three further regions contained fewer CPR surveys than the preset acceptance level and were not considered further. These clusters were in oceanic waters in the northwest of the study region and in a coastal strip which included the Clyde, Liverpool Bay and the Bristol Channel.

Following the threshold similarity test and removal of data-poor clusters, a total of ten clusters remained, hereafter to be called regions (Table 1). Given that the K-means clustering does not use information on location, the regions were well-resolved in space (Fig. 2). The regional boundaries showed a close affinity with shelf sea stratification and seasonal frontal boundary formation. The Celtic Sea regions (CM and CS) represent the transitional waters from the Atlantic at the shelf margins, to the coastal waters of the Irish Sea. CS stratifies between May-November each year when the increase in temperature and weak tidal currents prevent the generation of enough turbulent energy to maintain vertical mixing (Simpson and Hunter, 1974; Hill et al., 2008). The region CM marks the position of the Ushant Front which exists off the north-western coast of France (Le Boyer, 2009). The stratification in this area is weaker and it is usually seen as a transitional water body (Pingree et al., 1982). Both CS and CM extend northward following the contours along the western coast of Ireland, which is in agreement with recent *in-situ* observations of the currents and water column structure that detected strong clockwise baroclinic flows in the Celtic Sea (Brown et al., 2003). The continental shelf edge is marked by a southern shelf edge region (SE) and a northern Malin Shelf region (MS) which lies between the Rockall trough and Scottish coast. The positioning of the SE region is consistent with the known region of cooler water that exists over the shelf break between April and October (Pingree and Mardell, 1981; Joint et al., 2001). The off-shelf waters form regions broadly consistent with latitudinal bands.

3.2 Interregional variability in SST

All the regions showed a warming trend over the time period considered. Warming was greatest in the Celtic Sea (CS) and Celtic mixed (CM) regions of shelf, at the Shelf Edge and in the more southern and central oceanic regions (WT, ABS and ABN; Table 1). The influence of modes of variability affecting SST varied among regions. The AMO, itself a temperature signal, was present in all areas. The influence of climate indices varied, with the NAO a positive influence on SST in southern shelf and ocean regions and Irish Sea, but absent or with a negative association in central and northern off-shelf regions and Malin Shelf (MS). The East Atlantic Pattern (EAP) was only selected as part of the best fit model in the Rockall Trough (RT) region.

Ordination of the regions by PCA of the SST time series emphasizes the similarities in temperature among adjacent regions (Fig. 3). For example, the Irish Sea is placed in the ordination between the Malin Shelf and Celtic Sea mixed and stratified regions.

3.3 Interregional variability in chl-*a*

The central tendency (T) for spatially averaged *chl-a* in each region was calculated using values from March-October for each year. Off-shelf there was a general northward progression in the timing of the seasonal peak. The earliest peak occurred in the Warm Temperate region (mean T of 5.76) with a gradual progression towards later seasonal peaks in the more northward regions. There was a difference of nearly a month between the most southern region, WT, and the two northern regions RT and RB, which had mean T of 6.61 and 6.64 months respectively. On-shelf there was less of a difference between the earliest and latest seasonal peak. The earliest T (SE) was 6.21 months while the latest (6.49 months) occurred in the Celtic Mixed (CM) region. Changes in chlorophyll phenology are not discussed further here due to the much shorter time series of satellite data in comparison to CPR counts.

3.4 Interregional variability in copepod phenology and average annual abundance

The phenology of copepod abundances generally changed over time, as identified by improvements in fit when comparing the interaction between covariates model (monthly and long-term predictors) with the non interactive model. *Calanus* phenology changed with year in all regions except for *Calanus* I-IV juveniles in CM. By contrast, the improvement in

model fit from including an interaction was negligible for the *Paracalanus-Pseudocalanus* group in five of the nine regions. In the majority of cases, the seasonal patterns were unimodal. When the same time series contained bimodal and unimodal patterns in separate years, only the unimodal pattern was analysed in correlations. One region (ABN) was excluded from further analysis because, although the region contained >3000 CPR samples, gaps in the time series made it difficult to define an acceptable model fit.

The measure of phenology, T , varied within and between regions over time. For *C. helgolandicus*, the mean T was 6.4 months with an average range within region of 1.2 months. *C. finmarchicus* generally had the earliest centres of gravity (5.7 months), and their average range was slightly larger (mean range 1.6 months). The mean T for the *Calanus* I-IV category was between the values for *C. helgolandicus* and *C. finmarchicus* at 6.0 months, with a range of 1 month within time series. The *Paracalanus-Pseudocalanus* group had the latest mean T at 6.85; with a mean range of 1.3 months within the time series where a month x long term interaction was detected. Phenology of *Calanus* spp. among regions was correlated (minimum by region correlation between *C. finmarchicus*, *C. helgolandicus* and *Calanus* I-IV was 0.884, $p < 0.01$). The earliest mean central tendency tended to occur in the Warm Temperate or Abyssal South region (mean across all *Calanus* groups of 4.9 months). The latest regional T occurred in the Irish Sea (at a mean of 7.1 months across all three *Calanus* groups).

In the majority of cases, increases in regional SST anomaly were negatively associated with the timing of the seasonal abundance peak (Fig. 4, time series shown in Fig 5). This implies an earlier zooplankton “bloom” in warmer years. There were a few exceptions where this negative relationship with SST failed to hold. For *C. helgolandicus*, the region WT showed no correlation with central tendency and SST. For *C. finmarchicus*, the regions ABS and IS showed a negligible and positive respectively correlation with SST while for *Calanus* I-IV, the region MS showed a slight positive correlation between central tendency and SST. The *Paracalanus-Pseudocalanus* group in the Irish Sea also departed from the general pattern of negative associations between the timing of the seasonal peak and mean SST.

The annual average abundance of *C. helgolandicus* tended to be higher in warm years, with a positive correlation between abundance and SST in all areas except IS and SE. The strongest positive associations with temperature were in the northern regions of RT and MS. The pattern of mostly positive associations between annual copepod abundance and annual SST anomaly was reversed in the majority of cases in *C. finmarchicus*, *Calanus* I-IV and the

Paracalanus-Pseudocalanus group. There appeared to be little clustering of similar dynamics in adjacent regions except for *Paracalanus-Pseudocalanus*, where the patterns of positive abundance-SST correlations in the Rockall Trough (RT) and Malin Shelf (MS) regions contrasted with negative relationships in other areas

Typically the annual abundances of *Calanus* spp. (adults and juveniles) were quite variable over time (Figs 6, 7 and 8). Many regions had strong annual or multiyear peaks where abundances increased by up to an order of magnitude over background levels. Correlations between regions were relatively weak, meaning that the peaks were often not synchronous across the study area. The average Pearson's correlation among *C. finmarchicus* annual abundance time series was 0.14 SEM 0.051, with a similar mean for *C. helgolandicus* (0.16 SEM 0.039). With *Calanus* I-IV the mean inter time series correlation was slightly stronger, but still relatively weak (0.23 SEM 0.031). In contrast to the pattern with *Calanus*, the *Paracalanus-Pseudocalanus* group tended to decline in all areas (Fig. 9), resulting in a relatively high mean correlation among time series (0.47 SEM 0.061).

Changes in phenology could potentially affect annual abundance through mismatches among predator and prey species. In order to test this potential interaction, the association between central tendency month and annual average abundance was examined. A positive association suggests that abundances increase when the peak abundance occurs later in the year.

Conversely, a negative association suggests that a late bloom will lead to a lower annual average abundance. Many of the associations between time of peak and size of peak were weak. The clearest pattern was for *C. finmarchicus* which had a strong positive correlation in the northern region (MS) and strong negative correlations in the southern regions (IS and WT). *C. helgolandicus* had negative correlations in the two most northerly regions (RT, MS) in addition to shelf regions (CM, CS). The Irish Sea had the strongest positive association between peak timing and abundance for *Calanus* I-IV. In the regions where the phenology of the *Paracalanus-Pseudocalanus* group changed, the Irish Sea had a relatively strong tendency for late blooms to have lower annual abundances. In the northern off-shelf areas (ABS, RB and RT), late blooms tended to be associated with higher abundances.

4. Discussion

It was possible to use proxies for chlorophyll a to partition the study area into regions that were consistent with oceanographic structures related to currents and topographically-generated features. The regions generally showed different trends in phenology and abundance for *C. finmarchicus*, *C. helgolandicus*, *Calanus* I-IV and the *Paracalanus*-*Pseudocalanus* groups. These results have implications for the scale at which environmental indicators should be gathered for management decisions. Taking averages over larger scales than the regions described here runs the risk of obscuring patterns and changes in them. Furthermore, changes in abundance and phenology over time did not track temperature in the same way in different regions within or among species. This implies that local conditions are important and that inter-regional variability is not simply a reflection of environmental forcing correlated with SST.

No region was a clear outlier across all taxonomic groups and associations examined. The differences among regions seem likely to reflect the way in which the hydrography of each particular region alters climatic forcing, individual species' responses to the forcing and variations in advection of individuals to and from regions. An example of an advective influence on populations may be evident in the Warm Temperate (WT) region. While warmer years led to an earlier month of central tendency for *Calanus* spp. in most regions, this was not the case for *C. helgolandicus* in the WT region. In contrast to other regions, *C. finmarchicus*' average annual abundance had a weak positive relationship to SST in WT. There is a relatively high level of population connectivity for *C. finmarchicus* across the North Atlantic (Provan et al., 2009) suggesting that the patterns may not be due to locally evolved responses. Population connectivity also stresses the potential role of advection. Advective processes might have led to a decoupling of the link between seasonal peak and SST seen in other areas. Some support for this idea is provided by the work of Hatun et al. (2005). According to these authors, the NE Atlantic subpolar gyre was at its strongest and its boundary was displaced to the east in the late 1980s. Strong eastward protrusions of water masses are thought to inhibit the northward flow of sub-tropical water along the shelf-break, allowing sub-arctic species to penetrate farther east. This late 1980s period coincides with peaks of *C. finmarchicus*, the northern species, in the ABS and WT regions and to a lesser extent in the RB region.

Further influences on the advection of copepods into different regions may be linked to the NAO. During the 1970s and since 2000, water mass movements at intermediate depths may have acted to delay the arrival of *C. finmarchicus* from overwintering areas farther north in the Atlantic to the WT region. The supply of individuals is likely to be associated with movement of the water masses around 600 m, the proposed diapause depth for *C. finmarchicus* in the northeast Atlantic (Spiers et al., 2005). Water moving south at this depth from the main overwintering areas is likely to be Subarctic Intermediate Water (SAIW), and the influence of this water mass may be reduced in comparison to warmer saltier subtropical waters at times of lower NAO index. A comparison of data from cruises in 1988, 1993, 1998 and 2003 indicated the strongest intrusion of SAIW in 1993 following a switch from relatively low to higher NAO index values (Johnson et al., 2007); this pattern coincides with the WT *C. finmarchicus* peak identified in the current study. It is worth noting that this was a region-specific response to the NAO. Correlations between the NAO, AMO, EAP and the zooplankton response variables of *T* and average annual abundance were as divergent as the associations between these variables and SST (NAO, AMO and EAP correlations not presented here for brevity).

The two *Calanus* species act as a complementary warm affinity-cold affinity pair (Planque and Fromentin, 1996, Helaouët and Beaugrand, 2007). *C. finmarchicus*' average annual abundance declined in association with warmer SST in all regions except WT (with no relationship in RT). In contrast *C. helgolandicus*, the more southern species, became more abundant in the CM, CS, WT, ABS, RB, RT and MS regions in warmer SST years. When comparing the association between timing and annual abundance in the northern regions of RT and MS, *C. finmarchicus* tended to be more abundant when the central tendency month was later in the year. In comparison, later development of *C. helgolandicus* in the same regions was associated with lower average abundances. The differences in abundance between species may reflect the action of match-mismatch processes with the spring bloom, where the different *Calanus* species are responding to different phenological cues.

The patterns of the *Paracalanus-Pseudocalanus* group are similar to results seen elsewhere. There has been a general decline in average annual abundance, particularly in warmer shelf regions (Alheit et al., 2005; Eloire et al., 2009). The pattern of correlations between abundance and SST (and to a lesser extent phenology and SST) support the characterisation of the *Paracalanus-Pseudocalanus* as a temperate waters group that is moving north. Hence in

the northern part of the species ranges (excluding MS), warmer temperatures lead to higher annual abundances, while even warmer temperatures in the southern part of the study area seem to be associated with suboptimal conditions. The absence of a clear phenological signal in many regions may reflect the multispecies nature of the *Paracalanus-Pseudocalanus*, such that individual species' responses are masked by other members of the group.

While the on-shelf and shelf edge regions identified reflect oceanographic forcing by the tidal mixing front and the processes at the shelf break (Pingree et al., 1986; Joint et al., 2001), the south-north banding of off-shelf regions may reflect the progression of the spring bloom in the northeast Atlantic. The onset of the northeast Atlantic spring bloom begins in the south and moves northward at a rate of 20 km day⁻¹ (Siegel et al., 2002). Analysis of chlorophyll central tendency showed that the timing of the seasonal peak occurred progressively later in more northern regions. The difference between the most southern oceanic region, WT, and the northern RT region is 0.85 months. Over 0.85 months the distance travelled by the spring bloom would be approximately 500km, which corresponds to the distance between the WT and RT regions. The size of each region may be governed by the relationship between the temporal resolution of monthly averages and the speed in which the bloom travels northward. The variation between oceanic regions in zooplankton phenology and abundance trends suggests that some subdivision of the off-shelf regions is needed to capture details of the spatial variation in zooplankton populations.

The analyses of change in CPR data from the different regions indicate that there are limits to generality: regions do not track variables in the same way and trends in different regions were not necessarily correlated. As recognized by Leterme et al. (2005) analyses at scales smaller than the ocean basin scale are needed to understand the processes involved in long term changes in plankton communities. Picking apart the mechanisms that cause regions to vary will involve an understanding of how the regional conditions affect bloom formation and the interaction of this process with advective processes. This detailed drill-down into the dynamics of each region lies outside the scope of the current paper. The idiosyncrasies of particular regions may also interact with processes higher up the food chain. The study area overlaps the region considered by the North Western Waters Regional Advisory Council (NWWRAC), a stakeholder body convened to bring information and advice to the EC with respect to managing fisheries under the Common Fisheries Policy. It may be useful to

examine changes in fish stocks within the regions defined or in to examine cases where migration causes stocks to be influenced by zooplankton trends in different areas.

At a time when management policy is shifting from a sectoral-based to an ecosystem-based management strategy, information on a) how to divide the seas into meaningful ecosystem regions and b) the state of the biological systems within regions, has become increasingly important. The analyses presented in this manuscript demonstrate that it is possible to derive meaningful regions using an extension of Longhurst's (1998) approach. The regions were not simply replicates of each other containing slightly different environmental conditions. There was evidence that the underlying forcings work differently in different regions, such that responses to SST and the interactions between phenology and annual abundance were not constant. The regions defined here should be thought of as complementary to the larger management regions such as the EU Celtic Seas eco-region. While this study has focussed on the trophically important *Calanus* and *Paracalanus-Pseudocalanus* group (Heath and Lough, 2007), the relatively large sizes of the regions are likely to facilitate work to broaden the taxonomic basis for understanding change in planktonic communities (Ji et al., 2010).

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Table 1. Area of ecosystem regions and the details of associated CPR samples. Sea surface trends in each area show details of the corrected Akaike information criterion (AIC) best fit regression using Atlantic Multidecadal Oscillation (AMO), the East Atlantic Pattern (EAP), and the North Atlantic Oscillation (NAO) as predictors, including the overall regression r^2 . Also shown is the linear trend in standardized temperature anomaly over time, ΔT . Regions are ordered from the innermost shelf (Irish Sea) out across the shelf into oceanic waters moving in a counter clockwise direction.

Region	Abbrev.	Area	CPR. samples	CPR years	SST best fit predictors	r^2 (%)	ΔT
Irish Sea	IS	75,262km ²	3888	1970-2008	+AMO, +NAO	41	0.0096
Celtic Mixed	CM	170,667km ²	8191	1958-2008	+AMO, +NAO	48	0.0133
Celtic Sea (Stratified)	CS	180,306km ²	6502	1958-2008	+AMO, +NAO	41	0.0112
Shelf Edge	SE	92,745km ²	7205	1958-2008	+AMO, +NAO	53	0.0123
Warm Temperate	WT	568,994km ²	6847	1958-2008	+AMO, +NAO	65	0.0160
Abyssal South	ABS	751,643km ²	5687	1958-2008	+AMO	56	0.0119
Abyssal North	ABN	691,983km ²	3788	1958-1986	+AMO	52	0.0120
Rockall Bank	RB	348,183km ²	3028	1958-2008	+AMO, -NAO	56	0.0049
Rockall Trough	RT	473,202km ²	5718	1958-2008	+AMO, -EAP	52	0.0037
Malin Shelf	MS	294,759km ²	3241	1958-2008	+AMO	32	0.0036

Figure legends

Fig. 1. Residual variance (r^2) following K-means clustering of *chl-a* data with different numbers of clusters (K). r^2 values are shown as a solid line with mean number of pixels cluster⁻¹ as a dashed line. The vertical line represents the optimum selection of K based on asymptote detection. The inset figure shows the number of clusters >2000 pixels at each iteration of K. An optimum number of large clusters is indicated in the inset at K = 14.

Fig. 2. Locations of the ten clusters defined as ecosystem regions by K-means partitioning of satellite-derived *chl-a* data. The locations of CPR samples throughout the study area are marked by black dots. Red contours indicate the underlying bathymetry at the 200, 400, 800, 1600 and 3200 m depths. Abbreviations and attributes that relate to each region are described in Table 1.

Fig. 3. Principal Component Analysis ordination of regions by SST. Regions close to each other in the ordination have a similar pattern of variability in SST over time. 64 % of the variation in SST is associated with the first two principle components.

Fig. 4. Correlations between the timing of seasonal abundance peak (T) and standardized SST anomaly (first row), annual average abundance and standardized SST anomaly (second row) and annual average abundance and timing (last row) for each taxon. Gaps in the charts for the correlation between T and SST are where model fitting did not indicate an interaction between month and year.

Fig. 5. The central tendency (T) in decimal months, for *Calanus helgolandicus*, *C. finmarchicus* and the *Paracalanus-Pseudocalanus* group (black line) and local SST anomalies (red line) for each of the nine ecosystem regions. Where zooplankton abundances varied between bimodal and unimodal peaks, only the bimodal pattern is shown. 'No Change' is indicated where there was no interaction between month and year, implying that central tendency (T) did not change over the time series. Note: SST anomalies are inverted on the y axis. Abbreviations of each ecosystem regions are given in full in Table 1.

Fig. 6. Mean accepted numbers (3 m^{-3}) for *Calanus helgolandicus* in the nine ecosystem regions (three year running mean).

Fig. 7. Mean accepted numbers (3 m^{-3}) for *Calanus finmarchicus* in the nine ecosystem regions (three year running mean).

Fig. 8. Mean accepted numbers (3 m^{-3}) for the *Calanus stage* I-IV in the nine ecosystem regions (three year running mean).

Fig. 9. Mean accepted numbers (3 m^{-3}) for the *Paracalanus-Pseudocalanus* group in the nine ecosystem regions (three year running mean).

Fig 1.

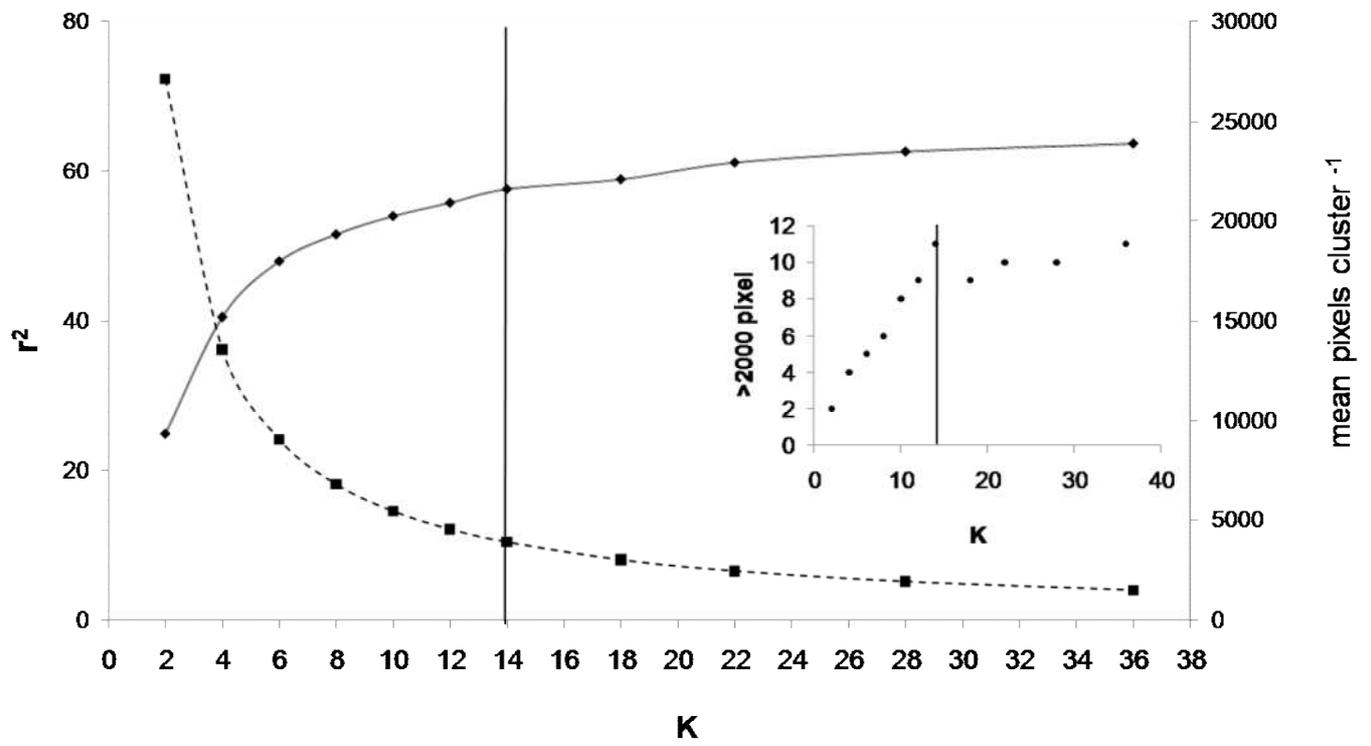


Fig 2.

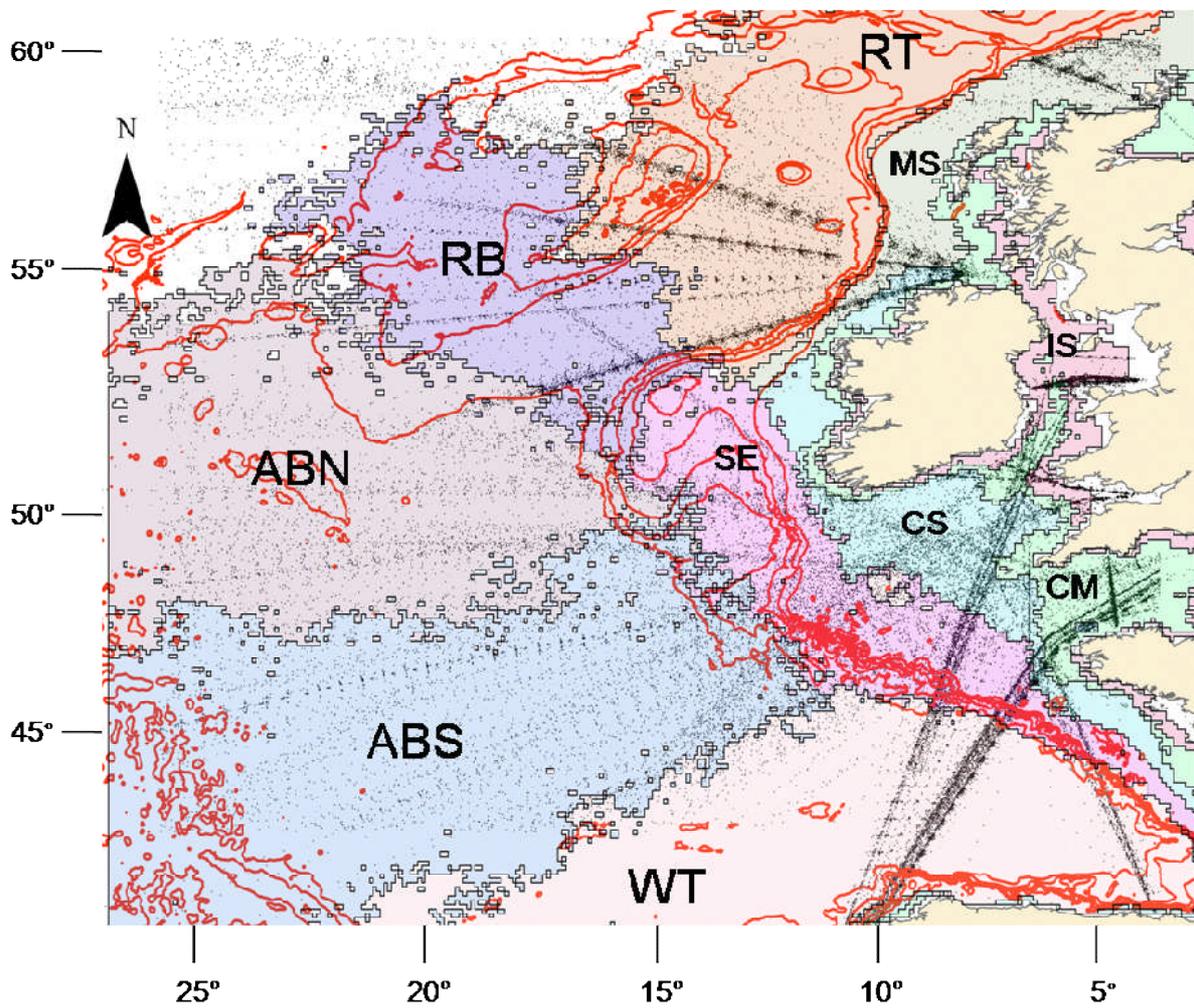


Fig 3.

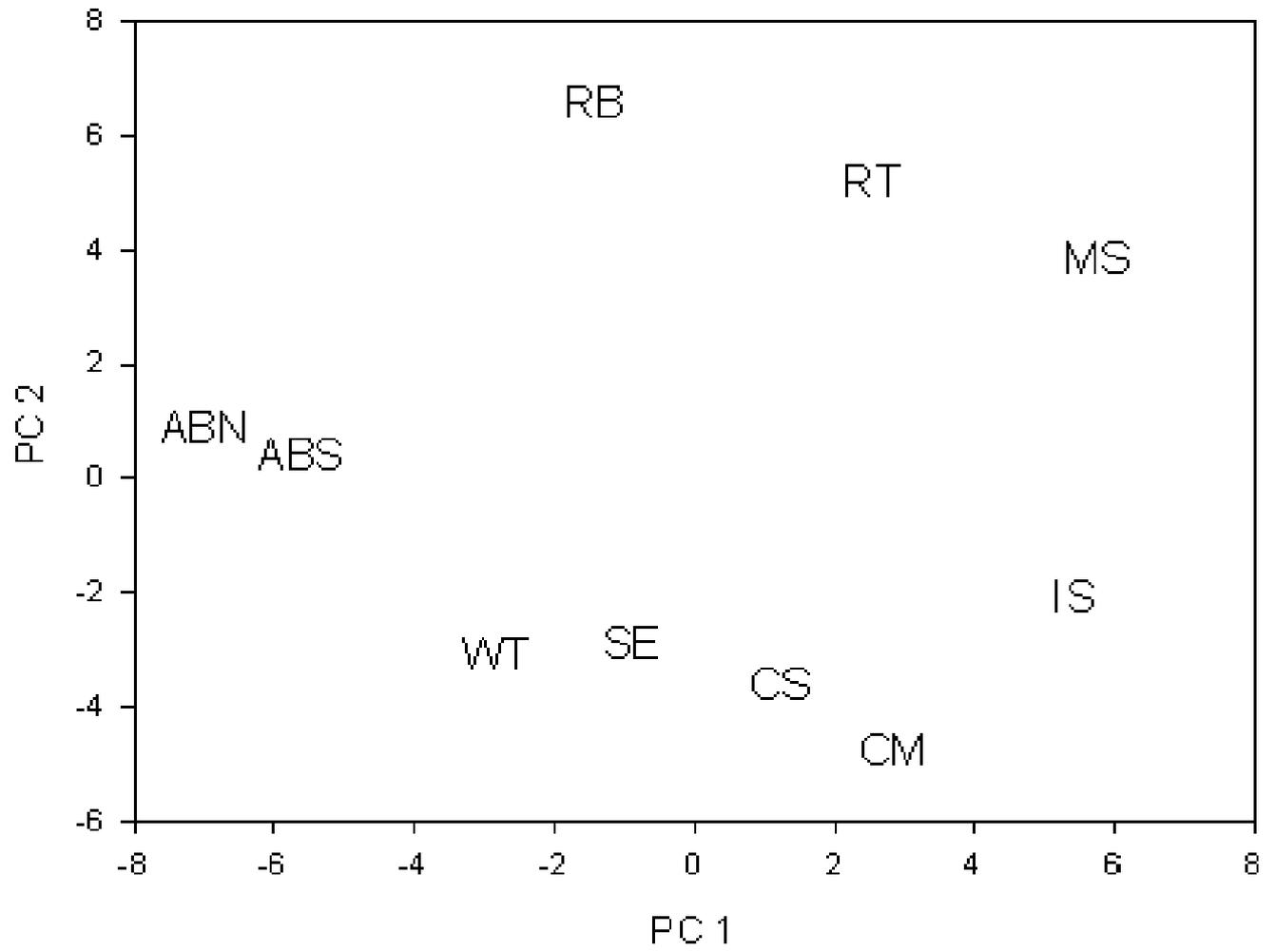


Fig 4.

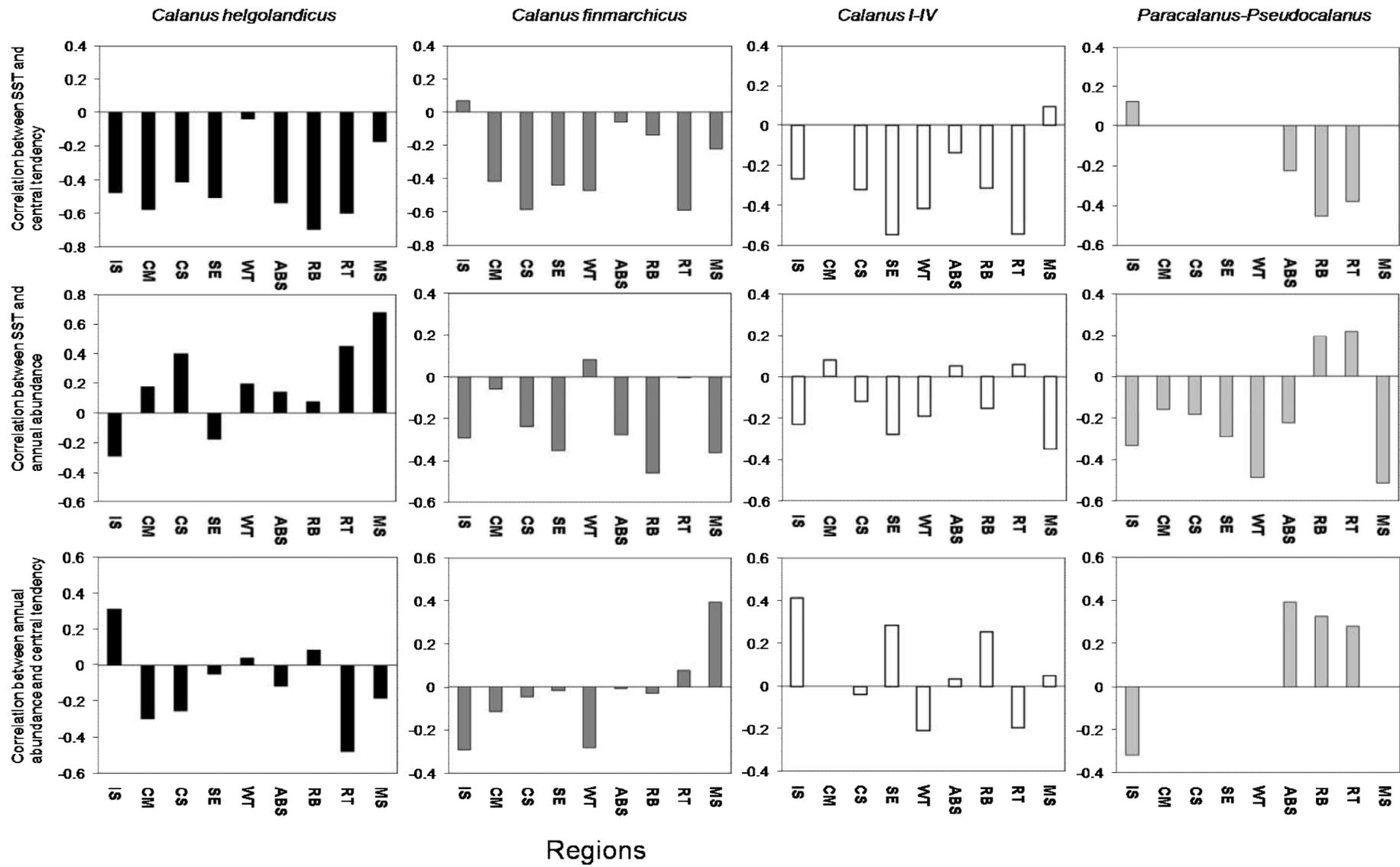


Fig 5.

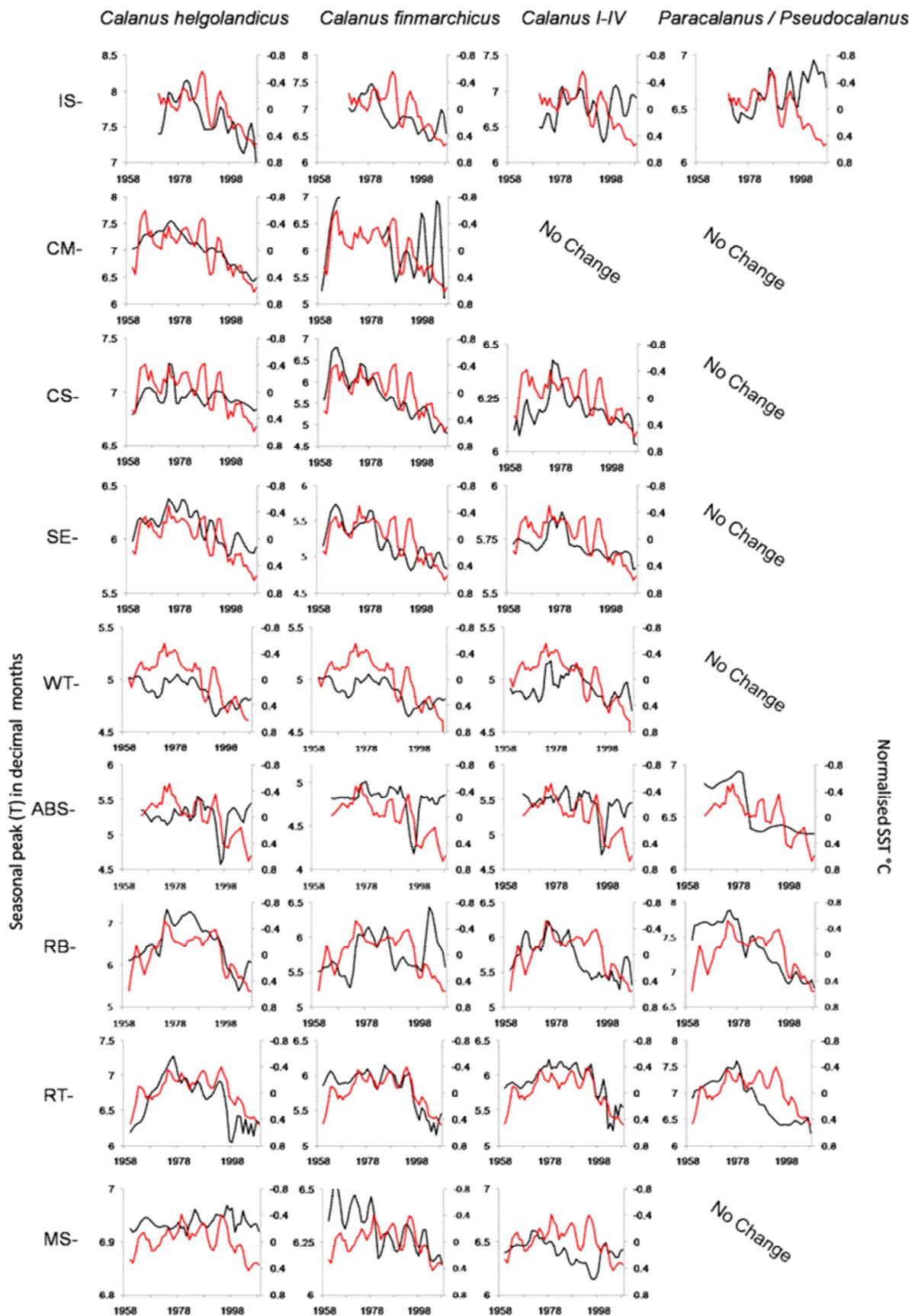


Fig 6.

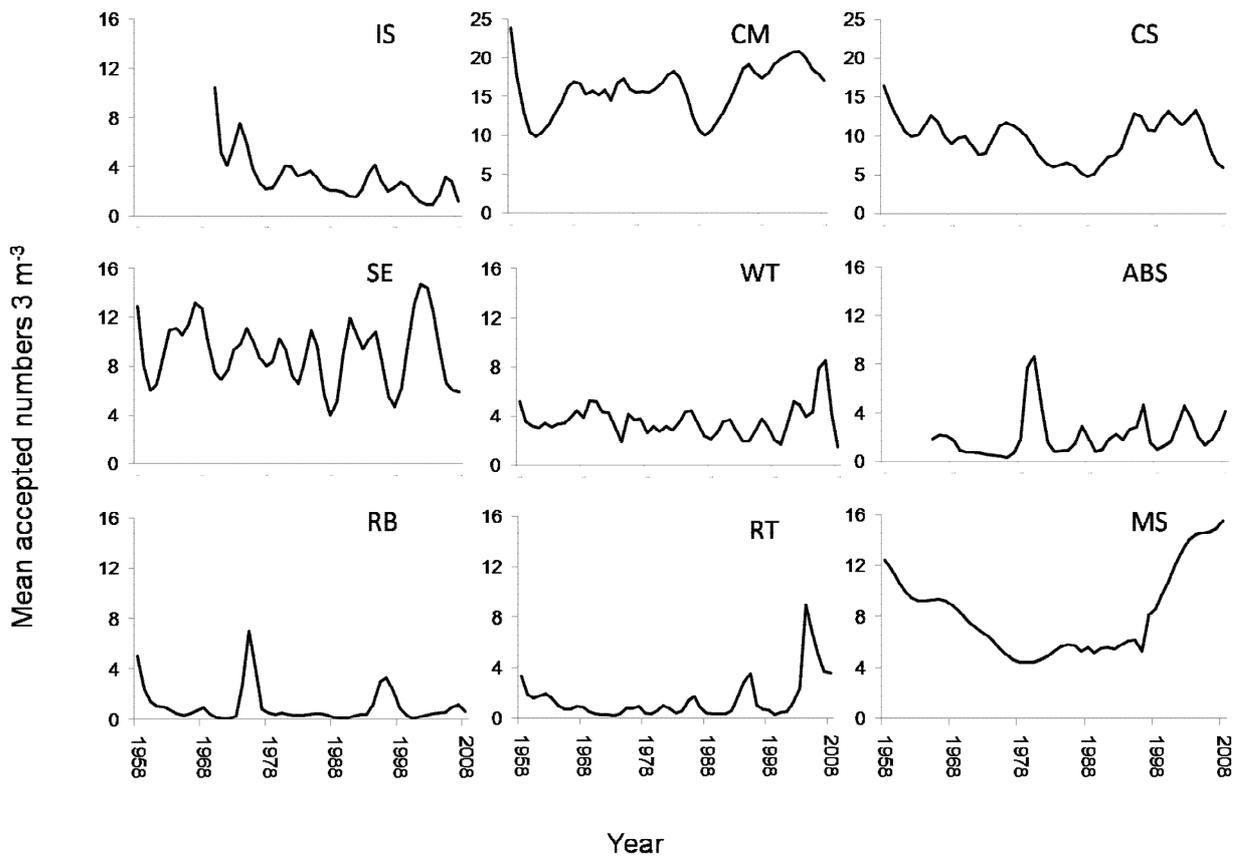


Fig 7.

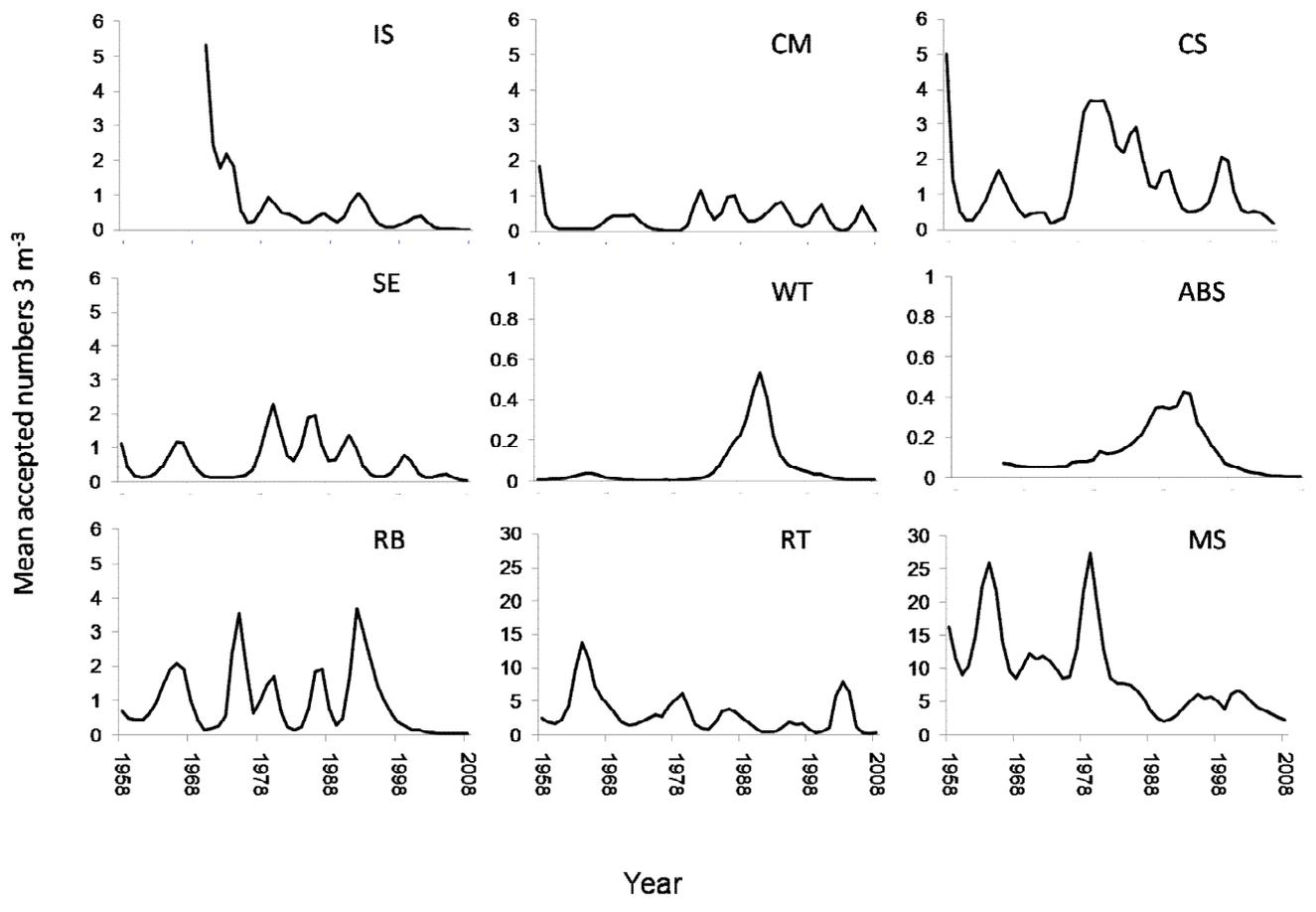


Fig 8.

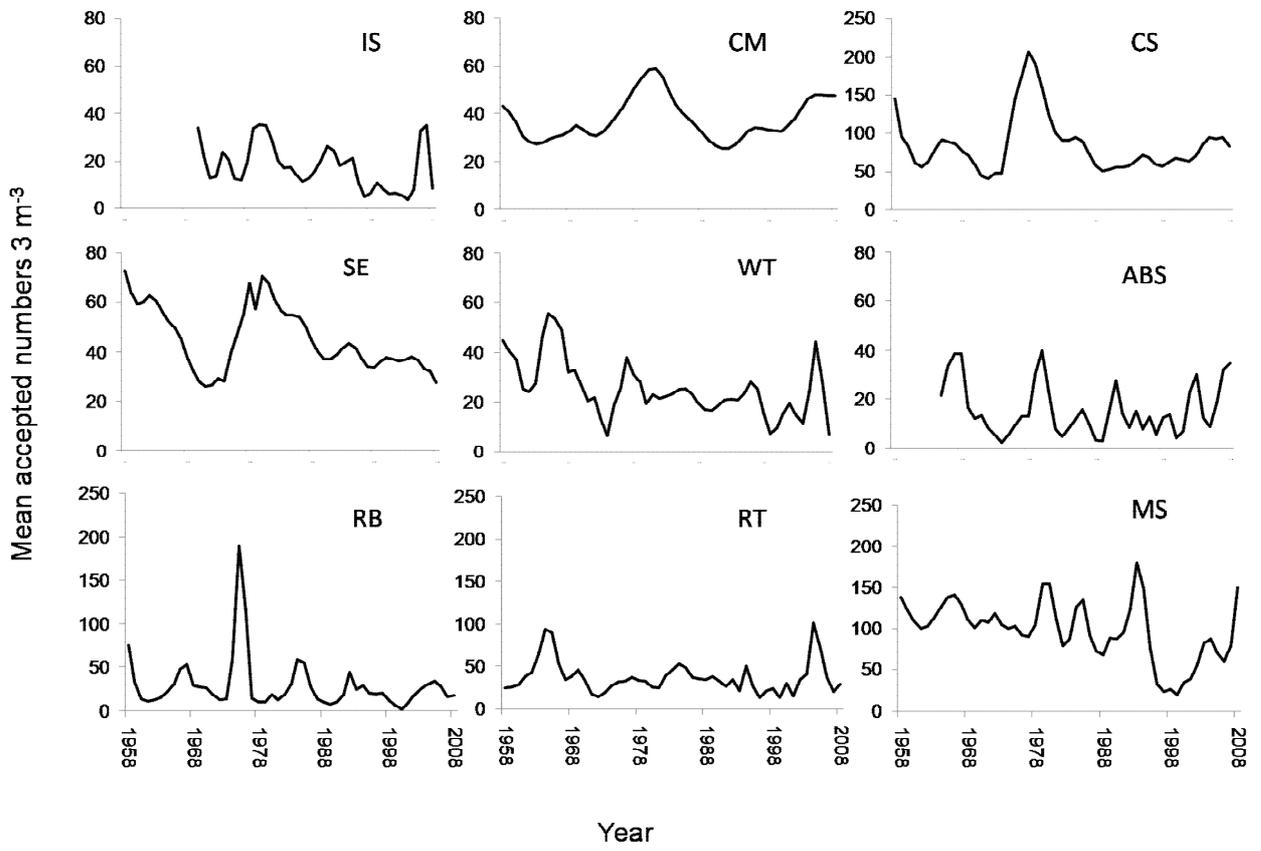
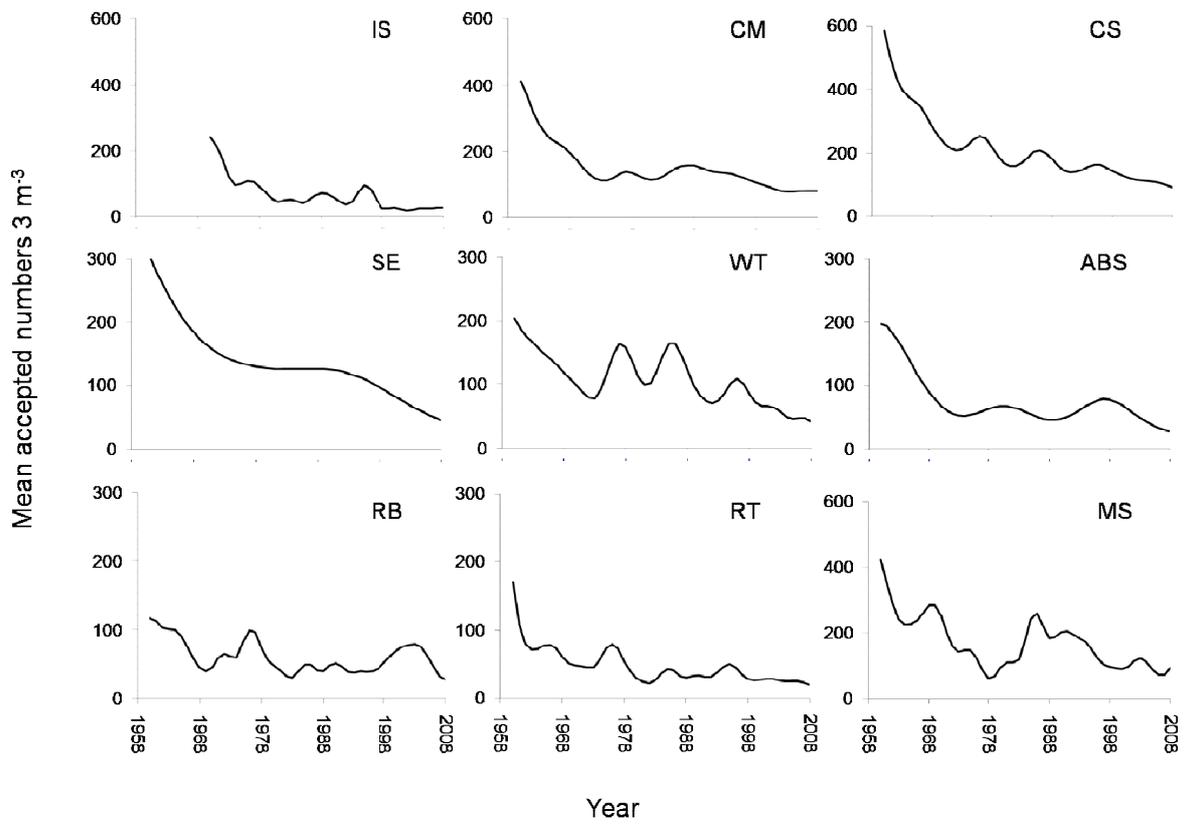


Fig 9.



Chapter 3

Trophodynamics and stability of regional scale ecosystems in the Northeast Atlantic

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Abstract

This study addresses the long term stability of three trophic groupings in the Northeast Atlantic at regional scales. The most abundant taxa representing phytoplankton, herbivorous copepods and carnivorous zooplankton were examined from the Continuous Plankton Recorder (CPR) database. Multivariate control charts using a Bray-Curtis similarity metric were used to assess whether fluctuations within trophic groupings were within or beyond expected variability. Two evaluation periods were examined: annual changes between 1960 and 1999 (2000-2009 baseline) and recent changes between 2000 and 2009 (1960-1999 baseline). The trends over time in abundance/biomass of trophic levels were region-specific, especially in carnivorous copepods, where abundance did not mirror trends in the overall study area. The stability of phytoplankton was within expected limits, although not in 2008-2009. Higher trophic levels were less stable, perhaps reflecting the added complexity of interactions governing their abundance. In addition, some regions were consistently less stable than others. Correlations in stability between adjacent trophic levels were positive at LME scale but generally non-significant at regional scales. The study suggests that certain regions may be particularly vulnerable to periods of instability in community structure. The benefits of using the control chart method rather than other multivariate measures of plankton dynamics are discussed.

Keywords: Regional ecosystems; plankton community structure; trophic indicators; plankton abundance; Northeast Atlantic

Introduction

There has been a global mean increase of $\sim 0.67^{\circ}\text{C}$ in sea surface temperatures (SSTs) over the last century (Trenberth et al., 2007); however recent changes in SST have been unprecedented, with larger increases over the past 10-15 years compared with the previous two millennia (Phillipart et al., 2011). The pattern of rising SST has been unevenly distributed in global oceans. For example, Belkin (2009) demonstrated that SSTs are increasing in all but two of the world's Large Marine Ecosystems (LMEs, www.lme.noaa.gov), but 10 of the 18 fastest warming LME's (i.e. those that have increased by $>0.60^{\circ}\text{C}$) are within the N.E. Atlantic. It is generally agreed that there have been dramatic changes in the abundance and biogeography of phytoplankton and zooplankton within the LMEs of the N.E. Atlantic (e.g. Edwards et al., 2001; Beaugrand, 2003) and the importance of global warming as a forcing agent is an area of intense research activity (e.g. Beaugrand et al., 2010). But the relative importance of environmental, climatic and biological processes affecting plankton assemblages depends on the scale being examined, so there is a need for a multi-scale approach to quantifying natural variability in pelagic ecosystems (Edwards et al., 2010).

There have been significant shifts in zooplankton dominance at large spatial scales, with the replacement of some species or species assemblages by others (Beaugrand et al., 2002; Reid et al., 2003), while phytoplankton have been shown to be increasing across the N. Atlantic (Leterme et al., 2005) and the North Sea (Edwards et al., 2001; McQuatters-Gallop et al., 2007). At the ocean basin scale (1000-10000 km) the strongest effects on phytoplankton (Barton et al., 2003; Henson et al., 2009) and zooplankton (Planque and Fromentin, 1996; Fromentin and Planque, 1996) appear to be associated with large scale multi decadal cycles in climate variation and SST. However, at finer scales, these cycles can be superseded by regional processes such as predator-prey interactions (Levin, 1992) and smaller scale environmental and hydrographic factors such as wind stress (Beaugrand, 2004), mixed layer depth (Henson et al., 2009; Reygandeau and Beaugrand, 2010) and bathymetry (Helaouët and Beaugrand, 2009). Phenology has generally been shown to change, with earlier abundance peaks associated with increases in SST in almost all regions (Edwards and Richardson, 2004; McGinty et al., 2011). However, longer term population dynamics over years and decades display strong regional differences for key indicator species such as copepods in the genus *Calanus* (Beare et al., 2002; McGinty et al., 2011).

Calanus copepods are important trophic components of ecosystems in the N.E. Atlantic and an obvious question to ask is whether regional-scale variability observed for these species is also observed more broadly e.g. within particular trophic levels? A community approach is intended to distinguish patterns that are more widely prevalent in N. Atlantic ecosystems from changes that may be more specific to a particular species (Lynam et al., 2010). Another worthwhile examination is that of regional scale stability of trophic relationships including whether perturbations at one level have a knock-on effect up the food chain (i.e. bottom-up regulation) (see Edwards et al., 2010 and references therein). Being able to quantify such information at many scales addresses policy and management objectives including assessing the long term viability of components in the food web as outlined in the Marine Strategy Framework Directive (Anonymous, 2010).

The present study investigates regional variability and how well this reflects larger LME-scale trends in the long term trophic stability of our study area in the N.E. Atlantic. The most numerically dominant species from three trophic assemblages (phytoplankton, herbivorous copepods and carnivorous zooplankton) were examined in nine pre-defined eco-regions (McGinty et al., 2011) of the N.E. Atlantic. Multivariate control charts including a distance or similarity metric were used to assess whether fluctuations within each trophic assemblage exhibited stochastic drift i.e. were within an expected natural variability, or whether more significant shift beyond expected variability had taken place. Fluctuations were evaluated against two contrasting baseline periods: the first examined the long term annual changes between 1960 and 1999, using the decade 2000-2009 as a baseline. Since exceptional warming has taken place in the most recent decade, the exercise was repeated using 1960-1999 as a baseline, against which the years between 2000 and 2009 were evaluated. The parallel comparisons of control charts across neighbouring eco-regions combined with the broad taxonomic scope of the present study (e.g. Ji et al., 2010) can contribute to the more detailed examination of cross scale ecosystem changes that are currently lacking for zooplankton datasets (Mackas and Beaugrand, 2010).

Methods

Defining the eco-regions

The study describes changes in the NE Atlantic in an area similar in extent to the Celtic Biscay LME, but including off-shelf areas (Fig 1). The procedure for defining the eco-regions within the study area used chlorophyll *a* (*chl-a*) as a proxy for variability in primary production, facilitating the clustering of regions that have similar temporal patterns: described in McGinty et al. (2011) as a finer-scale extension of methods proposed by Longhurst (1998) for defining biogeographic ‘provinces’. Briefly, this involved using the level 3, monthly composite images of SeaWiFS *chl-a* (pixel size - 9km x 9 km) for the months of March – October, 1998-2009. A k-means clustering method was first used to cluster the *chl-a* data; thereafter a cluster dendrogram was used to aggregate clusters with >95% similarity. This process resulted in nine clusters (= eco-regions) that were spatially well-resolved (McGinty et al., 2011). The term eco-region has been used a number of times in the ecological literature, here we use it specifically to refer to the areas identified by the chlorophyll clustering technique of McGinty et al. (2011). The on-shelf eco-regions showed a close affinity with the well known boundaries of transitional water bodies in the Celtic Sea and Irish Sea, while off-shelf, the divisions appeared to be more related to the onset of the spring phytoplankton bloom which occurs later with increasing latitude (Fig. 1). Due to the sparseness of available plankton data, the eco-region ABN was not used for the current study.

Trophic assemblage selection

The plankton data from separate eco-regions were extracted from the Continuous Plankton Recorder (CPR) database. The issues in using the CPR database are well known (Beare et al., 2003) with non-random sampling being one of the most critical features of the dataset. However its coverage both spatially and temporally makes it an indispensable data source for such studies. At the scales discussed Beaugrand and Edwards (2001) recommended that at least five samples per sampling (month) unit will capture most of the variability found in a particular area. Although the CPR will not be regularly sampled through time, establishing a lower bound limit of 3000 samples (50years x 12months x 5samples) ensured that the maximum number of months in each time series will be achieved (and caused the exclusion of eco-region ABN as mentioned above).

Species recorded in the CPR were separated into three trophic level communities: phytoplankton, herbivorous copepods and carnivorous zooplankton based on a thorough literature search on species behaviour and diet (e.g. Davis, 1984; Mauchline, 1998 and references therein; Richardson et al., 2006). The selection of herbivorous zooplankton was restricted to copepod taxa for several reasons, i) these have been identified as key trophic link between phytoplankton and carnivorous zooplankton (Williams et al., 1994; Richardson and Schoeman, 2004) and ii) over 100 species of copepod taxa have been differentiated in the CPR database, of which 92.5% of taxa have been identified to species level, allowing more accurate biomass estimates to be made (Beaugrand et al., 2001).

Trophically important species will tend to be numerically abundant or dominant contributors to biomass, therefore selection of trophic indicators was based on the most abundant (in the case of carnivores) or most dominant groups in terms of biomass (phytoplankton and herbivorous copepods). Phytoplankton biomass (B_p) was calculated by multiplying the summed number of cells by cell weight (μg) obtained from the literature (Biological Atlas of the Arctic Seas, 2000). The biomass of a herbivorous copepod species ($B_{h_{i,j}}$) in a CPR sample was found using the length/wet weight relationship in equation (1), where L is the length of species i as obtained from the literature (Richardson et al., 2006) and $x_{i,j}$ is the number of individuals for species i in each sample, j . Carnivorous zooplankton were quantified using the number of individuals due to the low taxonomic resolution for many of the groups.

$$1) B_{h_{i,j}} = (0.08 \times L_i^{2.1}) x_{i,j}$$

In addition to information on total abundance or biomass of each species, dominance values included a weighting for the frequency of occurrence of a species. Equation (2) characterises each species' relative importance (RI_i) within a trophic level, where $W_{i,j}$ is the abundance/biomass of species i in sample j , $Max(\sum_{j=1}^n W_{i,j})$ is the maximum value of individuals/biomass for a species within each trophic assemblage, and F_i is the fraction of n samples where species i is present. Equation 2 produces a value between 0-100, where 100 indicates a species with the maximum abundance/biomass that is present in all samples and 0 indicates that a species was not recorded within the eco-region.

$$2) RI_i = 100 \left(\frac{\sum_{j=1}^n W_{i,j}}{Max(\sum_{j=1}^n W_{i,j})} \times F_i \right)$$

Within each eco-region and trophic assemblage, species were ranked by *RI* value (largest to smallest) before calculating a cumulative sum (%) of abundance. Only species which contributed to the first 75% of abundance/ biomass were used in subsequent analyses. Hence infrequent or low abundance species were not analysed subsequently in multivariate control charts. For phytoplankton, the volume of the cell may differ by several orders of magnitude between species. In order to regulate this, the square root of the biomass was used for ranking the species.

As there may be missing months within the time series from an eco-region, the species' counts were modelled using a Generalized Additive Model (GAM) to interpolate values subsequently used for calculation of annual means. GAMs were fitted using a log link function, using the *mgcv* package within the statistical package R (see McGinty et al., 2011). Two models were compared for each species, the first (model 1) modelled the long term (t , month $1 \dots n$, where n is the total number of months in the time series) and seasonal component (m , $1 \dots 12$) separately while the second (model 2) model allowed both terms to interact. The model which yielded the lowest Akaike Information Criterion value was used. By implementing the GAM on each species' time series we can fill any data voids reasonably if the parameters of the model were significant. Model 1 and 2 are specified below;

$$\text{Model 1: } P(r, t) = Y_0 + f_1(m_i) + f_2(t_i) + \varepsilon_i$$

$$\text{Model 2: } P(r, t) = Y_0 + f_1(m_i t_i) + \varepsilon_i$$

Where $P(r,t)$ is the monthly probability distribution for zooplankton abundance classes in the time series and f are smooth functions of the covariates m and t . Y_0 is the model intercept and ε the error term

GAM predictions yield smoothed monthly abundance values for the years 1960-2009. These smoothed monthly values were used to generate the average annual abundance estimates for each species, which were first normalised by subtracting the temporal mean of the species and dividing by the standard deviation. By removing the seasonal trend before generating annual abundance estimates much of the autocorrelation was removed (see below for further

steps taken to remove autocorrelation). These smoothed and normalised values were then used for further statistical analysis.

Statistical analysis

Control Charts

Univariate control charts employ a test statistic such as the mean and specify control limits of two or three standard deviations above and below the mean. A system is said to be ‘out of control’ or behaving beyond expected stochastic processes when a point goes beyond these or other specified control limits. In the present study, the multivariate analogue was used to examine the stability of three trophic communities in nine eco-regions over the last 50 years. The departure of the community in each case was evaluated against a baseline centroid (see below) and a bootstrapped (95th) percentile range around that baseline. The Bray-Curtis distance from the centroid that would suggest significant divergence from a baseline is likely to differ between communities due differences in assemblage structure. To standardise these distances across all trophic communities for display purposes, distances were divided by the value at the 95th percentile so that rescaled differences above one indicated significance (i.e. assemblages were beyond expected limits given the baseline set of observations).

Determination of whether an eco-region was beyond expected limits was carried out annually over the evaluation period. A Bray Curtis similarity measure was used on either untransformed data (if variance < mean) or ln(x) data (variance > mean). To test the long term stability of each trophic assemblage at regional scales we used 2000-2009 as a baseline decade against which to evaluate annual variability. A trophic assemblage was considered stable if the number of years that were beyond expected limits fell within expected binomial probabilities (see below). Conversely, it was unstable if the number of years a community was beyond expected limits exceeded that which was predicted by binomial probability. In this context ‘out of control’ has the sense that the departure of an assemblage from the baseline (in terms of multivariate distance) is unusually large. This could be because dominant species have become rare and/or because rarer species have become dominant. Trophic fluctuations between 2000 and 2009 were also evaluated, this time using the years 1960-1999 as a baseline. This approach allowed an examination of the relative stability

across the whole dataset. It also enabled us to put recent changes to the trophic ecosystem into context with respect to the longer time series.

Large scale charts were calculated for comparison with regional trends. This was carried out by summing species abundance/biomass across all eco-regions for each trophic assemblage. Spearman correlations were calculated between the control chart distance time series in trophic communities at regional and large scales. The significance of each correlation was corrected for temporal autocorrelation by calculating the effective degrees of freedom using the modified Chelton method (Pyper and Peterman, 1998). The control charts were generated using the FORTRAN program 'ControlChart' developed by Anderson (2004).

When calculating the probability of a trophic assemblage for a particular year being within/beyond expected limits it is necessary to control for potential artefacts of multiple hypothesis testing. Significant departures from centroids were therefore evaluated for entire time series using binomial probabilities. The probability of being out of control follows a binomial distribution $B(n, x, p)$, where n is the number of trials, x is the number of times the ecosystem is out of control and p is the probability of encountering an out of control year. This was calculated separately for each baseline period ($n=40$ for 1960-1999; $n=10$ for 2000-2009).

The direction of change from the baseline centroid to the year being evaluated cannot be assessed from the control chart (a system could become significantly different based on an increase or decrease in abundance of the species present within the trophic assemblage). We therefore 1) examined the change in standardised abundance between years both within and beyond expected limits for the two baseline periods; 2) compared the variance around both baseline centroids and the distance between them and finally 3) related these changes to the changes in abundance at the level of our species or taxa groups.

Results

Thirty two taxa dominated the eco-regions across all trophic communities according to the ordering procedure in equation (2) (see Table 1). Within each trophic level there were two/three species which were ubiquitous across almost all eco-regions. The diatom group *Thalassoria* spp. was dominant in all nine eco-regions while the two most dominant dinoflagellate species (*Ceratium fusus* and *C. furca*) were found in all but one eco-region.

Within the herbivorous copepod group the juvenile *Calanus spp.* I-IV and *Acartia spp.* were found across all eco-regions and the euphausiids and chaetognaths were the most frequently observed carnivorous zooplankton groups across our study area. There were also some species that were endemic to a particular region or group of regions. The temperate species *C. helgolandicus* dominated the regions south of 55 ° N while the sub polar species *C. finmarchicus* dominated the two regions north of 55 ° N with a co-dominance in the region MS. The coastal species *Temora longicornis* was only found to be dominant in the IS region while the predatory copepod *Pleuromamma spp.* was only found to dominate offshore eco-regions. The control charts showed contrasting patterns, depending on which baseline period was used:

i) *Baseline 2000-2009*

The phytoplankton community was very stable in all eco-regions (Fig. 2a). In regions where the community deviated beyond the expected limits, the assemblage recovered quickly within 1-3 years. There was a slight trend for more departures from control towards the start of the time series, but generally departures were of short duration and without clear patterns across regions. There was a much higher degree of inter-annual variation at higher trophic levels and here, the number of years beyond expected limits exceeded the number we would expect to have arisen due to stochastic fluctuations (Fig 2b, c). For example, the number of years found to be beyond expected limits in both groups were almost half of all the years between 1960 and 1999. For the herbivorous copepods there was a period between 1960 and 1967 where multiple eco-regions went beyond the expected limits (Fig 2b). This also happened in the carnivorous zooplankton over the same period, although only in certain regions (Fig 2c). Carnivorous zooplankton were beyond expected limits in many regions between 1986 and 1989.

There was strong inter-regional variability in all three trophic levels, although this only surpassed a potentially stochastic pattern in some cases. Four eco-regions (MS, SE, CM and IS) within the herbivorous copepod community exceeded the number of years beyond expected limits that one would expect from stochastic processes (Fig 2b). For the carnivorous zooplankton there were two regions (SE and IS) exceeding such limits (Fig. 2c).

In order to evaluate how well the fluctuations in trophic communities at regional level reflected the larger LME scale, the summed responses across the study area were compared with those of the individual eco-regions. Correlation coefficients between fluctuations in the

trophic level communities and the summed total revealed the varying strengths in this relationship across the eco-regions (Fig. 3a). In the phytoplankton community, five eco-regions were positively correlated with the summed total after correcting for autocorrelation. Herbivorous copepods were only weakly correlated with the summed total and there was only one instance of a significant correlation (in the CS region). The carnivorous zooplankton community meanwhile displayed a combination of both positive and negative coefficients which were significant in five regions. Overall, while in most instances, regions were positively correlated with the summed total (15/27) only some of these were significant (11/27) and several (3/27) were negatively correlated with the summed total. The latter group were all members of the carnivore community (Fig. 3a).

To examine the extent to which fluctuations were synchronous between trophic levels, correlations were examined between the 'responses' (i.e. control chart centroid distances) for the three trophic levels on a regional basis. This revealed that the relationships between trophic levels were weak in almost all regions (Fig. 3b). However, three significant relationships were found between the phytoplankton and herbivorous copepod communities: in two regions (SE and WT) and also overall at the LME scale (after correcting for autocorrelation $r_{SE}=0.69$, $p=0.002$; $r_{WT}=0.725$, $p=0.001$; $r_{tot}=0.564$, $p=0.014$). There were two strong positive relationships between herbivorous copepods and carnivorous zooplankton with one occurring in the MS region ($r_{MS}=0.515$, $p=0.034$) and also a significant positive relationship at the LME scale ($r_{tot}=0.457$, $p=0.05$).

ii) *Baseline 1960-1999*

Evaluation of the years 2000 to 2009 with respect to the baseline 1960-1999 showed that trophic communities underwent a high degree of change in virtually all eco-regions during the latter half of the decade (Fig. 4). Despite regional variability within and across the trophic levels, there was a general trend post-2005 towards years being beyond expected limits. This was most noticeable in 2008 and 2009 and included the phytoplankton community. The summed responses for 2009 were three times greater than expected limits and this dramatic shift was widely observed across all eco-regions.

Overall trends

The distance between the two baseline centroids revealed that there was a shift in the centroid for the upper two trophic levels but this is less evident for phytoplankton (Fig. 5a). However

there was a large degree of variance between the years 2007-2009 for the phytoplankton community; a pattern also reflected in the control chart (Fig. 4).

There was a significant difference between the standardised abundance of species in years that were within expected limits and those that were beyond expected limits. For baseline 2000-2009 (Fig. 5b) the abundance of species in all trophic levels was significantly greater in years that were beyond expected limits than years within expected limits. For the 1960-1999 baseline (Fig. 5c), by contrast, the abundances were significantly lower in years beyond expected limits than for years within expected limits. This is in agreement with Table 1, where the vast majority of species have shown a marked decrease in abundance between baseline periods. The majority of taxonomic groups showed a significant decrease in abundance over time (25/32 taxa). Out of the remaining taxa five showed a significant increase in abundance while two showed no significant change in abundance.

After amalgamating species from all trophic levels across the study area, we observed a long period of relative ecosystem stability between 1960 and 2004, but evidence of profound ecosystem change in more recent years (Fig. 6). An nMDS plot using the Bray-Curtis similarity measure showed that the entire plankton community has altered in the most recent years analysed (2005-2009). This pattern has also been observed separately within each of the eco-regions (data not shown for brevity).

Discussion

There is strong evidence to suggest that the regional scale variability observed for trophically important *Calanus* copepods (Beare et al., 2002; McGinty et al., 2011) is also present more broadly within trophic communities. The most abundant representatives of three trophic level communities i.e. phytoplankton, herbivorous copepods and carnivorous zooplankton, displayed contrasting regional patterns in long term (1960-1999) 'trophic stability'. Some regions appeared more prone to departures from control than others. In many cases, there was a failure for the regions to follow the patterns of the overall study area (i.e. the scale of Large Marine Ecosystem, or LME).

Comparing across regions, the shelf and shelf edge areas were more likely to have communities significantly departing from a baseline. In particular, the SE region had the

largest number of significant distances from either baseline. This may reflect the transitional nature of this region, subject to particular oceanographic processes. For example the Shelf Edge Current (SEC) plays a fundamental role in the physical exchange processes and cross shelf fluxes around the SE and MS regions (White and Bowyer, 1997). The level of oceanic water transported by the SEC fluctuates on interannual timescales e.g. flow rates almost doubled from the long term mean in the years 1989 and 1998 (Reid et al., 2001). These changes have had a significant effect on the North Sea ecosystem by transporting exceptionally warm water into the region leading to a regime shift in the area (Reid et al., 2001). Strong interannual variability exhibited by the SEC may have had a similar effect on plankton in the SE and, to a lesser degree, the MS communities.

The regional scale distances from separate baselines were not always reflected in the pattern when data were summed at the LME scale. At larger scales trends may be smoothed, leading to loss of the signal from regional variability. A disparity between patterns at different scales has also been documented for intertidal (Denny et al., 2004) and seabird communities (Fauchald et al., 2011). In the present study, the degree to which the regions deviated from the LME in the plankton community appeared to intensify at higher trophic levels. For example, while the herbivorous copepod communities were weakly positively correlated with a LME trend, this pattern was more chaotic in carnivorous copepods, with both positive and negative correlations with the LME. The relative agreement between regional and LME trends within the phytoplankton trophic assemblages may be due to broad scale synchrony in the drivers for growth and development in this group. Previous studies have shown the basin scale importance of photoperiod (e.g. Eliertson, 1995) which will not vary considerably over our study area. However drivers that probably operate at regional scales have also been identified. The effects of variability in SST and wind stress are also known to influence phytoplankton dynamics (Edwards et al., 2001). Dutkiewicz et al., (2001) has modelled the effects of vertical mixing and has shown both regional and interannual variability in phytoplankton may arise because mixing can increase productivity through nutrient supply but also restrict productivity by removing phytoplankton to below critical depth. Further studies have shown similar levels of interannual variability in bloom dynamics where wind induced mixing can create both deleterious and advantageous effects on phytoplankton (e.g.- Ueyama et al., 2005). Annual fluctuations in nutrient availability through anthropogenic enrichment are probably only important in coastal regions (McQuatters-Gollop et al., 2007).

Notwithstanding these sources of variability, the stability of regional and large scale phytoplankton abundances was similar in the present study.

In combination with the effects of climatic and hydrographic forcing that have been shown to be important for phytoplankton communities, there are a number of additional biological factors that could perturb successful recruitment in zooplankton communities. Variability in the individual scale processes such as predation rates (Hirst and Kiørboe, 2002), prey availability (Baier and Terazaki, 2005) and migration from diapause or overwintering resting states (Hirche, 1983) can cause regional scale differences in population characteristics. Out of these possible biological controls, the migration and transport of zooplankton organisms from their overwintering areas appears to be one of the more dominant processes dictating interregion and interannual variability. Heath et al., (1999) found that inflow of *C. finmarchicus* into the North Sea was regulated by a complex interaction between deep water circulation and wind field at a centre of species abundance in the Faroe-Shetland Channel. Linked water transport and climate factors are also the proposed processes controlling interannual variability within the shelf regions. A more comprehensive study across a larger area revealed several centres of abundance across the N. Atlantic (Heath et al., 2004). One way to approach the question of basin scale variability is through the use of a structured population model driven by ocean transport and hydrodynamics e.g. Speirs et al, (2006a, b). Again using *C. finmarchicus* as the model species, Speirs et al., (2006a) found strong connectivity between centres of distribution in the N. Atlantic even when the influence of ocean transport had been factored out.

The most significant changes in trophic communities occurred in the most recent decade (2000-2009) by comparison with a baseline comprised of the previous four decades. Community similarity for the years 2005-2009, in particular, was drastically altered compared with previous years (Fig. 4). Trophic communities were almost universally beyond expected limits in 2008 and 2009, even for phytoplankton communities, which in some cases were more than two deviations above the expected limit. Nevertheless, despite trophic level-specific and region-specific contrasts, there was a common theme in all analyses. Irrespective of the baseline considered, the average biomass/abundance of each trophic assemblage was significantly different between years that were within expected limits compared with those that were beyond expected limits. This translated as a trend for decreased abundance/biomass to be characteristic of years which were beyond expected limits. Even with a reduced

biological detail, coarse averaging of species abundance/biomass and the subsequent comparison between baselines reveal a similar pattern for the vast majority of species used in this analysis. Out of thirty two taxa used in this study, twenty six were found to have decreased in abundance/biomass within the last decade. With the trophic wide decreases in species abundance/biomass so evident, the results highlight the exceptional changes that have occurred in plankton assemblages compared with respect to the latter half of the last century.

Recently there has been much debate about the abundance of phytoplankton in global oceans. Boyce et al., (2010) indicated a median decrease of 1% per year in the global phytoplankton biomass over the last century, based on the integration of various proxy and *in-situ* measurements of *chl-a* concentration. However this was subsequently called into question (McQuatters Gollop et al., 2011; Mackas, 2011; Rykaczewski and Dunne, 2011) based on possible overestimates of *chl-a* using secchi disk measurements (Rykaczewski and Dunne, 2011). In contrast, according to other datasets such as the CPR, Bermuda Atlantic Time Series (BATS) and the California Cooperative Oceanic Fisheries Investigations (CalCOFI), phytoplankton has apparently increased in many cases over the last 50 years (McQuatters Gollop et al., 2011). In the present analysis we derived direct biomass estimates from the most dominant species in the CPR dataset. This suggests that changes in phytoplankton biomass (1960-1999) while present were not significant. Rather, such changes were well within expected stochastic fluctuation. The data from this study alludes to a possible shift in community structure in the latter half of the last decade, particularly in the years 2008 and 2009 (Fig. 4 a,b,c) but it remains to be seen whether this cross-trophic deviation is a temporary effect possibly due to the effects of the anomalously cold winters (associated with extreme negative NAO values in the latter years of the decade) or whether it marks the beginning of a sustained and persistent change in the state of all plankton communities.

By contrast with phytoplankton, there is general accord about how the long term changes in zooplankton distribution and abundance have changed in the N.E. Atlantic over the last 50 years. Large poleward shifts have been observed in the distribution of herbivorous copepods, where assemblages with boreal affinity have been replaced by others more characteristic of warmer waters (Beaugrand et al., 2002). This distributional shift was attributed to the northward progression of the temperate/polar isotherm discontinuity which is currently found within our study area (Beaugrand, 2009). One suggested consequence of such shifts is the switch to an alternative ecosystem state or regime where the constituent species are

potentially smaller in size, lower in numbers and less nutritious, causing a cascade effect at higher trophic levels (Beaugrand et al., 2009). However there was little evidence in the present study to suggest that rarer species were becoming more abundant as these usually contributed no more than 5% towards the total biomass in any one year. Instead we found evidence of a significant decrease in biomass of the most numerically dominant zooplankton species. One possible explanation for this could be increased jellyfish abundance (i.e. ctenophores and medusae) in our study area (Licandro et al., 2010; Lynam et al., 2011) leading to increased predation rates on zooplankton. This would constitute top-down control of trophic dynamics, in a similar way to the effects caused by fish predators. Whether predation on zooplankton by jellyfish actually occurs at the scales to produce such an effect requires further investigation.

The stability of links between trophic levels over time is an area of increasing importance to management objectives (e.g. Anonymous, 2010; Edwards et al., 2010) and research activity is intensifying in this area (e.g. Beaugrand and Kirby, 2010a; Beaugrand and Kirby, 2010b). But because the dynamics of different trophic levels will operate at different scales, straightforward links between trophic interactions or direct climate forcing on these may be difficult to establish (Aebischer et al., 1990). Although there has been evidence of correlations between positive anomalies in abundance/biomass of plankton prey and cod (Beaugrand et al., 2003) or sandeel recruitment (Frederiksen et al., 2006) (bottom-up regulation) in the North Sea/SE Scotland respectively, in the present study there was little significant regional-scale correlation between trends in adjacent trophic levels. Such correlations, though present at LME scale (Fig. 3a), were mostly non-significant at regional scales and in the case of carnivorous zooplankton, small negative correlations were found in some regions. Again, this is likely to reflect the more complicated dynamics of predator turnover rates and different scales for processes affecting predator groups.

A potential cause of the apparent greater stability of phytoplankton in comparison to zooplankton between 1960 and 1999 is that the phytoplankton baseline contains some very unusual years between 2000 and 2009 (Figure 5). This may inflate the confidence limits, meaning that only very large departures from the centroid would be detected for 1960-1999. The observation that departures from the centroid were rare over a 40 year period emphasizes how unusual the changes seen in the decade 2000-2009 have been. An additional explanation for the differences between phytoplankton and zooplankton is that zooplankton are more patchily distributed, leading to a more variable sample collection.

However, the confidence limits are derived from the data and are based on frequency of departures (95th percentile) rather than absolute distance from the baseline. The more variable nature of zooplankton counts would not cause these groups to be more likely to be judged out of control.

Generally, when dealing with multivariate plankton assemblages, datasets have been reduced to a univariate measure to allow simple correlations to be made between the community and environmental variables. This has been done by either obtaining an average response across all species or through data reduction techniques such as Principal Components Analysis (PCA), where the principal modes of variability are used as univariate measures of community variability. While there are similarities between PCA and control chart approaches, with similarities among studies depending on the degree of pre-screening of data and any transformation applied, the difference with control charts is that distances from a baseline can be scaled, whereas PCA scores are more arbitrary. Both techniques aggregate data and require further analysis and disaggregation to understand which variables are responsible for multivariate structure. This is beyond the scope of the current study, but it would be possible to take the control chart for an eco-region and repeat the control chart analysis, missing out combinations of species to examine the groups most contributing to deviation from the baseline.

When deciding on a baseline for a control chart, a large number of different hypotheses can be tested. For example, one could compare the similarity of one decade to the preceding decade. We chose a combination of baselines that led to the questions a) how does the period 2000-2009 differ from the period 1960-1999? and b) how frequently have conditions typical of 2000-2009 occurred in the period 1960-1999? A possibility of using different baseline lengths is that the longer baseline samples more environmental variability (due to multidecadal patterns of variability), making detection of out of control events less likely in the shorter time series. In the analyses presented here, there is little support for this, even using the range of assemblages sampled between 1960 and 1999; there were still significant departures from the baseline in 2000-2009. The frequency of out of control events did not seem to differ among the different baselines. The ability to compare between baselines of different lengths adds a complexity beyond what can generally be carried out with PCA type approaches and may allow more targeted hypotheses to be tested (for example, baselines constructed for NAO positive or NAO negative years).

The two baselines used encompass a period when the SST anomaly in the North Atlantic has changed from positive in the 50's to negative during much of the 1960's and 70's to positive, particularly in the last decade. Phytoplankton communities appear to have been more synchronous and less variable over this time than zooplankton. Although adjacent trophic levels were linked at large scales, patterns at regional scale showed uncoupling of dynamics, particularly for zooplankton, which were beyond expected limits during periods when phytoplankton communities did not appear to be so. The patterns identified suggest changes have occurred in the structure of communities and the next challenge is to test whether such changes are linked to the functioning of ecosystems and how this differs from the changes in abundance that have generally been the focus of previous studies.

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Table 1. The thirty two most important taxa either numerically or as a large contributor to the overall biomass according to equation (2), for each trophic level. Also shown are the eco-regions where each taxon was found to be the most important and the biomass/abundance change between the baselines 1960-1999 and 2000-2009 (Increase, Decrease or No Change).

Taxon	Eco-regions present	Biomass/abundance change between baselines 1960-1999/ 2000-2009
Carnivorous zooplankton		
Euphausiids	IS CM CS SE WT ABS RB RT MS	Decrease
Chaetognaths	IS CM CS SE WT ABS RB RT MS	Decrease
Hyperiid	IS CM CS SE WT ABS RB RT	Decrease
Decapods	IS CM CS SE WT	Decrease
<i>Pleuromamma spp.</i>	WT ABS RB RT	Decrease
<i>Candacia spp.</i>	CS SE WT	Decrease
<i>Euchaeta spp.</i>	SE WT	Increase
<i>Corycaeus spp.</i>	SE	Decrease
Herbivorous copepods		
<i>Calanus spp. I-IV</i>	IS CM CS SE WT ABS RB RT MS	Decrease
<i>Acartia spp.</i>	IS CM CS SE WT ABS RB RT MS	Decrease
<i>Paracalanus spp.</i> and small copepods <2mm	IS CM CS SE WT ABS RB RT	Decrease
<i>Calanus helgolandicus</i>	IS CM CS SE WT ABS MS	Increase
<i>Centropages typicus</i>	CM SE WT ABS	Decrease
<i>Pseudocalanus spp.</i>	CM CS	Decrease
<i>Metridia lucens</i>	RB RT	Decrease
<i>Calanus finmarchicus</i>	RT MS	Decrease
<i>Temora longicornis</i>	IS	Increase
Phytoplankton		
Dinoflagellate		
<i>Ceratium fusus</i>	IS CS SE WT ABS RB RT MS	Decrease
<i>Ceratium furca</i>	IS CM SE WT ABS RB RT MS	Decrease
<i>Ceratium tripos</i>	CM CS SE RB RT MS	Decrease
<i>Protoperdinium spp.</i>	CM MS	Decrease
<i>Ceratium lineatum</i>	ABS CM	Decrease
<i>Ceratium macroceros</i>	WT	Decrease
<i>Dactyliosolen mediterraneus</i>	RT	Decrease

Diatom

<i>Thalassiosira spp.</i>	IS CM CS SE WT ABS RB RT MS	Increase
<i>Hyalochaete spp.</i>	IS CM CS SE WT ABS RB RT	Decrease
<i>Thalassionema nitzschioides</i>	IS CS SE WT ABS RB RT MS	Decrease
<i>Phaeoceros spp.</i>	IS CM CS SE WT ABS MS	Increase
<i>Rhizosolenia alata alata</i>	CM CS SE WT ABS RT	Decrease
<i>Rhizosolenia imbrica. shrubsolei</i>	CM CS RB MS	Decrease
<i>Rhizosolenia styliformis</i>	CM RB RT	No Change
<i>Thalassiothrix longissima</i>	ABS RT MS	No Change

Figures

Figure 1. The geographical distribution of the nine eco-regions used in the analyses. These are in clockwise order IS=Irish Sea; CM=Celtic Sea mixed; CS=Celtic Sea stratified; SE=Shelf Edge, WT=Warm Temperate; ABS=Abyssal South; ABN=Abyssal North (Not used); RB=Rockall Bank; RT=Rockall Trough; MS=Malin Shelf.

Figure 2. The control chart for each of the trophic communities for all nine eco-regions a) Phytoplankton, b) Herbivorous copepods and c) Carnivorous zooplankton for the years 1960-1999 using the years 2000-2009 as the baseline set of observations. Blue represents cells that are within expected limits, yellow represents cells that are beyond the 90th percentile from the baseline while red represents cells that are beyond the 95th percentile from the baseline. The overlaid time series (white markers and black line) for each trophic level shows the level of control when data are summed across all eco-regions. Years where the scaled centroid distance is above one were beyond expected limits (at the 95th percentile indicated by dashed line). The columns accompanying each trophic assemblage represent the binomial probability that the number of years beyond expected limits exceeded the expected amount. Those above the dashed line are deemed to be significant at the $p=0.05$ level.

Figure 3. Correlation coefficients a) between each eco-region and the summed total and b) between adjacent trophic levels within each eco-region with the same procedure applied at the LME scale in the final column 'Total'. Red columns indicate significant correlations where $p<0.05$ after correcting for temporal autocorrelation.

Figure 4. The control chart for each of the trophic communities a) Phytoplankton, b) Herbivorous copepods and c) Carnivorous zooplankton for the years 2000-2009 using the years 1960-1999 as the baseline set of observations for all eco-regions. The legend is as described in (Figure 2.)

Figure 5. a) Variability about the baseline centroids (1960-1999=large closed circle; 2000-2009=large open square) for each baseline period (1960-1999=small closed circle and stippled line; 2000-2009=small open square and solid line) of each trophic level category. Each panel represents a PCA performed on a matrix of the average abundance of species summed across all eco-regions. The centroid represents the arithmetic mean of each year for

both baselines The difference in abundance between years (mean \pm SE) when trophic communities were within expected limits (blue) compared with years that were beyond expected limits (red) across all eco-regions for b) 2000-2009 baseline and c) 1960-1999 baseline.

Figure 6. A nMDS plot of the summed numbers of individuals/biomass of all species from all trophic levels across all eco-regions for the years 1960-2009 using the Bray-Curtis similarity measure (triangle- 1960's, inverted triangle- 1970's, diamond-1980's, square-1990's, circle-2000's).

Figure 1.

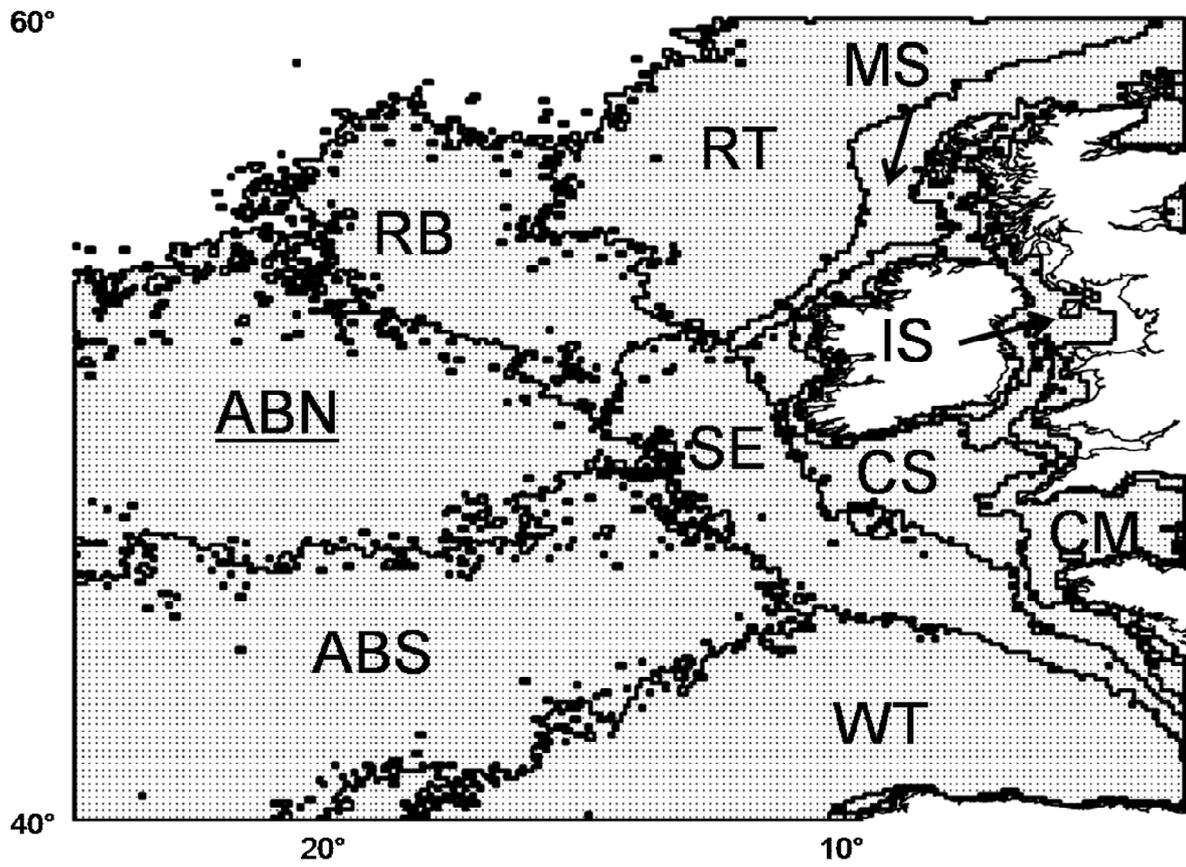


Figure 2.

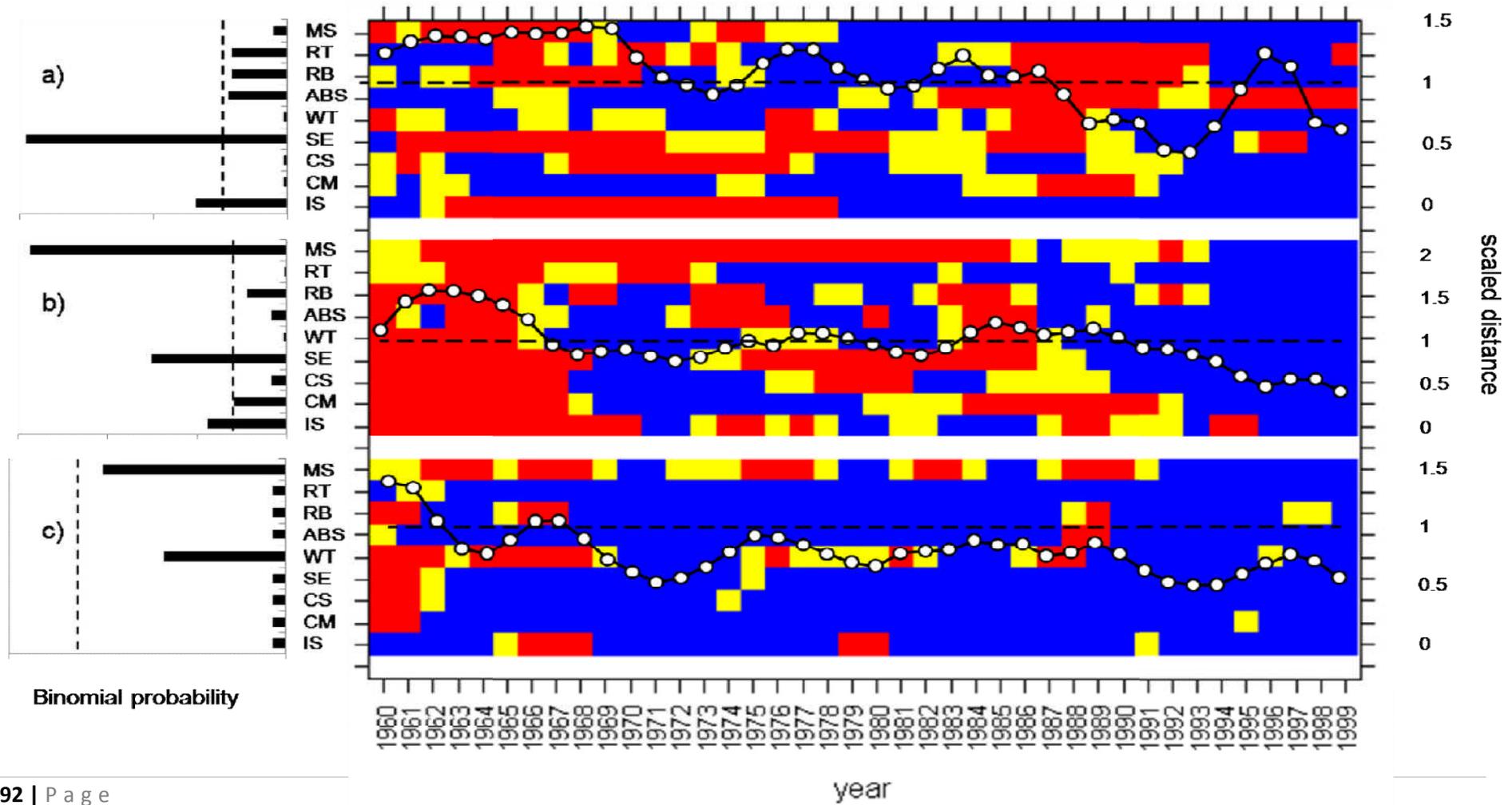


Figure 3.

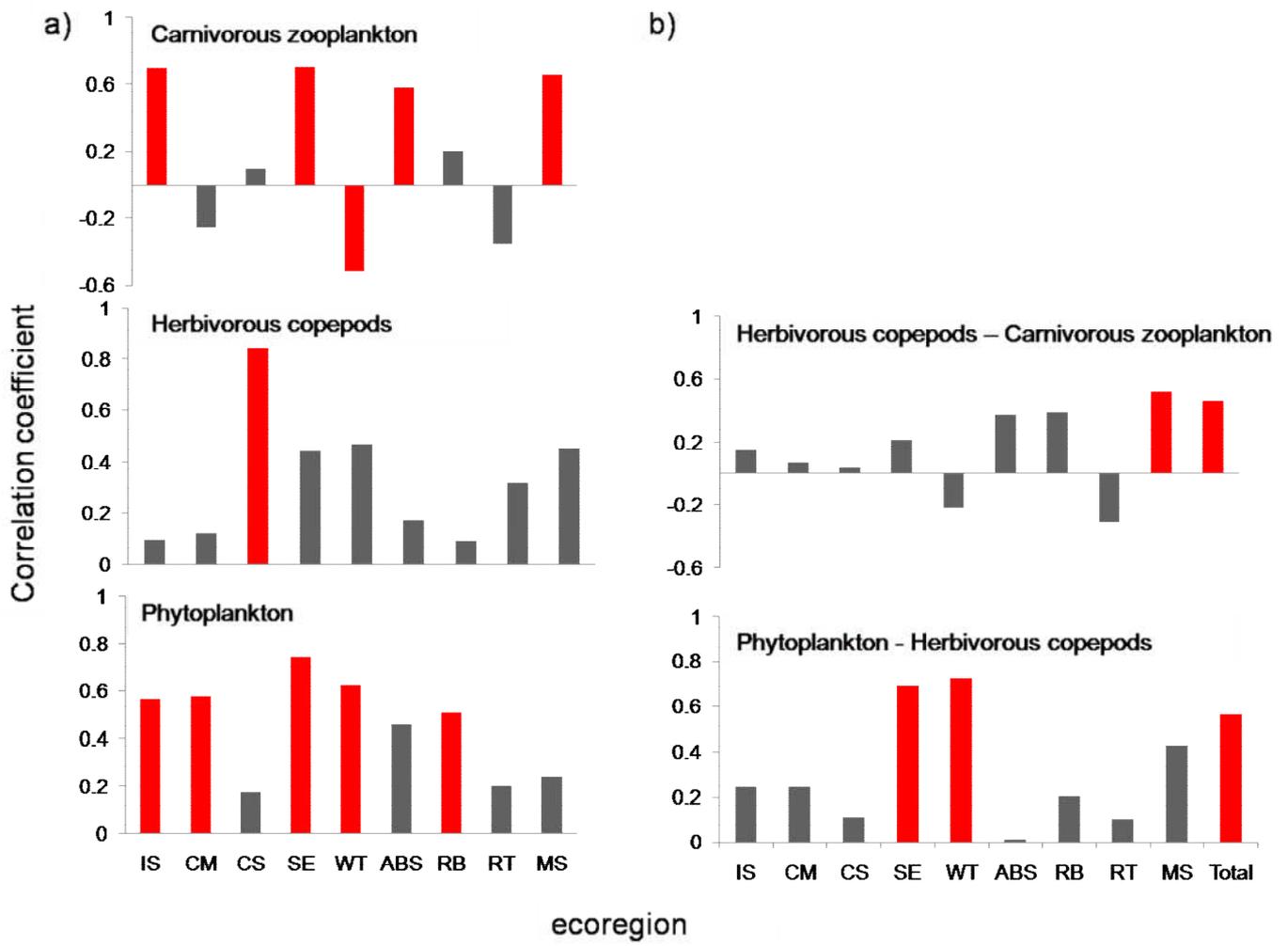


Figure 4.

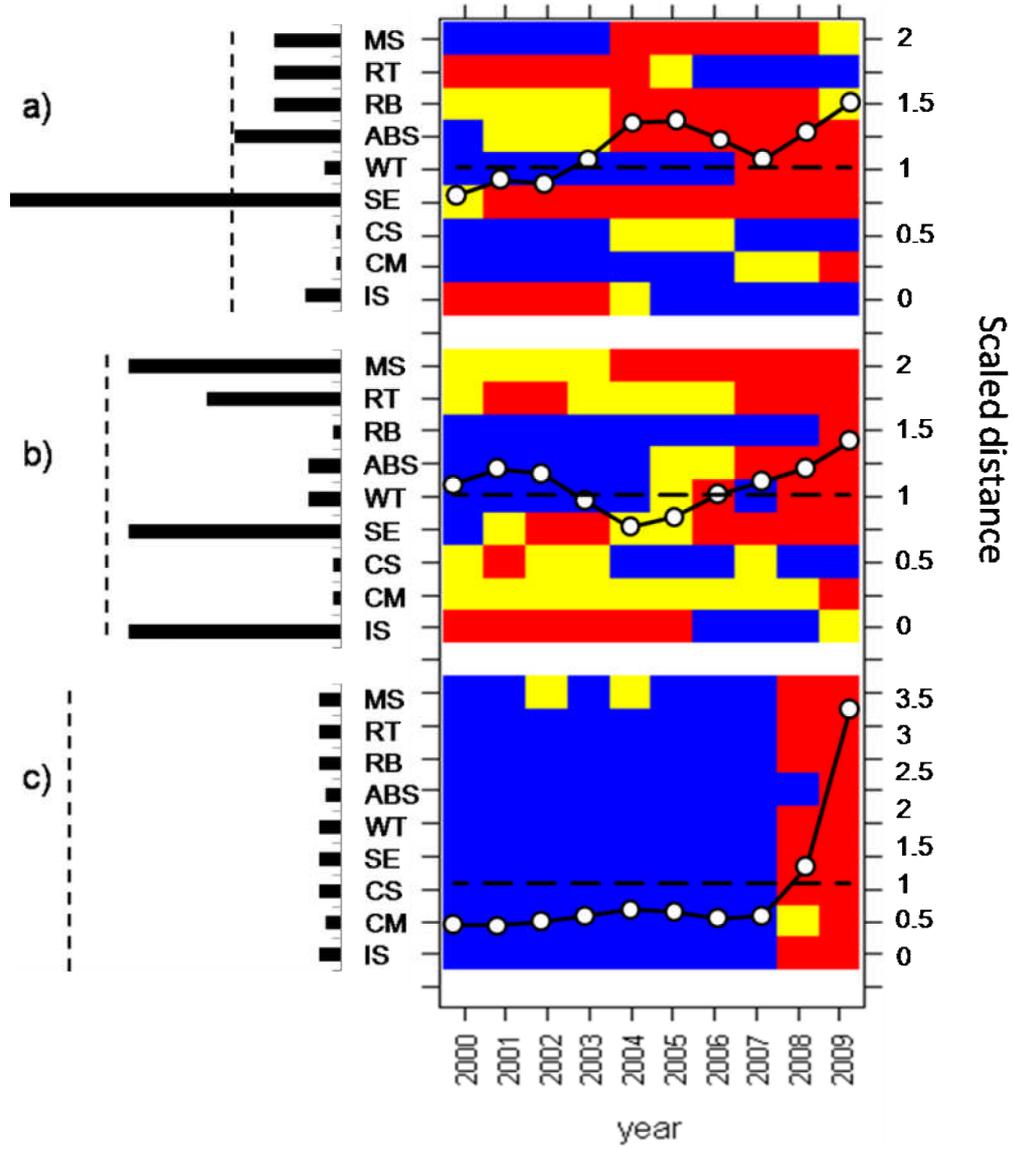


Figure 5.

a)

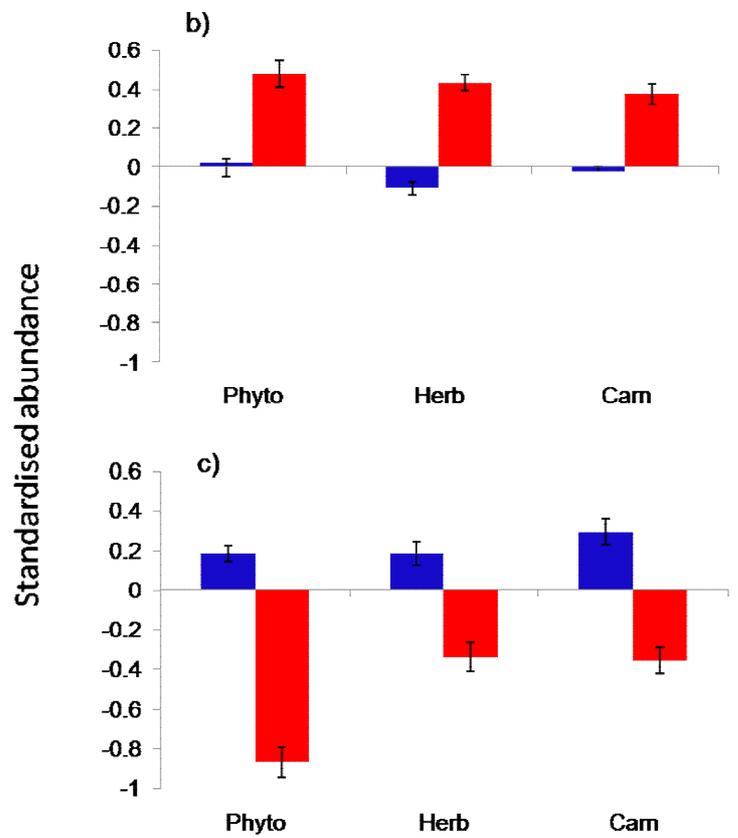
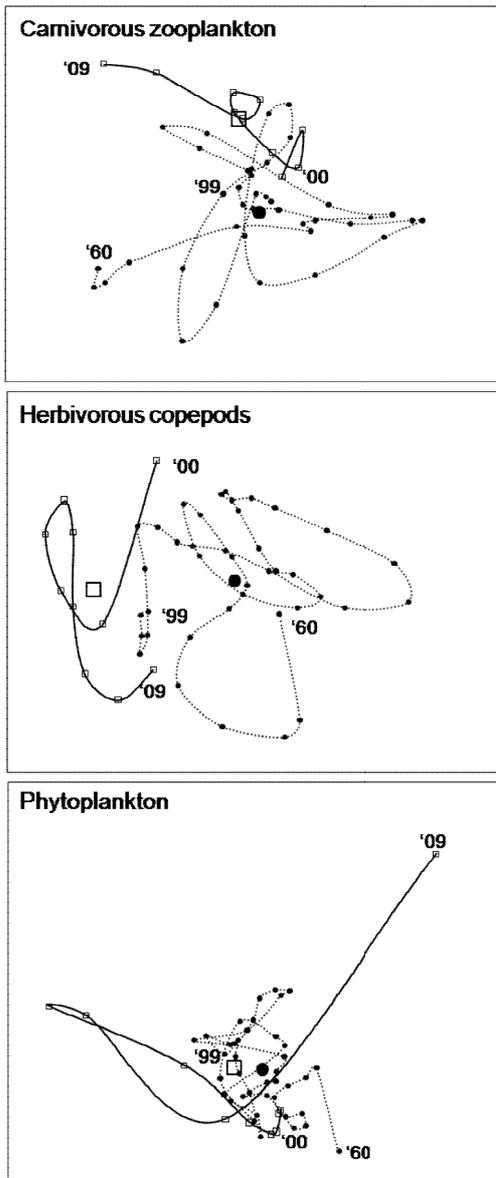
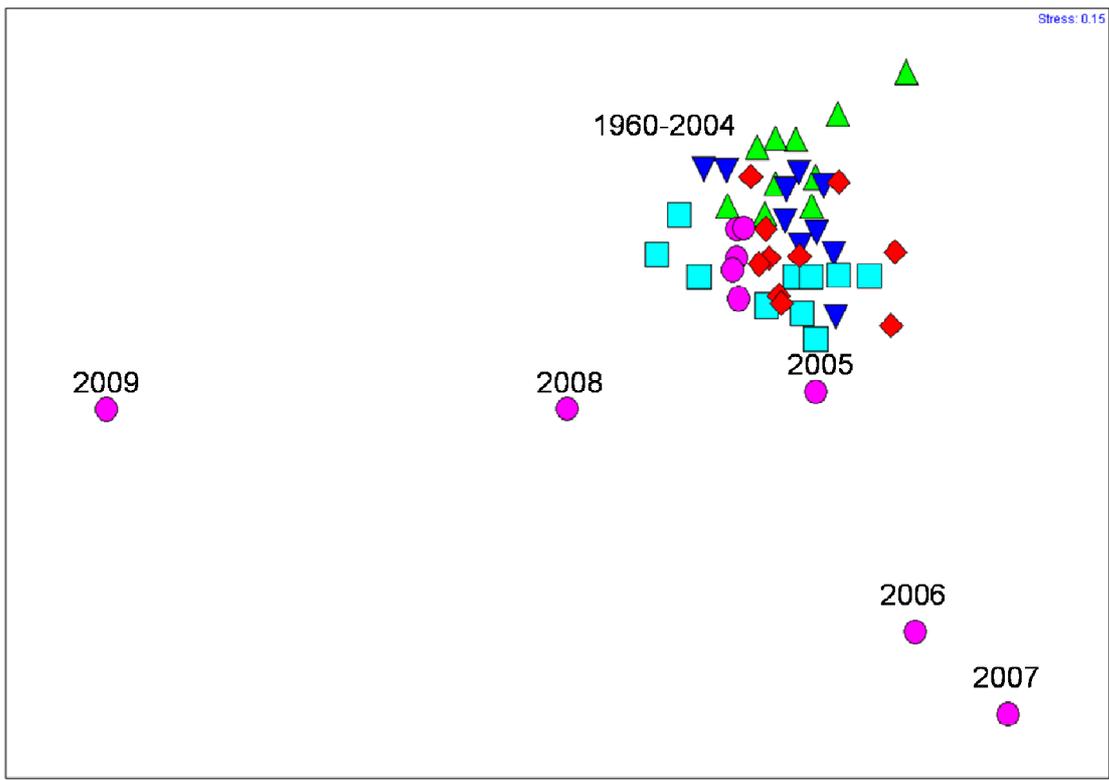


Figure 6.



Chapter 4

Local-Regional links in zooplankton populations around Ireland: Synchronous patterns with adjacent shelf and offshore waters

Submitted: *Estuarine Coastal and Shelf Science, in review*

Abstract

Regional variations to climatic and environmental forcing can cause broad scale variations to plankton dynamics. Despite differences between areas, migration and advection can cause dependencies between these areas also. Variability in zooplankton populations in bays and estuaries are explained through local environmental gradients but rarely consider possible external influences on dynamics. Time series for eleven of the most dominant copepod taxa are reconstructed from archived samples between 1973 and 1987 for Galway Bay. The abundance of each of these species were modelled using a generalised additive model to allow cross correlations with populations in the adjacent shelf and offshore regions which were derived from the Continuous Plankton Recorder.

Temporal changes in the species abundance within the bay were not aligned with the local environmental conditions (sea surface temperature) or with the major modes of climatic variability (North Atlantic Oscillation and Gulf Stream North Wall). The majority of copepod taxa (7/11) were found to show strong relationships with an adjacent region and in those cases one region tended to dominate with high R^2 values. Comparisons made with other regions yielded low and insignificant R^2 values (~5%). There were both synchronous and asynchronous patterns in the annual abundances of both populations. We have shown that populations within Galway Bay can co-vary strongly with adjacent regions and are likely to impose a strong influence on the community structure within the Bay.

The period between 1979 and 1982 also coincided with a significant shift in the community composition in pelagic ecosystems of the N. Atlantic and changes in the Galway Bay community were compared between these time periods (1973-1979 and 1983-1987) were compared. Within Galway Bay there was a significant change in the timing of the spring and autumn maxima for the majority of the taxa and a PCA revealed a shift in species' abundance between the two time periods.

Keywords: zooplankton, phenology, estuarine dynamics, shelf dynamics, interspecific relationships, Ireland, Galway Bay

1.0 Introduction

Oceanographic and environmental variability between open ocean, shelf and coastal areas can result in broad scale variations in planktonic population dynamics (McGinty et al., 2011). The resultant forcing processes can interact with anthropogenic impacts (nutrient enrichment) which typically exert more of an influence in estuaries and coastal regions (McQuatters-Gallop et al., 2007). Despite the differences between regions, migration and advection can cause dependencies between areas. The variability and ecological preference of zooplankton in many of the largest European bays have been described (e.g.-Taylor, 1993; David et al., 2005; Moderan, 2010). These studies attempted to explain the variability of the zooplankton with internal characteristics of the bay such as the change in temperature and salinity gradients. However a large degree of variability still remains unexplained and this might be explained by external influences, one of which may be through population interactions with adjacent water bodies.

Galway Bay is an open bay situated on the west coast of Ireland. The seasonal dynamics of several constituents of the plankton community were studied throughout the 1960's to 1980's including copepods (Fives, 1969), fish larvae (Fives, 1970), Chaetognaths (O'Brien, 1977) and Ctenophores (Yip, 1981) though there was no continued programme to maintain any long term sampling for the area. Fortunately many of the samples have been preserved as an archived sample set which covers the period between 1973 and 1987. Such samples sets are invaluable given that there are very few time series which are >10 years for marine ecosystems (Richardson, 2008). Long term datasets allow us to examine how climatic and environmental forcing can affect the abundance and distribution planktonic organisms and make regional comparisons with other time series (Richardson, 2008).

In order to obtain information on zooplankton abundance in the adjacent waters, data from the Continuous Plankton Recorder (CPR) were used. The CPR is a long term plankton dataset arising from regular sampling the N.E. Atlantic since 1958 (Richardson, 2006). However there exists a "sampling shadow" off the west coast of Ireland due to the position of the regular towing routes. This gives our sample set an elevated importance as the samples were collected in this "sampling shadow" off the west coast of Ireland. Previous attempts to fill the gap in the data have been undertaken before (Fives, 1969) but did not consider any direct relationships between Galway Bay samples and the CPR dataset. The CPR plankton sampler is unique in that it is designed to filter low volumes of water across from the upper 10m. of

the water column over vast areas of the ocean (about 3m^{-3} per 12 km). In contrast collecting plankton samples through a net haul process is restricted to fixed stations where volumes filtered is greater and species abundance can be several orders of magnitude more. However it was found that even at a single station site such as the “Dove” time series in the North Sea, strong positive correlations can be found between the interannual variations of species between net haul samples and CPR time series (Clark et al., 2001). Improved correlations were found when a grid of net hauls was compared against CPR samples that bisect the study area (Kane, 2009). The grid of net hauls smooths out the unique localised variation experienced by a single station net haul across a larger area.

The aim of this work is to reconstruct a time series of several important zooplankton taxa (calanoid copepods) within Galway Bay and investigate the conspecific associations with populations in adjacent areas. Species were selected based on (Fives, 1969). The period in question (1972-1987) occurs during a well documented period of change within pelagic ecosystems of the N. Atlantic (centred around 1977-1982) (Beaugrand, 2004). In the North Sea, the composition of the pelagic community moved from a cold water affinity to a warm water affinity community which was driven by an increase in sea surface temperature and a change in the wind intensity and direction. By comparing the two time periods prior and subsequent to those years, we examine whether there were any significant changes in the community abundance within the zooplankton of the Galway Bay area. Particular focus is placed on identifying the conspecific relationships between the populations of each copepod taxa in Galway Bay against the populations found in the broader scale eco region defined by the clustering of *chl-a* data (McGinty et al., 2011; see Fig 1). The present study examines Galway Bay, an area in a historical “sampling shadow” to examine the extent to which local coastal plankton dynamics are independent of or reflect patterns seen in larger adjacent areas. Strong relationships between the multi annual abundance patterns between Galway Bay and the eco region populations will provide evidence of population linkages and possible advection routes from the surrounding area.

2.0 Methods

2.1 Study area

Galway Bay is a semi enclosed bay situated on the west coast of Ireland. The bay is characterised as a well mixed estuary with freshwater inflow from the Corrib River on the

north east coast of the bay and an anti-clockwise circulation pattern controlled mainly by inflow rates from the south and outflow to the north. Both salinity and sea surface temperature are influenced by rates of fresh water inflow from the River Corrib and oceanic inflow from the south of the bay (Booth, 1975). Salinity varies between 24.0 in the inner bay to 34.9 in the outer Bay and flow rates from the Corrib change seasonally from winter daily means of $\sim 250\text{m}^3\text{s}^{-1}$ to summer daily means of $\sim 50\text{m}^3\text{s}^{-1}$ (Nolan, 2004).

2.2 Environmental data

Broad scale environmental variables were used as potential covariates as there were no long term oceanographic observations available from within Galway Bay. Sea surface temperature (SST) data were obtained from the two data points of the HadISST1 dataset (Rayner et al., 2003) that are positioned nearest to Galway Bay (Fig 1.). The NAO winter index (Hurrell, 1995) which is based on the difference of normalized sea level pressure between the Azores and Iceland was used as this previously has been demonstrated to be correlated with zooplankton time series (Fromentin and Planque, 1996). The Gulf Stream north wall (GSNW) index, found by obtaining the principal components of sea surface measurements at six longitudes between 79°W - 65°W (Taylor and Stephens, 1980), was also considered. The position of the north wall is thought to alter the position of storm tracks across the North Atlantic which would impact upon zooplankton distributions in the N.E. Atlantic (Taylor et al., 1992).

2.3 Zooplankton tows and CPR

Routine biological and oceanographic sampling was carried out in Galway Bay between 1972 and 1987 by the former Department of Oceanography in NUI Galway (now Earth & Ocean Sciences). There was no sample collection in the Bay during the period between 1979 and 1982. The two principal vessels involved in sample collection during this time were the “Queen of Aran” angling vessel and the *R.V. Lough Beltra*. Zooplankton were sampled either using a ring net (50 cm diameter) under an oblique tow or a discrete depth plankton sampler which sampled multiple depths simultaneously (Clarke and Bumpus, 1950). Both plankton samplers had the same mesh aperture ($250\ \mu\text{m}$) and were towed at similar speeds (1-2 kn) and over similar durations (~ 15 mins) to ensure maximum filtration efficiency of each tow. Sampling spanned inner Galway Bay where water depths are ~ 30 m to the outer bay where water depths can be up to 60m (Fig 1). 810 samples were collected in total but a proportion of

these samples had been analysed previously for other projects and some individuals had been removed. Records for such samples show where any loss of sample had occurred. In most cases the samples had been undisturbed. Although in a few cases (n=24) subsamples were previously taken from the whole sample. These subsamples were randomly selected and it is expected that all subsequent subsampling will still be representative. Eleven taxa of calanoid copepods composed of nine species and two taxonomic groups were selected for enumeration based on their ubiquity in Galway Bay (Fives, 1969) (see Table 1) and their known association with oceanographic conditions (Beaugrand et al., 2002). Zooplankton sampled from tows was identified using a dissection microscope and counted following a subsampling procedure that either counted all individuals until 300 individuals were enumerated or in cases where there are <300 individuals, until the whole sample had been counted.

Temporal patterns of copepods from Galway Bay were compared with regional patterns in these taxa from the temporal patterns found in the CPR time series for each available eco region (McGinty et al., 2011). Zooplankton data for the larger study area came from the Continuous Plankton Recorder (CPR) Warner and Hays (1994). The CPR data was divided into distinct eco regions following the methods of region classification defined by McGinty et al. (2011). Time series for the eleven selected taxa were extracted from every region in which they were found to be adequately represented (i.e. found in >10% of samples). All but one species (*Centropages hamatus*) were found at a high enough frequency in Galway Bay to be modelled in at least one of the eco regions.

2.4 Modelling copepod abundance

To enable cross correlation between the different time series, data were interpolated using Generalized Additive Model (GAM) smoothing routine. The model allowed for the generation of regular average monthly and annual abundance estimates for the zooplankton population in Galway Bay during the period between 1973 and 1987. The GAM included all available descriptor variables including spatial (Latitude, Longitude and Depth) and temporal (Year, Month, Julian Day) variates. Spatial coordinates were not found to improve model fit based on the Akaike's Information criterion (AIC) so only temporal descriptors were used. Julian Day proved to be a better fit than Month for the seasonal component of the model. Depth was also available as a discrete factor but through exploratory graphs and GAMs it was found not to improve the prediction of our models. GAMs were carried out using the

mgcv package (Wood, 2006) in the R environment (R development core team, 2008); all had a negative binomial error distribution and a logit link function. The long term variable *Year* (Jan 1973=1, Feb 1973=2, ... Dec 1987=180) and short term variable *Julian Day* (1, 2, 3... 365) were modelled additively (non interacting) and allowed to interact. All taxa took the form of Model 1 where both variables were allowed to interact.

Model 1
$$g(P_{r,t}) = Y + f(\text{Year}_i, \text{Julian Day}_i) + \varepsilon_i$$

The relative change in abundance for each month and the change in timing of the seasonal maxima between the two time periods (1973 to 1978 and 1983 to 1987) were evaluated for each species. The spring and autumn maxima for each year were evaluated by calculating the centre of gravity (T) of the monthly means according to Edwards and Richardson (2004) where x_m is the mean value of the species abundance in month Spring M (January=1, February=2, . . ., June=6) Autumn M (July=1, August=2, . . ., December=6).

$$\frac{\sum_1^6 m. x_m}{\sum_1^6 x_m}$$

2.5 Relationship between Galway Bay and broader eco regions

Comparisons were made between the annual species abundances in Galway Bay from plankton tows and the CPR time series in the surrounding eco regions in order to determine possible population linkages between Galway Bay and the surrounding seas. Annual abundances were used to reduce the autocorrelation in the dataset. Linear regressions were modelled for all available eco regions and curvilinear regressions were also applied when a visual inspection of the data revealed a possible polynomial relationship. The most parsimonious model was determined using the AIC corrected for small sample sizes. Akaike weights (w_i) give the likelihood of the model being the best fit of those compared. As a general rule, models which are within >10% of the highest model are considered as plausible models (Royall 1997)

3.0 Results

3.1 Temporal variation in the climatic and environmental variables

Typically the lowest SST occurred in March with temperatures ranging between 9.6-10.2°C. The highest temperatures were usually found in July/August with temperatures ranging between 14.8-17.2°C. There was a significant change in the mean annual SST between 1973 and 1987 (Fig 2a). A fitted least squares regression showed a significant increase in SST during this time. Owing to the inherent stochastic fluctuations within the NAO and GSNW index there were no changes observed within these index measures during this time (Fig 2b).

3.2 Relationship with CPR eco regions

The vast majority of the taxa found in Galway Bay were associated with at least one of the CPR eco regions between 1973 and 1987 (Fig 3.). All time series were also found to show no significant levels of autocorrelation in the data. Only *Centropages hamatus* was found to have no corresponding eco region with enough samples to model species counts. Of the taxa that were compared 7/10 were found to have a significant relationship with at least one of the eco regions. The stratified Celtic Sea region (CS) had the greatest number of significant associations with the Galway Bay (4/10). The three remaining species to show a significant relationship with an eco region were associated with the Shelf Edge (SE) (*Acartia clausii*), Rockall Trough (RT) (*Metridia lucens*) and with the Irish Sea (IS) (*Temora longicornis*). With the exception of IS, all the associated eco regions, share a border close to the Galway Bay area. In the 7/10 cases that showed a significant relationship between Galway Bay and eco region populations most were found to show a significant relationship with only that region. Only *Calanus juvenile spp.* and *C. helgolandicus* populations were found to have a significant relationship with more than one eco region which was the Celtic Mixed (CM) region. The comparisons made with other eco regions yielded low R^2 values (~5%). Also the strength of the significant models were such that the w_i showed that no other model for other eco regions were within the minimum cut off point (>10%) of the highest model.

3.3 Seasonal and interannual trends in Galway Bay plankton trawls

The only significant change in average abundance over the time period 1972-1987 was for *Acartia clausii* and *Centropages hamatus* which both showed a significant increase, and for *Candacia armata* which showed a significant decrease also. There was strong year to year variability for the remaining taxa, which, although they did not show a consistent change in absolute abundance, nevertheless changed in the amplitude, duration and timing of the seasonal blooms (Fig. 4). The highest total annual abundance for 7/11 of the taxa was found

to have occurred in 1978. This coincided with a strongly negative NAO phase the previous winter (1977) and also with a relatively low GSNW value for 1978.

Bimodal seasonal patterns dominated in the Galway Bay assemblage with all taxa showing seasonal maxima in spring/autumn for almost all years (Fig 4.). The pattern of change in the timing of the seasonal maxima varied between seasons. The average timing of the seasonal maxima for the two time periods (1973-1978 and 1983-1987) were compared. The change in timing of seasonal maxima also varied between taxa. In spring, there was an earlier seasonal peak in the 1980's compared with the 1970's, in 6/11 taxa, especially amongst the smaller sized individuals of the copepod community (Fig 5). Autumn maxima were both significantly earlier and later for a number of taxa (5/11). The magnitude of the autumn seasonal change was not as acute as in the spring. Again the smaller zooplankton taxa were the ones which tended to alter their seasonal timing in autumn, although two of the species (*Pseudocalanus elongates* and *Acartia clausii*) showed a later seasonal peak in autumn as opposed to their earlier seasonal peak in spring.

There were noticeable changes in the community composition of zooplankton over the two decades studied. A PCA of annual abundance revealed a strong dissimilarity between the 1970s and 1980s (Fig. 6). The year 1978 appeared as an outlier which is likely due to the fact that the majority of taxa displayed their highest abundance levels during that year. The ratio between the two *Calanus spp.* in a particular area can be used a useful index for boreal (*C. finmarchicus*) or warm water (*C. helgolandicus*) influence (Fig. 7). The warm water affinity species *C. helgolandicus* dominated across most years while the boreal affinity species was found to dominate in only three of the years. There was no obvious relationship between the NAO and the *Calanus* index although the years when *C. finmarchicus* was dominant tended to also be the years where the NAO was most positive.

4.0 Discussion

The modelling approach adopted in this study enabled us to put a time series of plankton tows from Galway Bay into the wider context of the N.E. Atlantic. The results demonstrated strong relationships between the zooplankton populations in Galway Bay and adjacent eco regions for most taxa, although which eco region Galway Bay followed depended on the taxon being examined. Populations tended to be significantly related to only one eco region suggesting

serial dependence with specific areas. This is the first time that a data series longer than 10 years has been produced for zooplankton distributions off the west coast of Ireland.

Nevertheless, the Galway Bay time series is still relatively limited (1973-1987) and it is therefore advantageous to be able to associate taxa found in Galway Bay with a regional category that has been more extensively sampled using CPR. Besides being important for understanding plankton dynamics themselves over time, this approach can provide information towards greater understanding of community interactions including wild and commercially farmed fish species off Ireland's west coast (Dransfeld et al., 2002) that prey on calanoid copepods during particular life stages (Beaugrand et al., 2010).

Population (a) synchronies between different populations of the same species have been documented in recent years ranging from time series within and between ocean basins (Alheit et al., 2007). With the focus on commercially fished small pelagics such as anchovies and sardines, studies investigating population linkages between zooplankton populations in different regions have been rare (Richardson and Schoeman, 2004; Mackas et al., 2006; Mackas and Beaugrand, 2010). We can infer as to the possible mechanisms which link Galway Bay with the associated eco region based on the type of relationship (positive or negative) observed.

The majority of the taxa were found to have a positive relationship with at least one of the corresponding eco regions. Positive relationships between the two populations are indicative of a synchronised change in abundance. This connection can be perceived as being as a result of a direct (advection from one region to another) or indirect (similar climatic, environmental conditions) interaction between Galway Bay and the eco region.

Conversely a negative relationship implies that there was an asynchronous change in abundance between the two regions. Equally connections can be seen as being through either direct or indirect mechanisms but the responses of each of the populations to the climatic variation or to their local conditions differ (Genner et al., 2004).

The presence of zooplankton taxa within Galway Bay could either be due to advection in of plankters or of established breeding and overwintering populations within the confines of the Bay. It is not known whether breeding populations exist in Galway Bay for the taxa that were examined in this study. Preliminary observations on *C. helgolandicus* and *C. finmarchicus* revealed little evidence of established breeding populations within Galway Bay (Leahy, 1983). The populations of both species within the Bay are therefore likely to be dependent

upon oceanic inflow into the area. Most of the other taxa, with the exception of *T. longicornis*, are associated with shelf and transitional water bodies (Beaugrand et al., 2002), so it would be expected that much of the population changes in the Bay are also dependent on the advection of oceanic water.

The CS region had the greatest number of associations with zooplankton populations in Galway Bay; most of which were positive but one of which was negative. The association with this region is most likely due to the strong jet like currents that originate in the Celtic Sea and travel anti-clockwise around Ireland's west coast, particularly in the summer months (Brown, 2003). The species *A. clausii* and *M. lucens* which are both transitional shelf edge species (Beaugrand et al., 2003) were found to be most strongly associated with offshore and shelf edge regions (SE and RT respectively). There is a clear physical separation between these offshore waters and Galway Bay especially since a strong Irish Shelf Front separates inshore and offshore waters at this latitude. Plankton dynamics on either side of front are known to vary considerably with an earlier onset of the phytoplankton spring bloom and an advanced zooplankton grazing community inshore. However there are frequent oceanic water influxes onto the continental shelf through the Porcupine Sea Bight which could facilitate species transport into Galway Bay from the SE in particular (McMahon et al., 1995).

The abundance of *T. longicornis* in Galway Bay was significantly correlated with the IS region although there is no known connection between the two populations. Instead the explanation of this association may reflect that *T. longicornis* is primarily a neritic species and the population synchrony is due to the oceanographic conditions of both areas being similar with a tidally mixed water column and lower salinities (Hill et al., 1997).

While phytoplankton was not considered in this study, due to the lack of concurrent sample collections, observations were made between 1974 and 1998. Spring blooms within the Bay developed in February/March in 1974/5 (Pybus, 1996) but was found to be much later in more recent years (O'Boyle, 2010). The community is dominated by diatoms such as *Skeletonema* and *Thalassiosira spp.* in spring which gives way to a more varied diatom/dinoflagellate community structure throughout the summer although diatom spp. still remain most abundant (O'Boyle, 2010). Thermal boundaries which form at the mouth of Galway Bay separate the stratified shelf and mixed coastal waters. Diatom blooms still dominate the mixed side of the boundary especially at spring tides (Roden and Raine, 1994) suggesting that tidal inflow regulates nutrient transport.

There was a clear dissimilarity in zooplankton community structure in Galway Bay between the two decades 1970s and 1980s. This coincided with a time of measured changes in ecosystems right across the N.E. Atlantic and indeed the whole Northern Hemisphere. For example, in the North Sea, a shift has been observed in a suite of biological and environmental datasets including diversity of calanoid copepods and abundances of *C. helgolandicus* and *C. finmarchicus* (Beaugrand et al., 2004). Similar shifts have been observed in other animal groups including fish species and seabirds (Kenny et al., 2009). These changes were attributed to altered ocean-climate interactions of which changes in SSTs were the principal manifestations (Weijerman et al., 2005). An abrupt climatic and zooplankton shift was also observed in 1977 off the Californian coast suggesting basin wide changes were concomitant across the Northern Hemisphere (McGowan, 2003). In Galway Bay we also observed a change in the timing of seasonal maxima of zooplankton, principally in spring, with maxima showing earlier in the 1980's compared with the 1970's. This corresponded to an increase in SST which is in agreement with findings elsewhere (McGinty et al., 2011) and is most likely a physiological response of the plankton to rising temperatures (Edwards and Richardson, 2004).

Overall the environmental and climatic variables used in this study proved to be poor predictors of zooplankton variability within Galway Bay. In particular the large atmospheric circulation patterns such as the NAO were unable to capture the variability at the scale of Galway Bay. Cannaby and Sinan Husrevoglu (2009) found that the influence of the NAO close to Ireland's coastline was negligible. The ratio between the two *Calanus spp.* which show links with the NAO at basin scales (Fromentin and Planque, 1996) do not follow this pattern at local or regional scales. As a result, the dependencies in using climatic/environmental data to characterise large scale plankton dynamics do not simply translate to the local or regional scales and other processes (i.e.- biological) must be considered to adequately model the data.

We used the regional classifications, defined previously, to place the coastal sample set in Galway Bay into its LME context. These linkages could also be applied to other large estuaries on the European shelf. Much of the spatial and temporal structure has been modelled within these estuaries. The variation of plankton community structure within these estuaries is attributed to local environmental gradients and changes to the temperature (David et al., 2005; Marques et al., 2006; Moderan, 2010), turbidity (Sautor and Castel, 1995; Moderan, 2010), salinity (David et al., 2005; Marques et al., 2006) and freshwater inflow

(Castel, 1993). Much of the variance remains unexplained in these areas with up to 60% of the variance not accounted for by local environmental characteristics of the estuary (Irigoien, 2011). One possible source of this unexplained variance may be from the external influences of adjacent populations. In the Bay of Biscay freshwater discharge from the Gironde and Adour estuaries are known to influence the wider plankton structure (Albaina and Irigoien, 2004; Albaina and Irigoien, 2007) but the reverse effect of estuarine populations regulated by adjacent populations have not been addressed. We have shown that annual abundances in Galway Bay can co-vary quite closely with adjacent populations and as a result may exert a strong influence on the community structure within the estuary. Therefore we would consider it pertinent to include some function which describes the dynamics of the adjacent populations to an estuary in further studies.

Acknowledgements

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Table 1. The outcome of the regression models for each species. Included are the eco regions compared with the Galway Bay population for each species, the R^2 value and the region selected (subscript). Significance values ($<0.001^{*}$, $**<0.01$, $*<0.05$, NS= not significant). The Akaike weights w_i (scaled between 0-1) gives the likelihood the selected model is the best of those compared.**

Species	Ecoregions Modelled	Regression models R^2	Akaiake weights w_i
<i>Acartia clausii</i>	IS CM CS SE WT ABS RB RT MS	0.634** _{SE} Curvilinear	0.863
<i>Calanus Juvenile spp.</i>	IS CM CS SE WT ABS RB RT MS	0.713*** _{CS} Linear	0.973
<i>Calanus helgolandicus</i>	IS CM CS SE WT ABS RB RT MS	0.693*** _{CS} Linear	0.834
<i>Calanus finmarchicus</i>	IS CM CS SE WT ABS RB RT MS	0.104 ^{NS} _{SE} Linear	0.223
Small copepods (< 2mm)	IS CM CS SE WT ABS RB RT MS	0.434** _{CS} Linear	0.524
<i>Metridia lucens</i>	CM SE WT ABS RB RT MS	0.563** _{RT} Curvilinear	0.734
<i>Centropages typicus</i>	CM CS SE WT ABS	0.324 ^{NS} _{ABS} Curvilinear	0.419
<i>Candacia armata</i>	CM CS SE WT	0.950*** _{CS} Curvilinear	0.999
<i>Pseudocalanus elongatus</i>	CM CS SE MS	0.261 ^{NS} _{CM} Curvilinear	0.612
<i>Temora longicornis</i>	IS CM	0.388* _{IS} Linear	0.957
<i>Centropages hamatus</i>	N/A	N/A	N/A

Figure 1. (Main) Locations of the 810 plankton samples collected in Galway Bay (circles). The two SST locations from the HADSST1 model are also shown (Had1 and Had2, squares). (Inset) the locations of each of the nine eco regions used for analysis. The region ABN was not modelled due to insufficient sampling in that area. The red square indicates the location of Galway Bay.

Figure 2. a) the normalised (1961-1990) SST values from the Had 1 and Had 2 datapoints. The dashed line represents the least squares regression fit to the data and b) The NAO winter index (December, January, February) (solid line) and the Gulf Stream index (dashed line) between 1973 and 1987.

Figure 3. Best fit linear and curvilinear regressions for the annual abundance of each of eleven taxa (species and groups) in Galway Bay and for the selected eco region (see Table 1).

Figure 4. Time series plots (Jan 1973-Dec 1987) for each of the eleven taxa that were modelled using GAM in Galway Bay. Also shown is the SST time series taken as an average of the Had 1 and Had 2 datapoints. No samples were available for the period Jan 1980-Dec 1982. Please note differences in scale across the taxa.

Figure 5. The change in the centre of gravity in decimal months of the a) Spring and b) Autumn seasonal maxima for each of the eleven taxa over a 14 year gap between 1973 and 1987. The figure is centered to the centre of gravity between 1973 and 1978 (Mean +/- SE) and the relative change in the centre of gravity (decimal months) between 1973-1978 and 1983-1987 is shown. Species are listed in ascending order from the most positive to most negative change. Significant changes ($p < 0.05$) in the timing of the seasonal peak are indicated by an asterisk *

Figure 6. A Principal Component Analysis (PCA) of the average annual abundances of eleven taxa (species and groups) in Galway Bay. 72% of the variability was accounted for by the first two principal components

Figure 7. The ratio between the average annual abundance of the two *Calanus* spp. in Galway Bay: *Calanus helgolandicus* (black) and *Calanus finmarchicus* (white).

Figures

Figure 1.

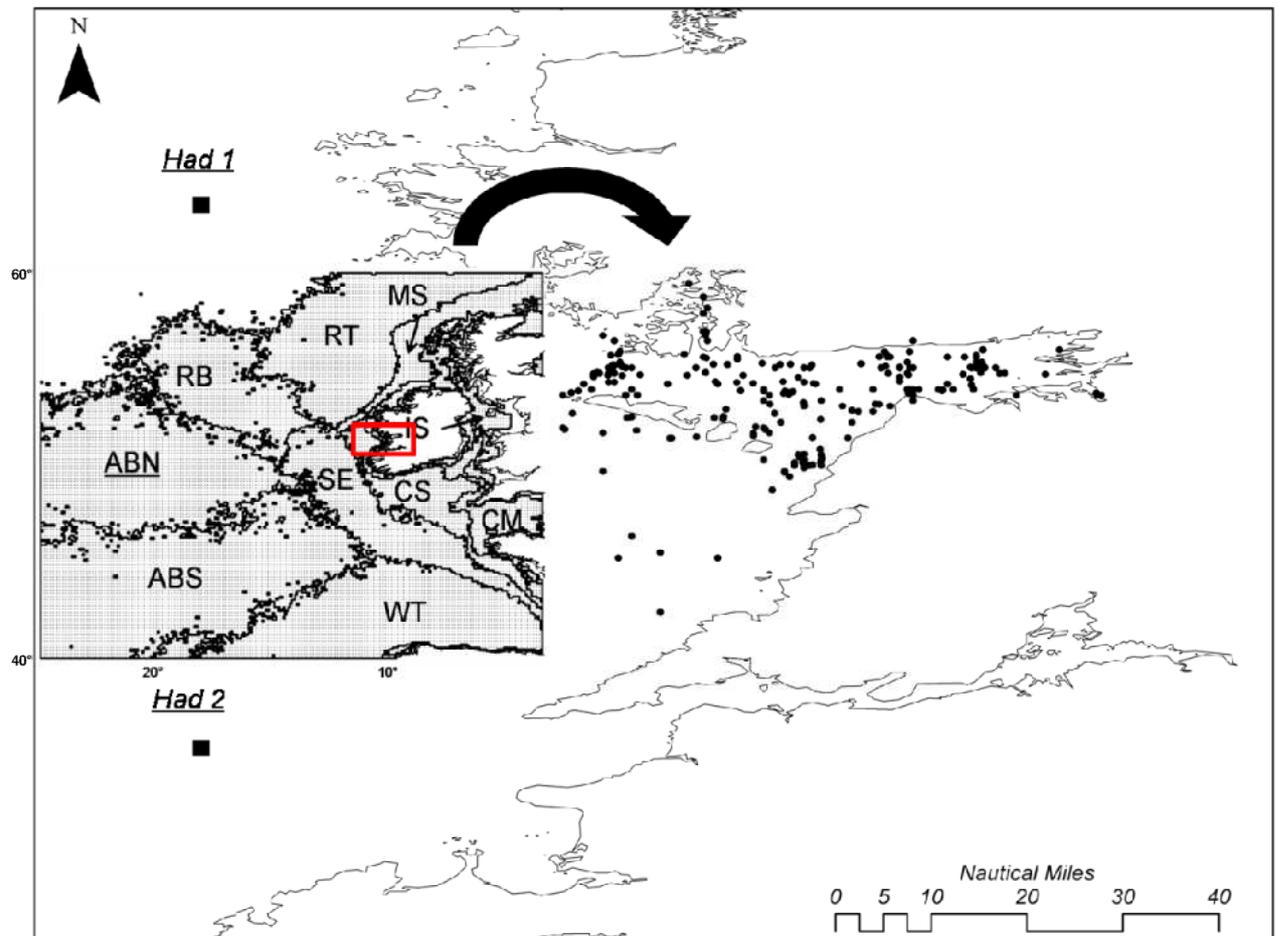


Figure 2a,b.

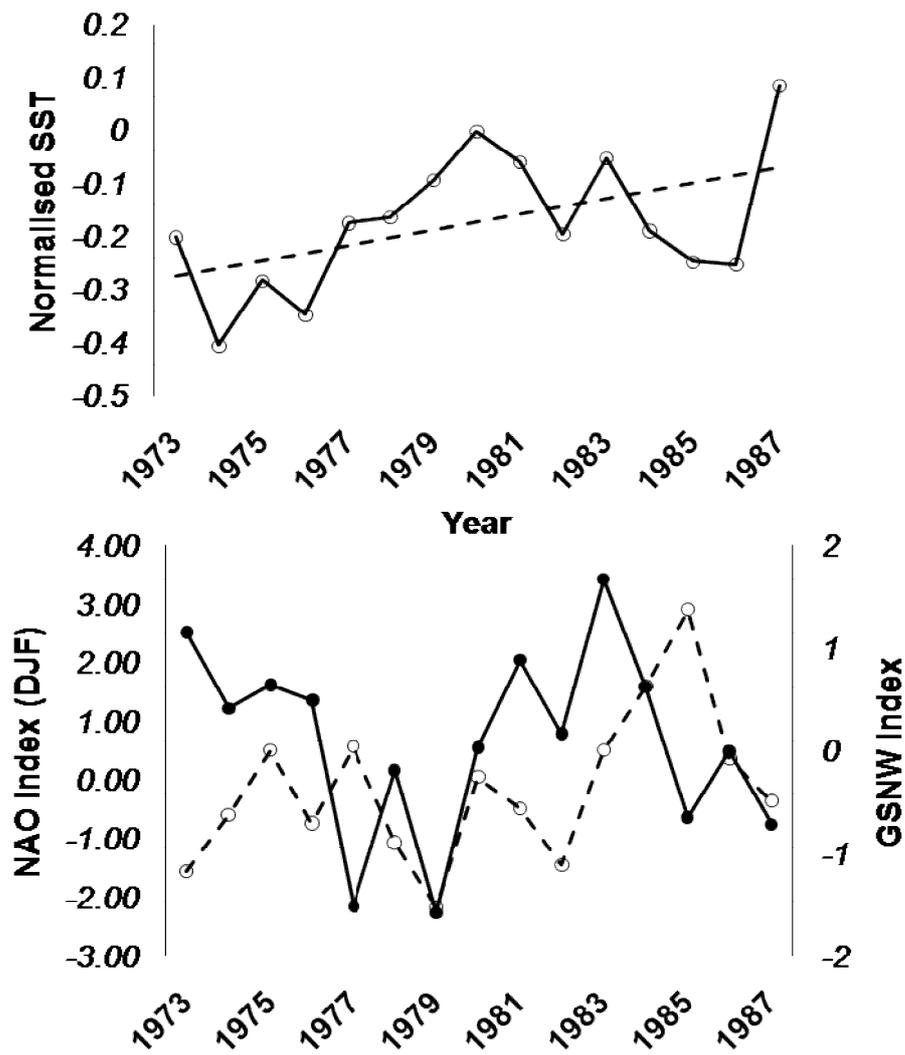


Figure 3.

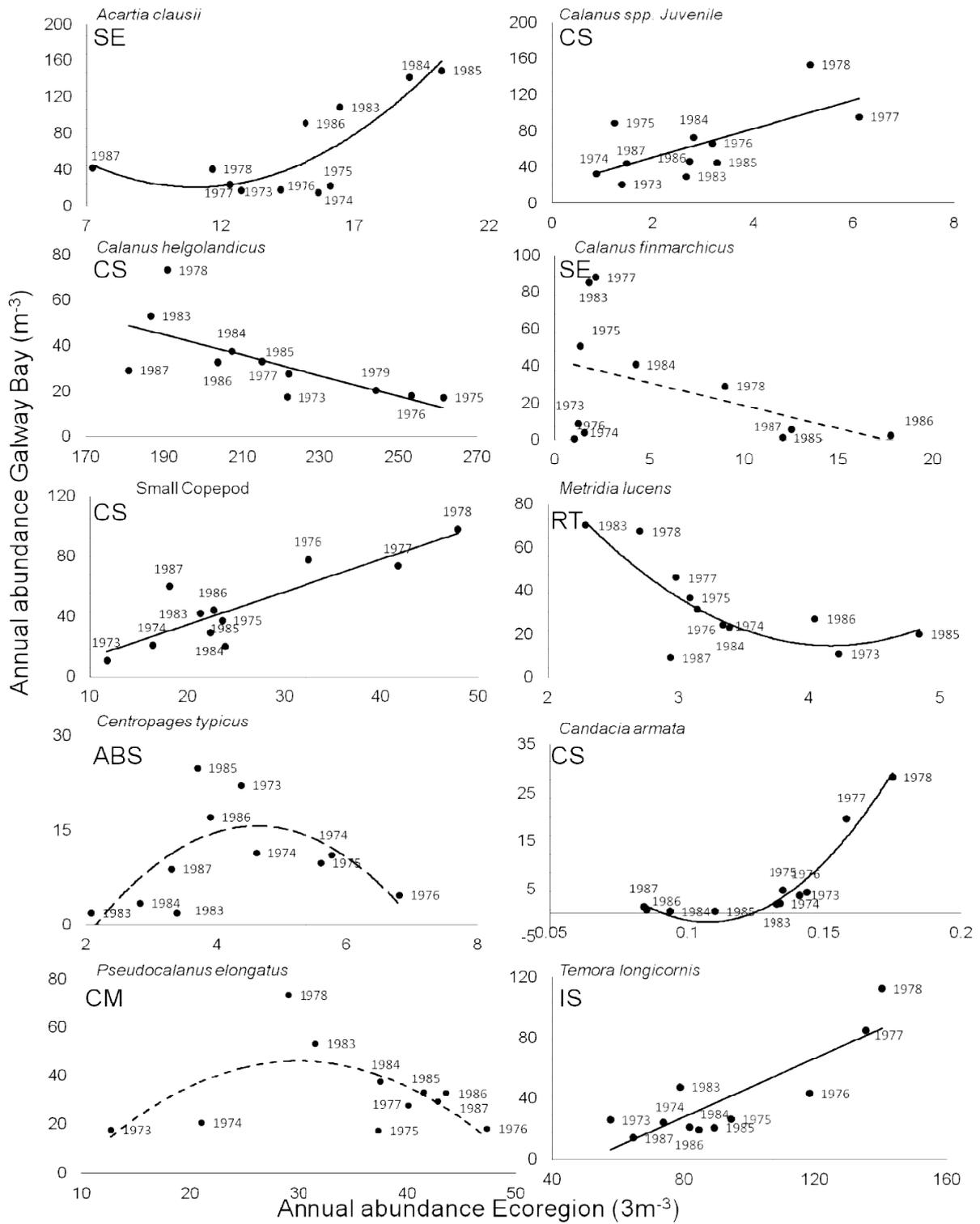


Figure 4.

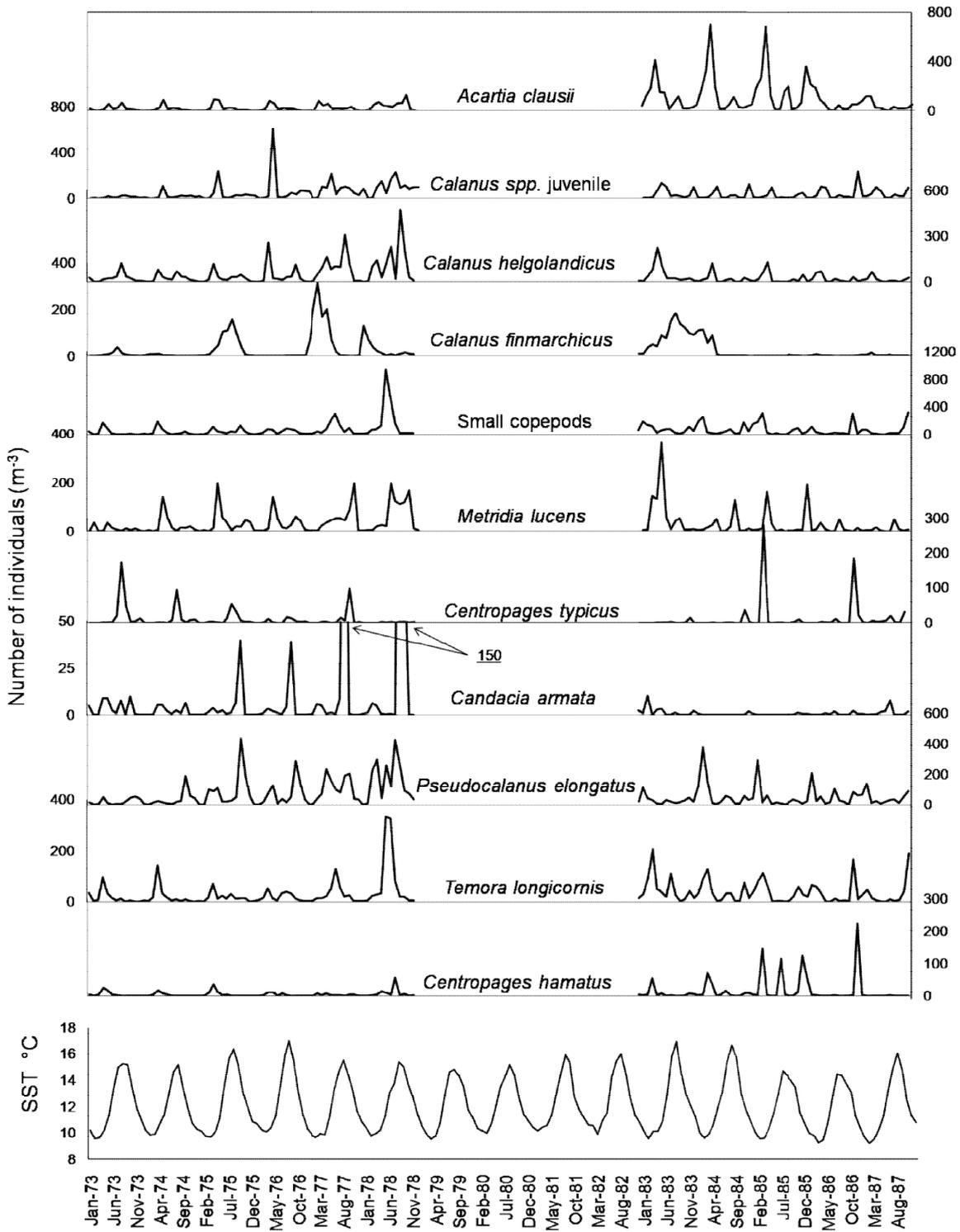


Figure 5.

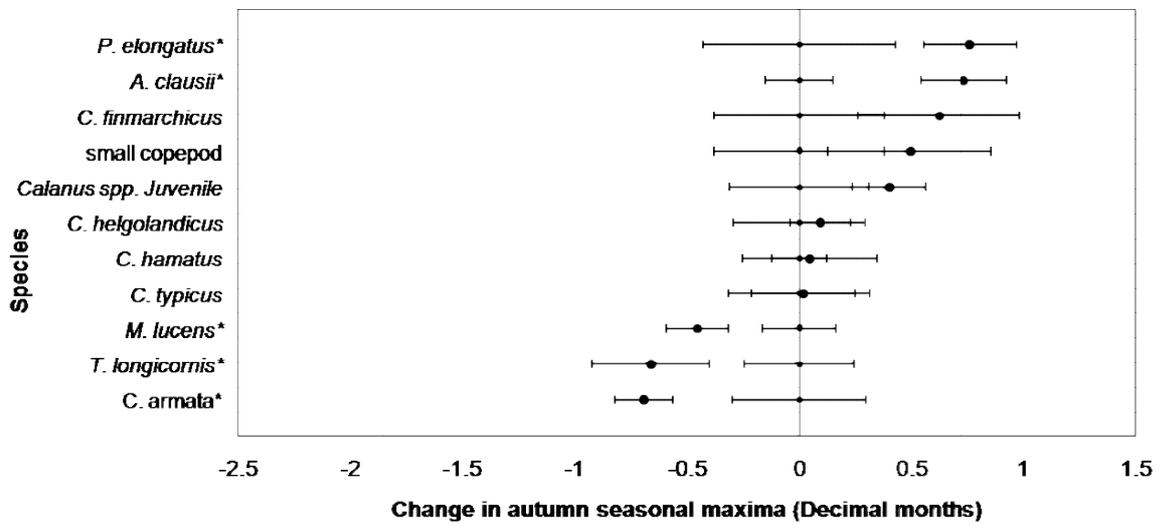
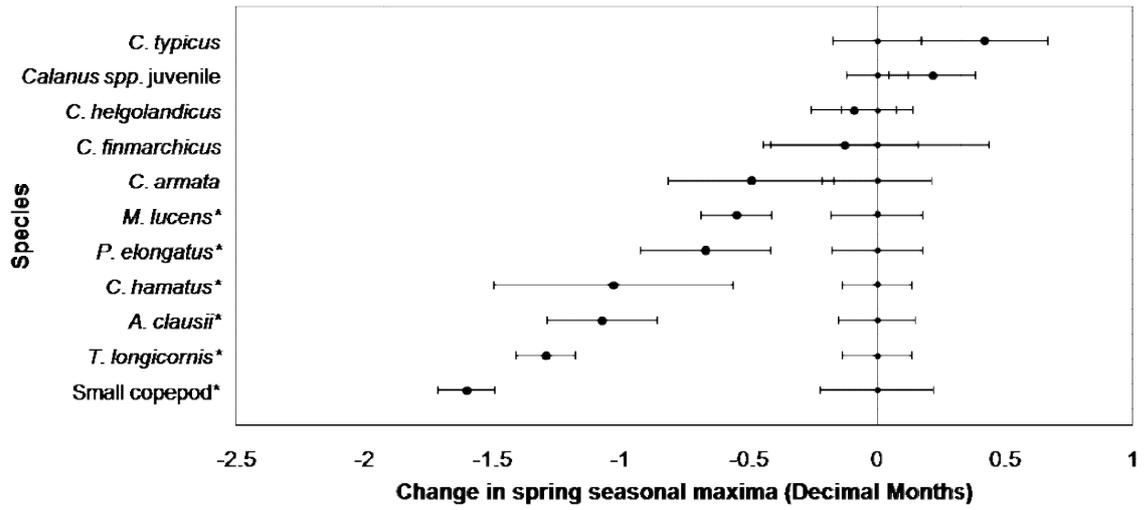


Figure 6.

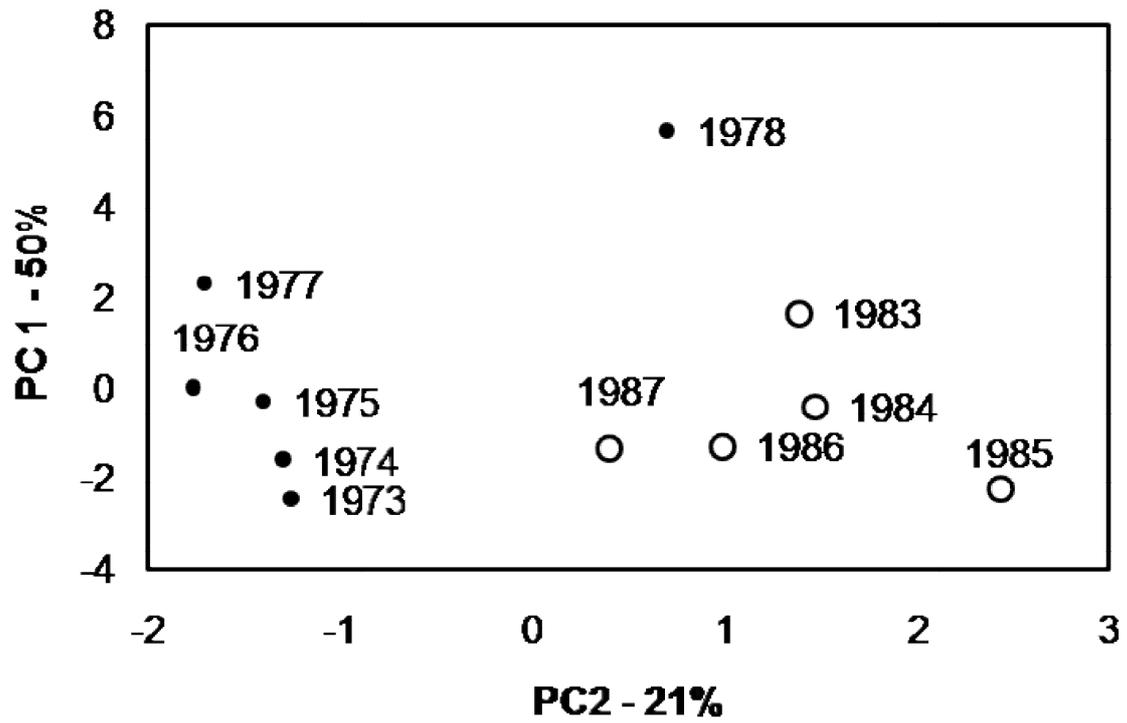
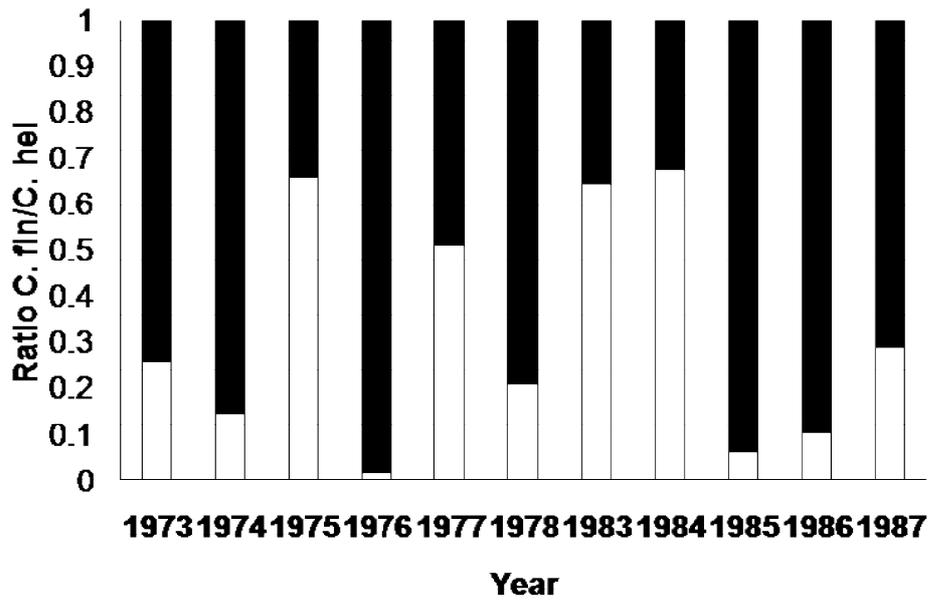


Figure 7.



Chapter 5

Zooplankton variability and the origin of zooplankton assemblages of the Celtic Boundary Front

Abstract

The Celtic Boundary front (CBF) is a thermohaline front dividing the waters in the permanently mixed Irish Sea and seasonally stratified Celtic Sea. Patterns of zooplankton variability have been assessed across similar fronts revealing strong community differences between water masses and a transitional community which show elevated biomass. *Acartia clausii* dominated the entire region and contributed ~50% of the total biomass. It is believed that swimming and migration behaviour specific to this species has enabled the population to proliferate across the entire frontal region. Clustering revealed four clusters dividing the Celtic Sea, Irish Sea and water above the Celtic Deep. Typically zooplankton biomass was much lower above the Celtic Deep in an area with a high Potential Energy anomaly (PEA) $>100 \text{ j m}^{-3}$. Species were found to prefer particular environmental conditions along a high-low gradient of temperature, salinity and chlorophyll concentrations. There was still a large degree of unexplained variability which could be partly explained by geographical distance between stations. Environmental variables explained $< 5\%$ of the variability within the Irish and Celtic Sea groups but almost 25% of the variance could be explained in the Celtic Deep group. SIMPER analysis revealed that the three major zooplankton assemblages had similar within group similarity and that the Celtic Deep group was the most distinct. All species with the exception of *Metridia lucens* were found to be lower in the Celtic Deep cluster. Similar species variability within the three groups eliminated the possibility that sampling bias, missing dense aggregations within this area was responsible. These findings are counter intuitive to what was expected as dense aggregations of biogenic material tend to aggregate at frontal boundaries. Limitations in our survey design have prevented any strong explanations to be developed for this result. It is hoped that the results of this work can be used with a local hydrodynamic model to help us to understand the Celtic Deep anomaly through tracking the seasonal development of the assemblages at the front.

Keywords: Celtic Front, thermohaline, zooplankton, clustering, assemblages, SIMPER

Introduction

Over the last forty years the water column structure of the Celtic Boundary Front (CBF) has been studied extensively. The formation and development of the CBF is largely understood and much of their development can be modelled using isopleths defined by the h/u^3 criterion (McMahon et al., 1995; Simpson and Hunter, 1974). The CBF is classed as a “Type II” thermohaline front (Hill and Simpson, 1989). The onset of the CBF can be seen from May when the warming of the sea surface, leads to thermal stratification as there is insufficient turbulent energy available to mix the water column of the Celtic Sea (Simpson, 1976; Hill et al., 2008). The Southern and Eastern areas of the Irish Sea remain vertically mixed year round as tidally generated turbulent energy remains sufficient (Hill et al., 1997). Beneath the thermocline, a dense pool of relatively saline cold waters develops which represent the vestiges of the previous winter (Horsburgh et al., 1998; Hill et al., 2008). The warming of these waters are very slow (2°C every 100 days) and the waters remain much cooler than the surface waters until the break down of the thermal stratification in Autumn (Hill et al., 2008). The CBF forms in the St. George’s channel and develops a characteristic “S” shaped meander in the position of the CBF which is thought to be due to the topographical constraints placed on the jet like baroclinic flows in the area (Pingree, 1976; Brown et al., 2003).

The chlorophyll and nutrient concentrations across the front have been analysed quite comprehensively (Savidge, 1976; Pingree et al., 1978). Subsurface chlorophyll levels generally peak at the CBF with the horizontal spatial extent of the abundance peak ranging from ~1-10nm and similar boundary peaks are also observed in the nitrate concentrations (Savidge, 1976). At the boundary of tidally generated fronts it’s generally considered that the chlorophyll accumulation arises as a result of the entrainment of the phytoplankton species from the frontal convergence (Le Fevre, 1986; Simpson et al., 1979; Franks et al., 1992). This enhanced primary biological productivity is known to benefit higher level organisms creating biodiversity hotspots attracting large numbers of higher trophic level organisms (Munk et al., 2003).

Recurrent studies assessing the meso scale dynamics of the phytoplankton and zooplankton community structure, have been performed further south along the Armorican and N.W. Iberian shelf in recent years (e.g.- Gil et al., 2002; Albaina and Irigoien, 2004; Fernandez et

al., 2007). These have found that, using high frequency sampling, where distances between stations range between ~5-8nm, it is possible to relate local hydrographical conditions to zooplankton species distributions (Gil et al., 2002; Albaina and Irigoien, 2007a). These fronts differ from the CBF as the near shore fronts off Spain which are “Type 1” upwelling fronts that develop from the upwelling of cold dense oceanic water up the continental slope to the narrow shelf plateau of this area. They do however impact upon zooplankton distributions in the same way by generating a strong environmental gradient dividing zooplankton communities. Frontal structures can lead to the development of distinctive zooplankton populations on either side of the boundary which form distinct communities with species which have a particular water body association (Ashjian and Wishner, 1993). It may also be the case that transitional waters are detected which exhibit their own unique zooplankton community structure (Albaina and Irigoien, 2007b) or that one species may come to dominate due to specific advantages due to its life history strategy and display a cosmopolitan distribution right across the frontal area (e.g.- *Nannocalanus minor*; Ashjian and Wishner, 1993).

Elsewhere on the European shelf, similar patterns of zooplankton variability at thermally stratified frontal regions have been detected. In the N.W. Mediterranean Molinero et al., (2008) found clear distribution patterns in phyto- and zooplankton across a thermal boundary front. Both these regions have been examined at a high sampling frequency over a number of years generating an understanding into the seasonal and multi annual fluctuations in hydrobiological interactions (Fernandez de Puelles and Molinero, 2008). In contrast less is known about the distribution of the mesozooplankton around the CBF. While we have a detailed understanding of the physical characteristics and the nutrient and chlorophyll variation for the area, the mesozooplankton community structure across the CBF remains largely unknown.

The aim of this study was to characterise the zooplankton community structure on both sides of the CBF using a high frequency Eulerian sampling grid. The linkages between the zooplankton taxa and the environmental variables were investigated in order to classify taxonomic preferences to the local hydrographical conditions. Recent evidence has hinted at the possibility that geographic distance across scales ~50 nautical miles (nm) may be a greater influence on zooplankton assemblage variation rather than prominent environmental predictors (Irigoien et al., 2011). This hypothesis is not new in other ecosystems such as

benthic marine habitats (Belgrano et al., 1995) but has only recently been applied to zooplankton assemblages on the Armorican Shelf (Irigoiien et al., 2011).

The outcome of this study may enable us to make comparisons between the zooplankton dynamics at the CBF and with other similar structures on the European Shelf. The CBF is much more of a dynamic frontal boundary in contrast with the shelf fronts. Being on the continental plateau and close to the U.K and Irish coasts the front is affected by local spring-neap tidal cycles shifting the position of the surface boundary fronts (Simpson and Boyer, 1981) and the level of phytoplankton production around the boundary interface (Sharples et al., 2003). Therefore, particular focus will be placed on the differences with the between and within group variability of identified zooplankton communities and their temporal resilience to shifts in the position the CBF.

Methods

The location of the study area can be seen in Fig 1. Samples were collected between the 14th-19th June 2009 onboard the *R.V Celtic Voyager* within a high frequency Eulerian sampling grid of 44 stations, each separated by ~8 nm. The CBF had already established during the previous month and was apparent from the remote sensing data from the AVHRR 1km (satellite which measures ocean radiance to generate sea surface temperature data) which were obtained via the Plymouth Marine Laboratory (PML) gateway. Satellite data were used onboard, along with the *in situ* temperature measurements in order to track any changes in the boundary front and allow equal sampling on each side.

Zooplankton samples were collected by means of a WP-2 zooplankton net with a mesh size of 200 μm (Unesco, 1968). The depth never exceeded 110 m at any station and net casts were towed vertically at a constant velocity from 10 m above the sea floor to the surface. Filtration efficiency was calculated using the formula $R = H \times \frac{B}{A}$ where H =Total Mesh area, B = Net porosity and A =Area of mouth opening. Values below 10.5 (arbitrary units) are considered to be effective in preventing clogging of the net (Hernroth, 1987). Net samples were preserved immediately in 4% buffered formalin solution for subsequent enumeration. A sensor array (CTD; SBE 911) was used at each station to give a depth profile of the temperature, salinity, conductivity, fluorescence and density (expressed as sigma-t) at each station. The Potential energy anomaly (PEA) is used as a measure of stratification intensity at

each station and is defined as the energy required (per unit depth) to completely homogenise the water column. The equation for the PEA as defined by Simpson et al, (1977) is:

$$\frac{1}{D} \int_{-H}^n g z (\bar{p} - p) dz$$

where g is the gravitational acceleration, z is the vertical coordinate, $-H$ up to the sea surface n , $p(z)$ is the density profile in a water column of depth $D = H + n$.

The preserved zooplankton samples were examined in the lab under a stereo microscope and enumerated and separated to either the level of genus or species for the major haloplanktonic groups and the meroplanktonic forms were usually identified to family level or more general categories. Where possible, copepod species were separated by development stages where copepodites refer to the stages I-IV and adults are V-VI. For each sample a suitable number of subsamples are taken until at least 300 individuals had been encountered. The counts for each of the samples were scaled up for the whole sample and given in densities m^{-3} .

Statistical analysis

The biological data were stored in an ($n \times p$) matrix where n =species and p =stations. The number of individuals for each species was log transformed $\log_{10}(x+1)$ to downweight the higher values, which have a greater impact on the similarity between stations. Stations were clustered using a Bray-Curtis similarity metric on the most dominant species abundances (>1% of total) in order to reduce the double zero effect (similarity can be high when many zeros are present at each station) and clustered using a complete linkage clustering method. Similarity between and within the major groups were determined using the SIMPER routine in the Primer package (Clarke and Warwick, 2001). Because the Bray-Curtis dissimilarity measure includes the contribution of each species to the variation, the average dissimilarity between two sites can be expressed in terms of the average contribution from each species. The standard deviation provides a measure of how consistently a given species will contribute to the dissimilarity. A good discriminating species contributes heavily to the dissimilarity and has a small standard deviation.

In some cases, a single species has been found to dominate the zooplankton community around frontal features. A K-dominance plot was used to summarize the relative abundances

within each cluster. Dominance by a few species can be interpreted as opportunistic growth in response to local conditions or selective retention of the abundant species.

To contrast the contribution by species of different sizes to the observed patterns biomass estimates were made using the average length-weight relationship for zooplankton. Length weight relationships for almost all organisms follow a power law of the form ($W=aL^b$), where a and b are constants, L is the body length (mm) and W is the wet weight (mg). The relationship described in Peters (1983) where ($W=0.08 \times L^{2.1}$) can be fit to almost all species of plankton and has been used successfully on a number of occasions on plankton data (e.g. Beaugrand, 2003; Brander et al., 2003). The wet weight was obtained for all species where length data was available. For this dataset length measurements were found for 97% of the total number of individuals counted.

A combination of both a canonical correspondence analysis (CCA) and a generalised additive model (GAM) were used to relate the environmental variables with zooplankton abundances. The significance and R^2 value of each environmental vector were calculated using a Monte Carlo resampling procedure. Those variables which were deemed significant ($p<0.05$) were used for both the GAM and variance partitioning evaluation (VPE) (Borcard and Legendre, 2000). VPE is analogous to generating partial R squared values for each explanatory variable but in the case of VPE the relationship does not need to be linear. The CCA is a constrained ordination procedure that can be used to interpret the abundance and distribution of a species matrix with a number of environmental variables. Multivariate GAM models can be used on a species matrix using similar model validation methods to those used in univariate GAMs. The resulting output produces a smoothed 2 D contour surface of environmental gradients on the CCA plots which allows an easier visualisation and interpretation of species/station ordination with the environmental variables (Surface and bottom temperature, PEA, Surface salinity, fluorescence; *chl-a*). Mantel and Partial Mantel tests were used to determine the strength of correlation between the species and environmental matrix (Mantel) and the correlation between the species and environmental matrix conditioned on the geographic distance (Partial Mantel). Variance partitioning is used to determine the percentage of variance explained by both the environmental and geographic distance matrices. The method is performed for both the within and between group variability. The significance of the partitioning was tested with a Redundancy analysis (RDA) on the species and environmental matrix with geographical distance used as a conditioning factor. A permutation ANOVA on the RDA output tested whether the variance explained was significant. All analyses were

performed using functions within the *vegan* package (Oksanen et al., 2006) for the R programming environment (R Development Core Team, 2008).

Results

Water column structure across the boundary front

The characteristics of the water column for this time of year were found to be in agreement with the known hydrography of the area. Satellite imagery of the SST for the CBF for the week between 14th and 21st June shows the position of the boundary front layer (Fig 1; inset). The “S” shaped meander of the frontal boundary is readily apparent as the western protrusions of water from the Irish Sea in the Celtic Sea and a larger tongue of Celtic Sea water extending northwards over the Celtic Deep.

Vertical profiles were taken along three transects marked in (Fig 1) that crossed the boundary front from the Celtic Sea into the Irish Sea (Fig 2 a,b,c). The strong vertical thermal gradient found on the Celtic Sea side shows that the summer thermal stratification was already well established. Surface temperatures in the Celtic Sea were in excess of 13 °C. This isopleth can be used to indicate the position of the Celtic boundary front. Across the boundary temperatures abruptly dropped to between 11 and 12.5° C. There is also an abrupt discontinuation in the thermal gradient and the relative difference between the surface and bottom temperatures (SI) decrease from >4°C to <1°C Fig 2 a,b,c. Within the Celtic Deep trough there is a pool of colder (9°C) and saline (35.1) waters visible in all transects (Fig 2 a,b,c). The Potential Energy Anomaly (PEA) revealed high stratification intensity in stations above the Celtic Deep with a PEA of between 77- 108 J m⁻³. In contrast to stations within the Irish Sea the PEA at these stations were over one tenth the intensity found above the Celtic Deep with values consistently <10 J m⁻³ (Fig 3). The two CTD profiles from either side of the front showed a stark contrast between the structures of the two water columns (Fig 4). Station 17 (see Fig 1 for location) taken within the Irish Sea had a relatively homogenous water column both in temperature and fluorescence (chlorophyll). In contrast at station 44 (see Fig 1 for location), which was located within the Celtic Sea had a sharp and pronounced thermocline in the upper 50m. where the water temperatures changed by over 5°C across the gradient. There was also a subsurface fluorescence peak between the 20-40 m depths.

Zooplankton community structure

Forty eight taxa were found within the stations samples (Table 1). Copepods tended to dominate the samples contributing to almost 75% of the total number of individuals: *Acartia clausii* was responsible for over 60% of that number. Any of the other high abundance categories belonged to other small Copepod spp that are < 2mm in length. *Pseudocalanus elongatus*, *Temora longicornis* and the small copepod category (copepodite stages of *Pseudocalanus*, *Paracalanus* and *Ctenocalanus* and unidentified copepods <1.5mm) are also highly abundant within this region. Other members of the zooplankton community which were found in considerable numbers included the cladoceran *Evadne* spp. and the Appendicularians.

Zooplankton biomass varied across the sampling grid, displaying a close affinity with the position of the CBF (Fig. 5). The highest biomass was found in the Celtic Sea in the S.W. corner of the grid. Wet biomass in this area ranged from 98-310mg m⁻³. In contrast the stations found across the Celtic Deep show particularly low zooplankton biomass ranging from 7-45 mg m⁻³. The stations within the Irish Sea showed intermediate levels in zooplankton biomass with a greater range in values from 21.43 mg m⁻³ in the southward protrusion to 211.24 mg m⁻³ in the N.W. corner of the grid.

Based on the cluster dendogram, four major groups were defined across the CBF (Fig 6a). The first cluster (Celtic Sea; filled triangle) grouped those stations found in the stratified part of the Celtic Sea situated in the south west of the sampling grid. The second cluster (Irish Sea; filled circle) identified those stations within the tidally mixed Irish Sea and the third (Celtic Deep 1; cross) and fourth (Celtic Deep 2; filled square) identified stations which are found in the tongue of water above the Celtic Deep which protrudes northwards into the Irish Sea. Similar to the zooplankton biomass, the clustering of the stations is spatially coherent and is divided by the 13°C isopleth which marks the boundary of the CBF (Fig 6b).

In all clusters the most numerically dominant species was found to be *A. clausii* but the overall abundance and composition of the most abundant taxa vary within each cluster. Average similarities within clusters vary between 70% (Celtic Deep 2) and 78% (Irish Sea) (Fig 7). The Irish Sea cluster was largely dominated by small copepod species. Species with coastal or neritic associations such as *Temora longicornis* and *Centropages hamatus* are numerically abundant within this cluster (Fig 7).

The Celtic Sea cluster had a much more even community assemblage. While *A. clausii* remained the most dominant species in this cluster, it did not numerically dominate the community in contrast to other clusters. Non copepod members of the mero- and holozooplankton community are found in relatively high numbers including the cladoceran *Evadne spp.* which was the second most dominant taxa, and Appendicularia and echinoderm larvae are regularly found in the samples. This area also has the highest abundance of zooplanktonic taxa out of the major clustering groups. For example the total number of individuals counted in the Celtic Sea cluster were almost 10 times greater than the number of individuals within the cluster groups found above the Celtic Deep (cross and filled square) (Fig 7). The cluster which contains two stations was the most different in comparison to all other clusters (Fig 7). While the average abundance of *A. clausii* was largely similar to other Celtic Deep cluster, the other species had relatively low abundance levels $<10 \text{ ind m}^{-2}$ (Fig 7).

The SIMPER analysis examining the between group variability found that the average dissimilarity between regions varied between 32.68% (Irish Sea: Celtic Sea) and 48.85% (Celtic Sea: Celtic Deep 2). The Celtic Deep cluster grouping was the most distinct of the three regions investigated. The change between the Irish Sea and Celtic Sea clusters are characterised by lower species abundances in the Irish Sea for most taxa, in particular the cladoceran genera (*Evadne spp.* and *Podon spp.*) and echinodermata larvae and higher abundances for neiritic copepod species such as *T. longicornis* and *C. hamatus*. The Celtic Deep cluster showed much lower species abundances compared to the two other clusters with the only exception being *Metridia lucens*. The species which contributed to the dissimilarity with the Celtic Deep clusters were reasonably similar for both the Celtic Sea and Irish Sea clusters. The taxa which contributed greatly to the dissimilarity were the cladoceran genera, gelatinous plankters (Hydromedusae and Appendicularia) and several copepod species (*C. hamatus*, *C. typicus*, *T. longicornis* and *A. clausii*)

The first 8 species in each region make up over 95% of the total number of individuals for each cluster grouping and these taxa tended to be members of the Copepoda class (Fig 8). The Celtic Deep cluster (cross) was the most distinct from the other groups with 85% of the abundance dominated by only 1 species (*A. clausii*).

Relationship with environmental variables

The correlation between the species and the environmental matrix using the CCA explained 72% of the variance. All of the five environmental variables were found to be significant at

the $p=0.001$ level (Table 2). The first four environmental vectors were oriented along the y axis in the CCA biplot creating a similar gradient pattern for the taxa. Increases in surface temperatures coincided with increases in salinity, SI and *chl-a* which would be the pattern, observed travelling across the front from the Irish to Celtic Sea.

The influence of environmental variables on the relative position of species in the CCA ordination is shown using contours from GAMs fitted to the species matrix using the four dominant environmental variables overlaid on the biplot. These visualise the preferred environmental condition for each of the 35 most abundant species in the vicinity of the CBF. Surface temperature (red) and salinity (green) contours are displayed in (Fig 9) while chlorophyll (red) and SI (green) contours are displayed in (Fig 10)

Using the fitted outputs for the two most important environmental variables (surface temperature and salinity) a scatter plot displays distinct clustering of stations based on the clustering of species abundances (Fig 11).

Both the mantel and partial mantel tests were significant (mantel $x_m=0.177$, $p<0.001$; partial mantel $x_{mp}=0.156$, $p<0.001$) with little difference found between the two tests. However further analysis into the partitioning of variance reveals that with between group variability, the geographical distance explains a greater amount of the variation in zooplankton community structure in contrast to using only environmental variables (Fig 11). Within group variability for the Celtic Sea and Irish Sea cluster reveal a similar pattern with geographical distance prevailing over the environmental variables in terms of variance explained. The Celtic Deep 2 cluster however, showed the environmental variables to be marginally better in explaining the within group variability. The overall variation explained within the Celtic Deep 2 cluster was almost double the levels explained within the other two clusters (46%; Celtic Deep to 34% and 22% within the Celtic Sea and Irish Sea clusters respectively)

Discussion

The results from this study suggest that although the CBF is a dynamic feature which is subject to periodic fluctuations in its boundary position, the zooplankton assemblages that were identified are likely to be found again if the sampling were to be repeated while the front is still present. Similar within group variability was found for the three principal cluster groups with the differences between the highest and the lowest percentage being $< 10\%$. Similar standard deviations were found for each of the highest contributing species to each

cluster which would suggest even further that the assemblages are stable over the summer months until the break down of the CBF.

The Irish and Celtic Sea clusters displayed the greatest level of similarity with each other while the Celtic deep clusters were more dissimilar with much lower levels in zooplankton biomass. Combined with measurements of current velocities parallel to the front which are strongest around the Celtic Deep and weakening further west (Brown et al., 2003) we believe that the greatest amount of cross frontal mixing occurs in the SW. This generates a zooplankton assemblage that is more insular from the surrounding communities. There was no evidence to suggest the presence of any transitional communities within the boundary front. Instead we saw zooplankton assemblages divided by the frontal boundary producing a sharp ecotone between the communities.

Perhaps the most interesting feature is the low zooplankton biomass and abundance found in the area above the Celtic Deep. The hydrographic conditions of the water column are similar to those found in the Celtic Sea in the SW of the sampling grid. Both areas have a well developed thermocline and a peak in fluorescence which is most likely the subsurface chlorophyll maxima at approximately 15-20 m. One clear difference between both areas of the grid is the average levels of the PEA. The maximum values for the PEA are all found above the Celtic Deep which is indicative of a stronger gradient between the bottom and surface waters. This may reduce the level of vertical nutrient fluxes into the upper water column above the Celtic Deep, rapidly depleting the available nutrients. This will create an island effect where the waters above the Celtic Deep will actually create an area of low biomass where typically plankton biomass is thought to propagate. Such thermohaline fronts usually facilitate phytoplankton growth which in turn results in high zooplankton abundance which benefit from the rapid phytoplankton turnover (Franks, 1992). However owing to the characteristic topography of this area we find the contrary to be true.

The only species that was found in higher concentrations in this region was the oceanic species *Metridia lucens* and the region over the deep also had the only records for another oceanic species, *Parapontella brevicornis* (Beaugrand et al., 2004). 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). In comparison with shelf waters, oceanic waters typically have lower biomass but higher nutrient concentrations (Beaugrand et al., 2002). However maximum fluorescence above the Celtic Deep is higher than both the Celtic

and Irish Sea. This prevents us with a difficult conundrum as the observations of low zooplankton biomass in this area are in direct opposite to what would be expected in this region. Similar variation in the community structure compared to the Irish and Celtic Seas remove the possibility that within this cluster the discrepancy is caused by missing dense aggregations. Unfortunately nutrient data were not collected during the cruise which could have assisted in identifying the potential productivity of different water bodies and their origin.

Each of the zooplankton species showed a preference to particular conditions along the environmental gradients. Most of the environmental variables (with the exception of bottom temperature; TB) largely follow the same patterns which mark the conditions experienced when crossing the front from the Irish Sea (low surface temp, *chl-a*, salinity) to the Celtic Sea (high surface temp, *chl-a*, salinity). The species occupied certain environmental bands indicative of water bodies that they are known to be associated with. For example *Centropages hamatus* and *Temora longicornis* are two of the most dominant species in the Irish Sea and these species occupy environmental bands associated with Irish Sea conditions. On the other extreme are the two oceanic species of *Metridia lucens* and *Parapontella brevicornis* which occupy the higher gradient bands.

Albaina and Irigoien (2011) suggested that geographical distance between stations can act as a better predictor of zooplankton distribution compared to environmental characteristics as species display associations with distribution centres rather than water masses. We found a marginal improvement in the level of variance explained with geographic distance over the whole sampling grid and this improvement was even greater in the Irish and Celtic Seas clusters where environmental predictors explained < 5% of the variance. This is most likely due to the fact that environmental changes within these areas are significantly less than comparing across the whole sampling grid. The geographic distance likely picks up some of the spatial variability caused by the inherent patchiness of plankton distributions and the predator-prey interactions within this assemblage. In addition the environmental influences on distributions may be underestimated as measured variables may not capture the combinations of processes having most influence on zooplankton abundances.

Within the Celtic Deep the balance of environmental and distance related processes appeared to be different to the Celtic Sea and Irish Sea clusters. Environmental and geographic distance explained 25% and 23% respectively, levels greater than the variance explained over

the whole grid. The influence of environmental variability alone was similar to patterns within the Irish Sea and Celtic Sea clusters.

The copepod species, *A. clausii* displayed a cosmopolitan distribution and was found to be the most abundant in all clusters. On average the species contributed to half the total biomass in each sample and was as high as 85% of the biomass in some areas. The ubiquity of *A. clausii* across the front agrees with several other studies which have found similar single species domination across frontal boundaries (Olsen et al., 1994). The abundance of *A. clausii* in areas adjacent to the CBF (Irish Sea and Celtic Sea) is comparable to other species collected around the CBF (Gowen et al., 1998) but do not dominate the water column (e.g. *C. helgolandicus*). Zooplankton aggregations at frontal boundaries are not as a result of passive transport by current flows but are active responses to current flows (Genin et al., 2005). Zooplankton species can actively swim against current flows and maintain position in a water column causing subsurface aggregations. Although the physical or biological cues have not been identified possible sensitivity to pressure may be responsible (Genin et al., 2005).

Different species behave in a multitude of ways with different diurnal migration patterns, and swimming speeds. *A. clausii* and, to a lesser degree, small copepods belonging to *Paracalanus* and *Pseudocalanus spp.* be found at high densities at with wide distributions as their particular behaviour is selected for by the environmental conditions of the frontal region. The density gradients of the CBF increase in strength with depth with strong current velocities showing a negligible response to the spring-neap tide cycle which is in contrast to the surface waters (Brown et al., 2003). Wind driven frontal mixing at the sea surface provides a limited amount of cross frontal exchange (Wang, 1990). *A. clausii* may maintain a position high in the water column which allows greater dispersal, while other species may undergo vertical migrations where they meet more barriers to horizontal movement due to the greater differences between water masses at depth. Foraging activity in *A. clausii* is higher and more successful in turbulent water than calmer waters which may give the species a particular advantage at the frontal area (Saiz and Alcatraz, 1992).

The source populations of the species at the front are difficult to discern without adding a temporal element to this study. With some species it is possible to at least consider their likely origins based on previous work in the Irish and Celtic Sea and the results from this study. As mentioned previously, *C. hamatus* and *T. longicornis* along with two copepod species (*P. elongatus* and *A. clausii*) have known associations with the Irish Sea contributing

to between 79 and 83% of the total zooplankton biomass (Gowen et al., 1998). Species such as *Parapontella brevicornis* and *Metridia lucens* are of an off shelf and oceanic origin (Beaugrand et al., 2002) and have most likely arrived through Atlantic water found at depths under the Celtic Sea.

A Hydrodynamic model has been developed in the Irish Marine Institute modelling the seasonal development of the stratification process in the Celtic Sea and would be useful in understanding the temporal evolution of the zooplankton assemblages around the CBF. The results of this work could be used in cooperation with the hydrodynamic model in order to further elucidate the temporal zooplankton dynamics at the CBF.

As an aside it is worth mentioning that a number of individuals of the Lusitanian species *T. stylifera* were found at station 23 in the Celtic Sea (Lindley and Daykin, 2004). Primarily distributed off the Iberian Peninsula this species has been regularly sampled in recent years in the Bay of Biscay and as far north as the English Channel. This northward movement of the species distribution is thought to be attributed to warming sea temperatures pushing its biogeographical range northwards. This species, in conjunction with another sub tropical species *C. chierchiaie*, have been recommended as climate change markers for the Celtic Sea.

In conclusion, the Celtic Boundary Front marks the boundary between separate zooplankton assemblages, where changes between distinct species compositions occurred over relatively short distances. There was little evidence for a transitional assemblage at the front. The most distinct groups of zooplankton occurred over the Celtic deep. These were generally low in biomass and species poor, in one case dominated by *A. clausii*. As abundances were low over the Celtic deep, it seems likely that the dominance in this area was not due to opportunistic growth, but may be due to better dispersal of *A. clausii* in the frontal zone. The behaviour that allows *A. clausii* to persist where perhaps other species are removed by advection may also contribute to this species being the most widely found and most abundant species on both sides of the front.

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Table 1. The forty eight taxa found in the forty four Eulerian time series grid in ascending order. The mean, standard deviation (Stdev), minimum (Min) and maximum (Max) values are shown. Also shown are the shortened species codes used for the CCA ordination plots

Species	Code	Mean	Stdev	Min	Max
<i>Acartia clausii</i>	AC	521.369	541.778	22.2865	2417.21
<i>Evadne spp.</i>	EV	169.225	353.919	0	1302
<i>Para/Pseudo spp.</i>	SMT	116.208	80.1476	5.441	354.744
Copepods small	SM	69.927	62.7769	3.263	266
<i>Appendicularian</i>	AP	55.818	85.2011	0	448.1
<i>Temora longicornis</i>	TL	49.6764	76.0288	0	392.784
<i>Pseudocalanus elongatus</i>	PE	42.8734	30.4534	1.452	140.03
<i>Echinodermata larvae</i>	EC	19.1596	47.7985	0	266
<i>Centropages hamatus</i>	CHa	10.7941	20.8238	0	126.027
<i>Hydromedusae</i>	HM	8.02834	10.6296	0	47.1
<i>Cirrepeda larvae</i>	CI	7.71218	11.7048	0	53.05
<i>Calanus stage I-IV</i>	CJ	7.03914	8.64182	0	42
<i>Oithonia spp.</i>	OI	4.9292	6.93811	0	36.192
<i>Podon spp.</i>	PN	4.86057	10.1363	0	47.1
Polychaeta all	PO	4.58707	7.2724	0	36.41
Decapod larvae <2mm	DS	3.88141	4.48223	0	17.5
<i>Centropages typicus</i>	CT	3.13841	6.27499	0	32.673
<i>Calanus helgolandicus</i>	CH	3.12894	4.73665	0	24.505
<i>Microcalanus spp.</i>	MI	2.39116	2.71113	0	8
Gastropod veliger	GA	2.116	4.54479	0	24.503
<i>Metridia lucens</i>	ML	2.1064	5.10848	0	29.125
<i>Tomopteris spp.</i>	TO	1.4336	5.02853	0	32.674
<i>Chaetognatha</i>	Cgn	1.39736	1.54632	0	5.04

<i>Harpacticoida</i>	HA	1.03009	2.21899	0	9.802
<i>Ctenocalanus spp.</i>	CT	1.0163	3.68526	0	20
<i>Corycaeus spp.</i>	CO	0.96418	1.95708	0	9.802
Decapod larvae >2mm	DL	0.58134	1.11953	0	6.099
<i>Tiguiropsis spp.</i>	TI	0.50532	1.06699	0	4.67
<i>Candacia armata</i>	CA	0.26057	1.09438	0	6.84
Bivalve veliger	BI	0.15768	0.4168	0	2.1
<i>Parapontella brevicornis</i>	PB	0.14289	0.66289	0	3.267
<i>Pleurobrachia pileus</i>	PP	0.13643	0.18003	0	0.922
<i>Hyperia galba</i>	Hyp	0.1217	0.4799	0	3
Amphipoda		0.10182	0.38786	0	2
Fish larvae		0.09994	0.15181	0	0.616
<i>Isias clavipes</i>		0.09623	0.37293	0	2.004
<i>Zaus spp.</i>		0.09326	0.29659	0	1.155
<i>Calanus finmarchicus</i>		0.08468	0.27821	0	1.124
<i>Mysidacea</i>		0.07182	0.21345	0	1.306
<i>Diaxis pygmaea</i>		0.06188	0.21207	0	1.005
Monstrilloida spp.		0.03921	0.1933	0	1.225
Scyphomedusae		0.02998	0.14896	0	0.949
<i>Euchatea hebes</i>		0.02849	0.18463	0	1.225
<i>Temora stylifera</i>		0.02849	0.18463	0	1.225
Caligiloid		0.02426	0.05566	0	0.237
Ostracoda		0.02337	0.15147	0	1.005
Euphasacea		0.00979	0.05139	0	0.331
<i>Sapphirina spp.</i>		0.00953	0.0469	0	0.29

Table 2. The five environmental variables used for the CCA analysis including the strength of association with the first two CCA axes. The goodness of fit (R^2) of each of the variables is also shown. All variables are significant to the 0.001=* level**

Variables	CCA1	CCA2	R^2
Potential Energy Anomaly (PEA)	-0.2221	-0.975	0.4723***
Chlorophyll (CHL)	-0.4649	-0.8853	0.4647***
Surface temperature (ST)	0.06226	-0.9981	0.6389***
Bottom temperature (TB)	0.86072	0.50908	0.4234***
Salinity (Sal)	-0.6917	-0.7222	0.4762***

Table 3. The results of the SIMPER analysis between three of the four cluster groups. Celtic Deep 1 was not used due to an insufficient cluster size (n=2). Species are ordered in terms of their greatest contribution to cluster dissimilarity up until 75% of the dissimilarity has been accounted for.

Species	Av Abundance (Irish Sea)	Av. Abundance (Celtic Sea)
<i>Evadne spp.</i>	6.85	563.55
Echinodermata larva	4.79	57.78
<i>Podon spp.</i>	0.52	15.61
Appendicularian	33.93	143.8
<i>Centropages typicus</i>	0.74	9.4
<i>Calanus stage I-IV</i>	3.75	16.89
Hydromedusae	8.6	13.88
Small copepods	49.01	145.82

Polychaeta larvae	3.48	10.5
Cirrepeda	13.99	6.75
<i>Oithonia spp.</i>	2.79	9.52
<i>Acartia clausii</i>	382.44	1135.23
Gastropod larvae	0.64	5.96
<i>Temora longicornis</i>	56.8	58.98
<i>Calanus helgolandicus</i>	1.3	6.03
<i>Centropages hamatus</i>	19.4	10.79
Decapod larvae	3.83	7.37
Av. Dissimilarity=		32.68

	Av Abundance (Irish Sea)	Av. Abundance (Celtic Deep 2)
Appendicularian	33.93	0.69
<i>Temora longicornis</i>	56.8	37.73
<i>Centropages hamatus</i>	19.4	0.4
Cirrepeda	13.99	1.06
<i>Evadne spp.</i>	6.85	0.28
Hydromedusae	8.6	2.23
<i>Metridia lucens</i>	0.66	6.13
<i>Acartia clausii</i>	382.44	118.61
Echinodermata larvae	4.79	0.78
Decapod larvae	3.83	0.68
Polychaeta	3.48	0.51

<i>Oithonia spp.</i>	2.79	3.69
<i>Microcalanus spp.</i>	3.04	0.63
Small copepods	49.01	28.18
<i>Calanus stage I-IV</i>	3.75	2.06
<i>Pseudocalanus spp.</i>	36.72	57.11
	Av. Dissimilarity=	38.15
	Av. Abundance (Celtic Sea)	Av. Abundance (Celtic Deep 2)
<i>Evadne spp.</i>	563.55	0.28
Appendicularian	143.8	0.69
Echinodermata larvae	57.78	0.78
<i>Temora longicornis</i>	58.98	37.73
<i>Acartia clausii</i>	1135.23	118.61
<i>Podon spp.</i>	15.61	0.17
<i>Centropages hamatus</i>	10.79	0.4
<i>Centropages typicus</i>	9.4	0.18
<i>Calanus stage I-IV</i>	16.89	2.06
Small copepods	145.82	28.18
Polychaeta	10.5	0.51
Hydromedusae	13.88	2.23
Decapod larvae	7.37	0.68
<i>Oithonia spp.</i>	9.52	3.69
<i>Metridia lucens</i>	0.6	6.13
	Av. Dissimilarity=	48.85

Figures

Figure 1

The location of the stations sampled as part of the Eulerian time series across the Celtic Boundary Front. Plankton and CTD stations are shown as filled circles. CTD only is shown by the filled square. The weekly composite of the AVHRR sea surface temperature for the period between 14th and 21st June 2009 is also shown (INSET). The position of the three transects are shown by the open rectangles at a), b) and c)

Figure 2

Three transects a), b) and c) which correspond to the lettering in Fig 1 showing vertical profiles of temperature and salinity across the Celtic Boundary Front (CBF). Also shown in the upper row is the stratification index (SI) marked by the dashed line and the total zooplankton abundance (ind m⁻³) through each of the three transects.

Figure 3

The Potential Energy Anomaly (PEA) (J m⁻³) for each station viewed on the Eulerian time series grid. The symbols (filled/open circles) for each station are scaled in proportion to the amount of energy required to homogenise the water column (i.e. Greater PEA corresponds to a more stratified water column). The open circles represent the category with the highest PEA values.

Figure 4

Two CTD profiles at two stations (17 and 44) located on either side of the CBF. Temperature (solid line) and fluorescence (dashed line) which serves as a proxy for chlorophyll concentration are shown.

Figure 5

The zooplankton biomass (mg m⁻³) for each station viewed on the Eulerian time series grid. The symbols for each station are scaled in proportion to the total zooplankton biomass found in the sample

Figure 6

- a) A cluster dendrogram of the 44 plankton stations using the Bray-Curtis similarity metric and the complete linkage clustering method. Four clusters have been defined using a cut-off distance of 0.45. Each cluster is classified by a particular symbol hereafter. Cluster 1 (triangle), cluster 2 (circle), cluster 3 (cross) and cluster 4 (square)

- b) The cluster association of each station viewed on the Eulerian time series grid. The location of the CBF is also shown (red line)

Figure 7

The four panels show the fifteen most abundant species in each of the four clusters. Average similarity within clusters identified by the SIMPER analysis is shown for three of the four cluster groups. Each cluster can be identified by the symbols which were used in Fig 5.

Figure 8

The k dominance plots for the taxa found in each of the four clusters. Each cluster can be identified by referring to the symbols used in Fig 4

Figure 9

The first two axes of the Canonical Correspondence Analysis (CCA) which both cumulatively explain 74% of the variance. The species are displayed in the ordination (species codes can be found in Table 1) while the orientation of the environmental vectors are displayed by the blue arrows. Overlaid are the contours found by using the *ordifit()* function on the data. Shown here are the surface temperature (red) and salinity (green) gradients

Figure 10

As fig 9. Overlaid are the contours found by using the *ordifit ()* function on the data. Shown here are the chlorophyll (red) and stratification intensity (SI) (green) gradients

Figure 11

The 44 stations graphed as a function of the smoothed GAM variables which display the highest R^2 levels from Table 2. These are surface temperature and salinity. The cluster association based on the taxa abundances for each of the stations are shown.

Figure 12

The partitioning of variation between the environmental variables and geographical distance of stations on the species matrix

Figure 1

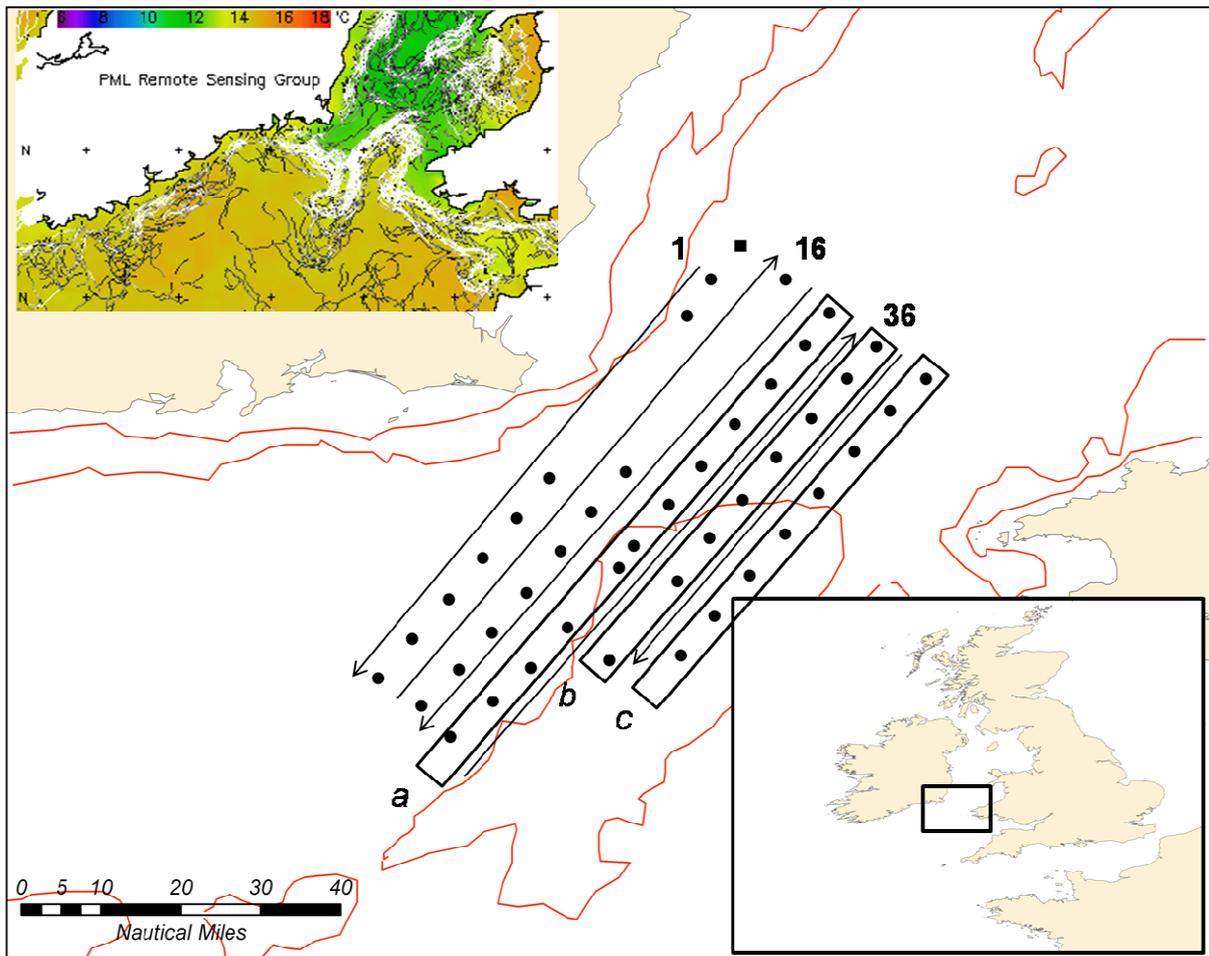


Figure 2

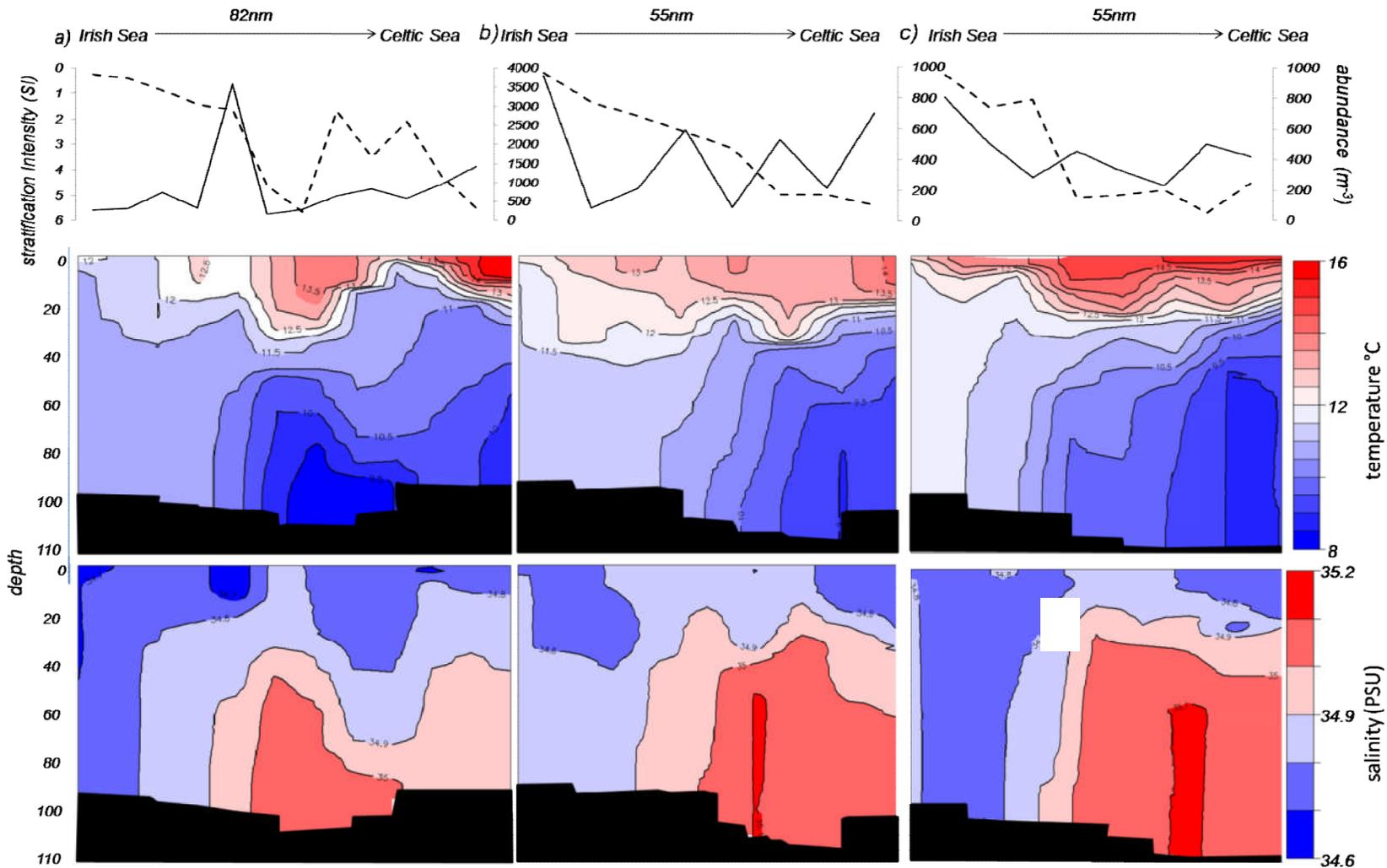


Figure 3

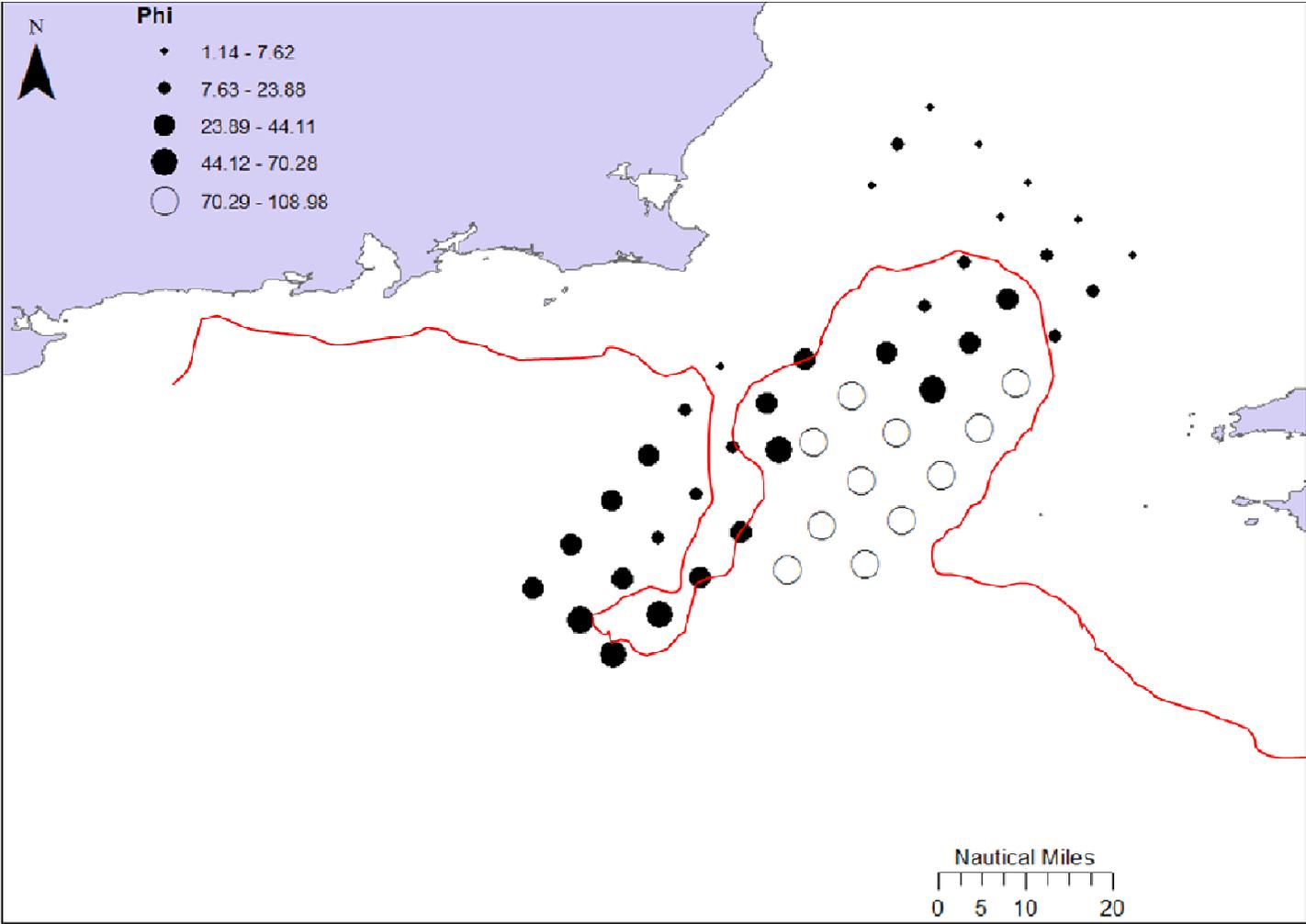


Figure 4

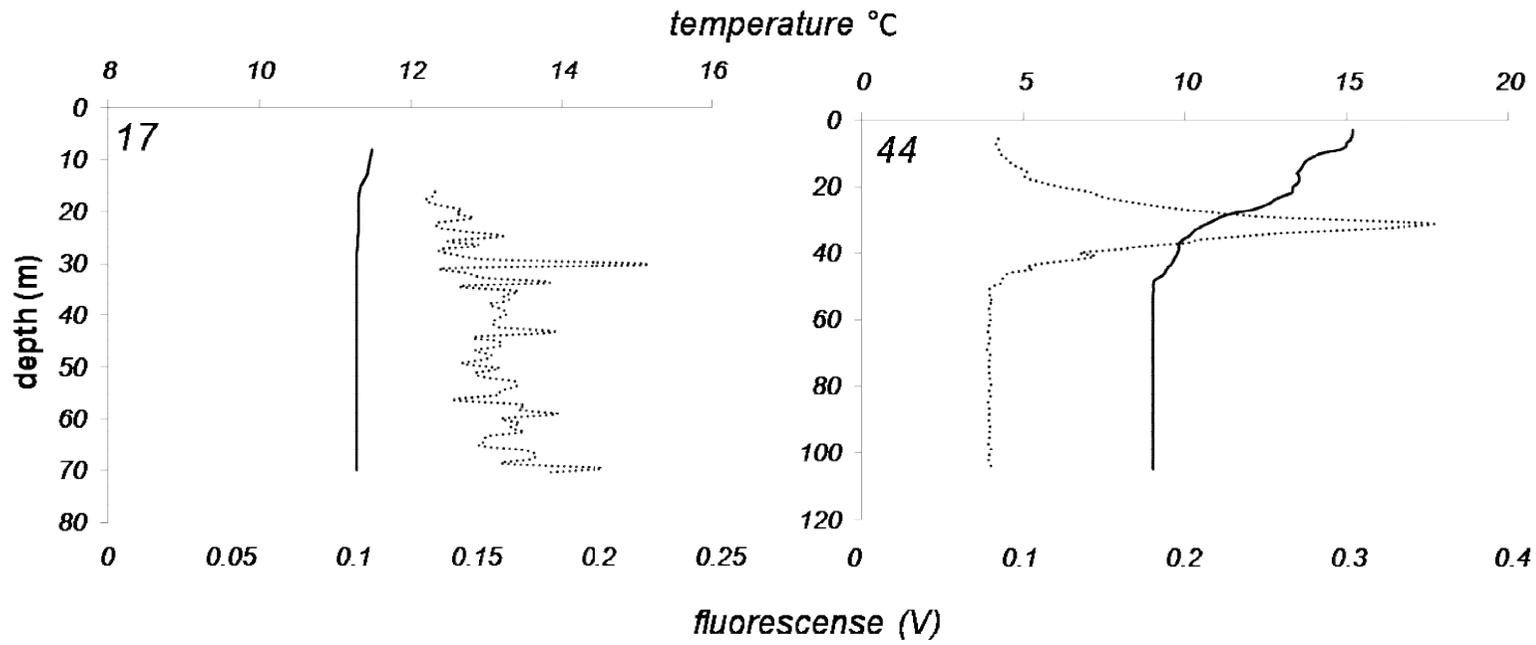


Figure 6 a,b

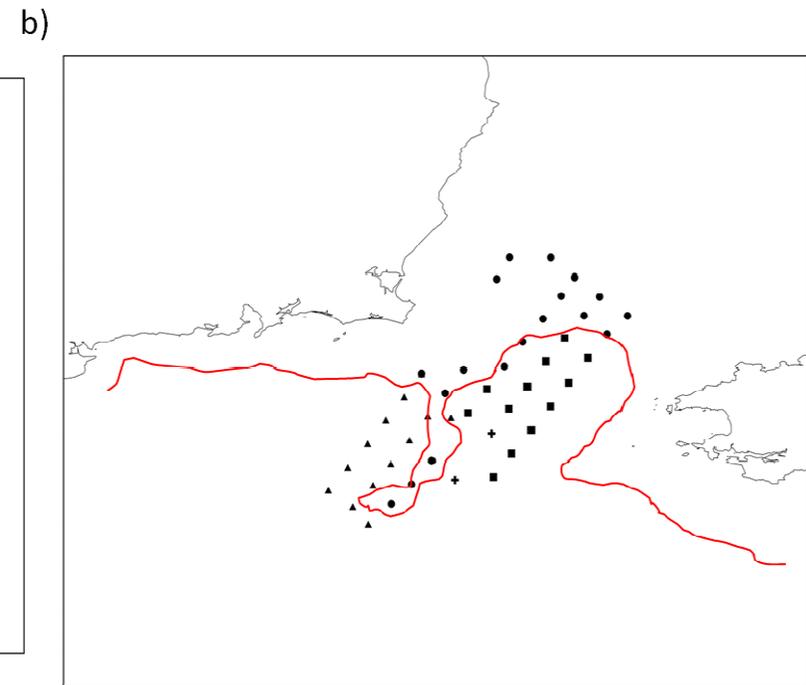
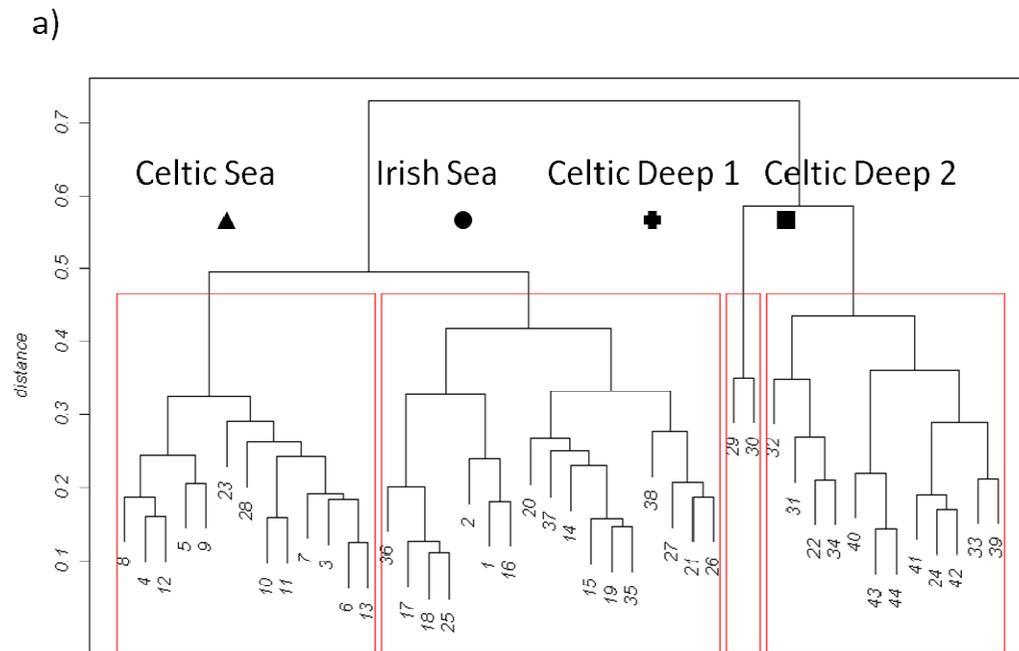


Figure 7

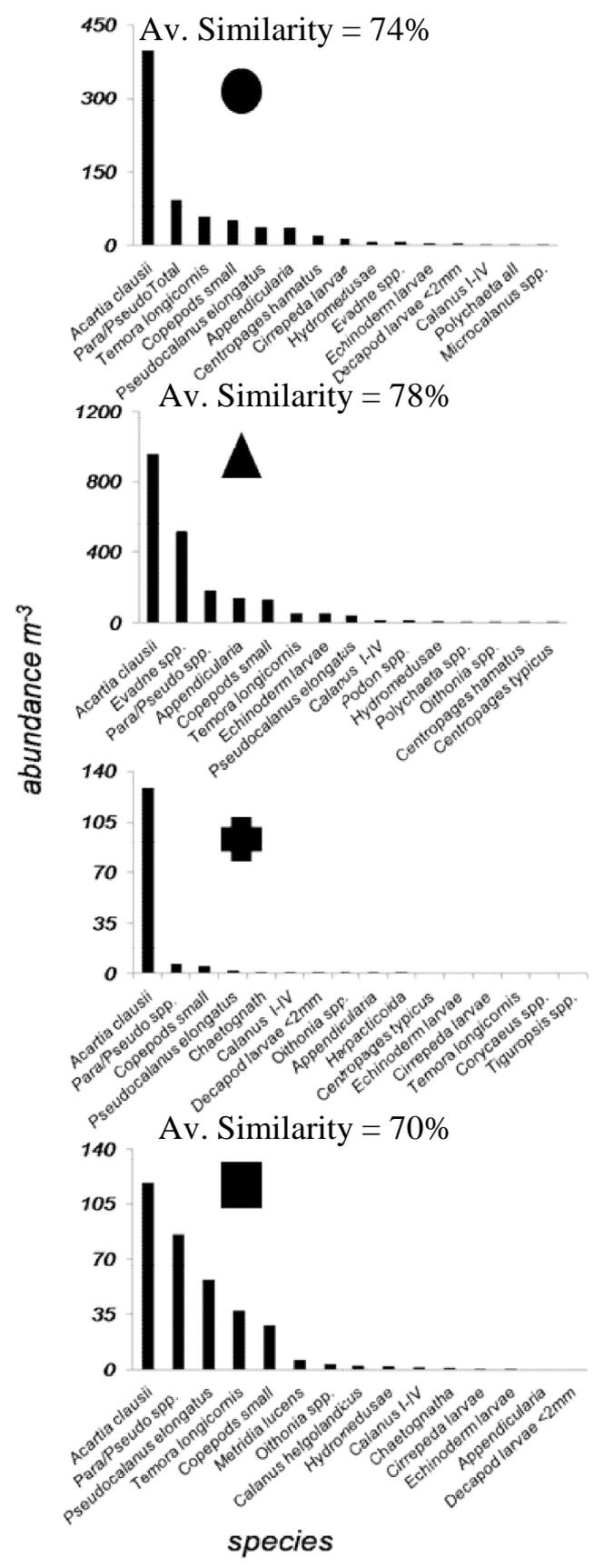


Figure 8

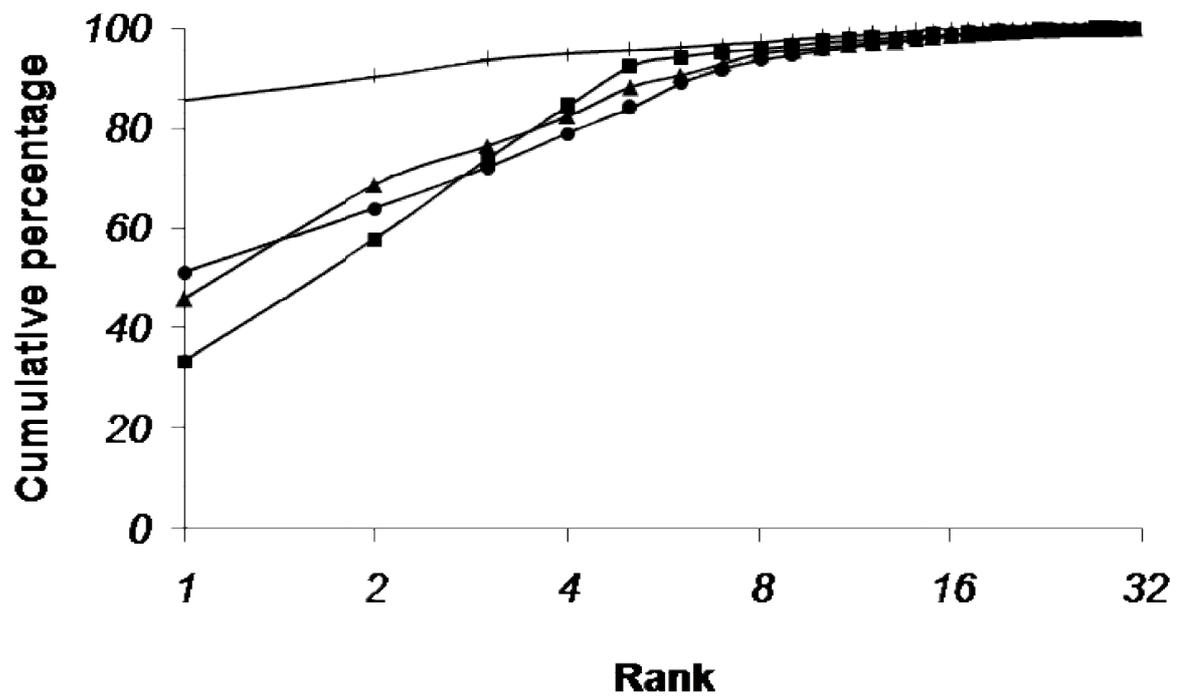


Figure 10

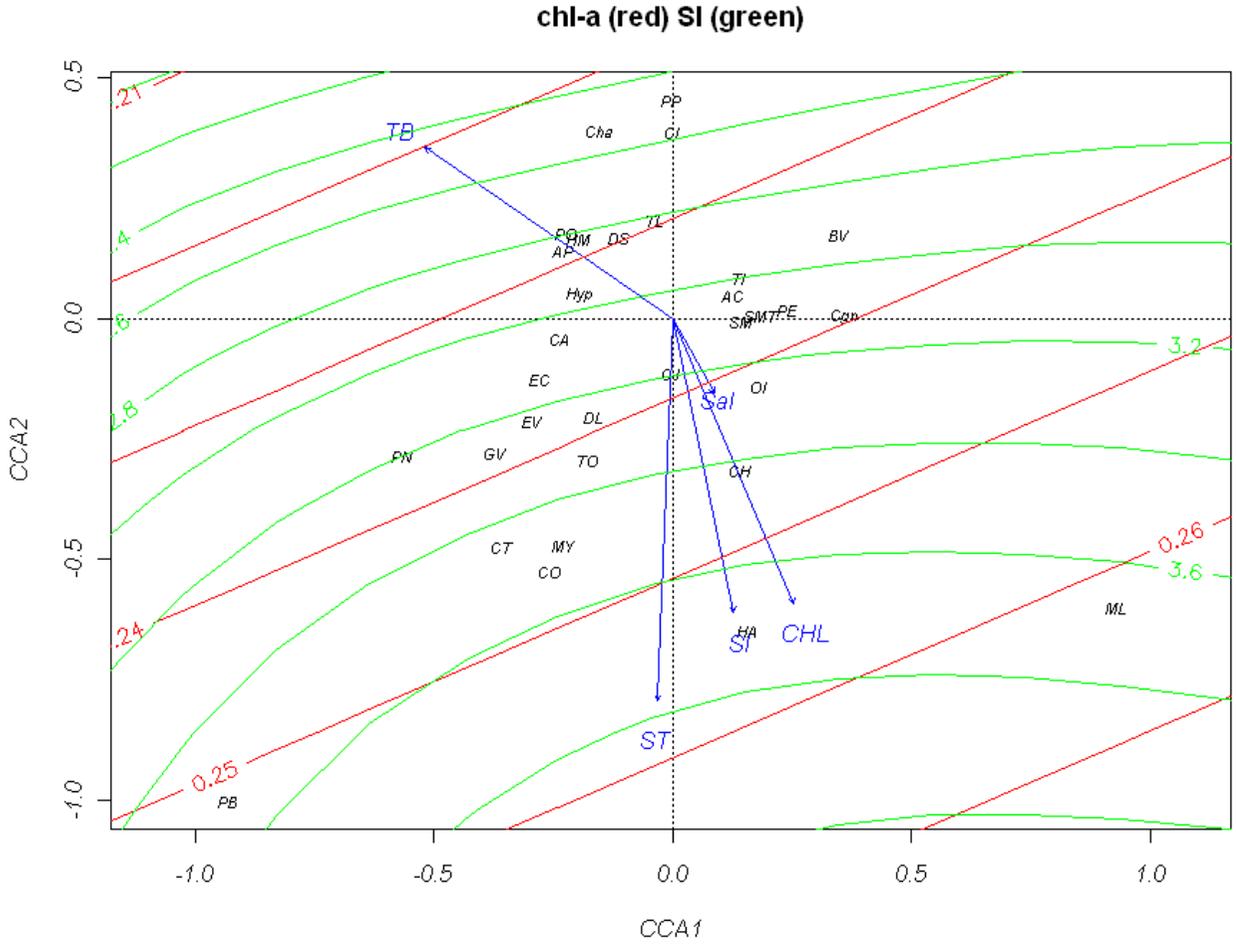


Figure 11

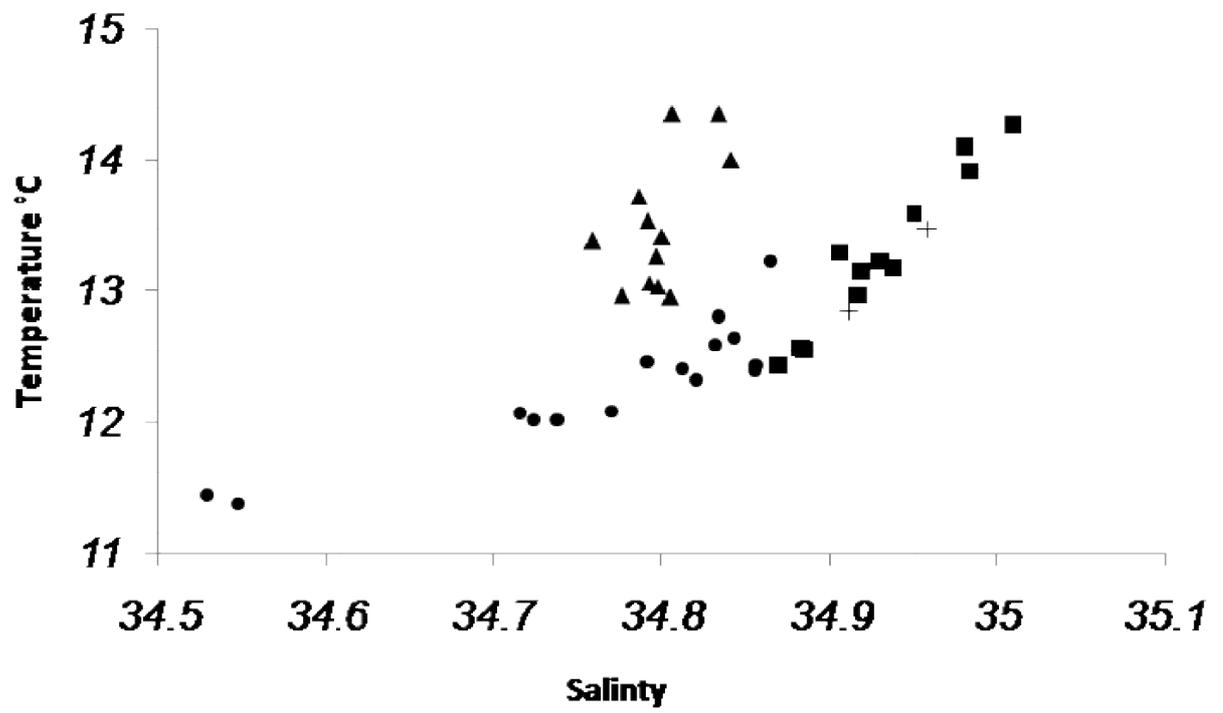
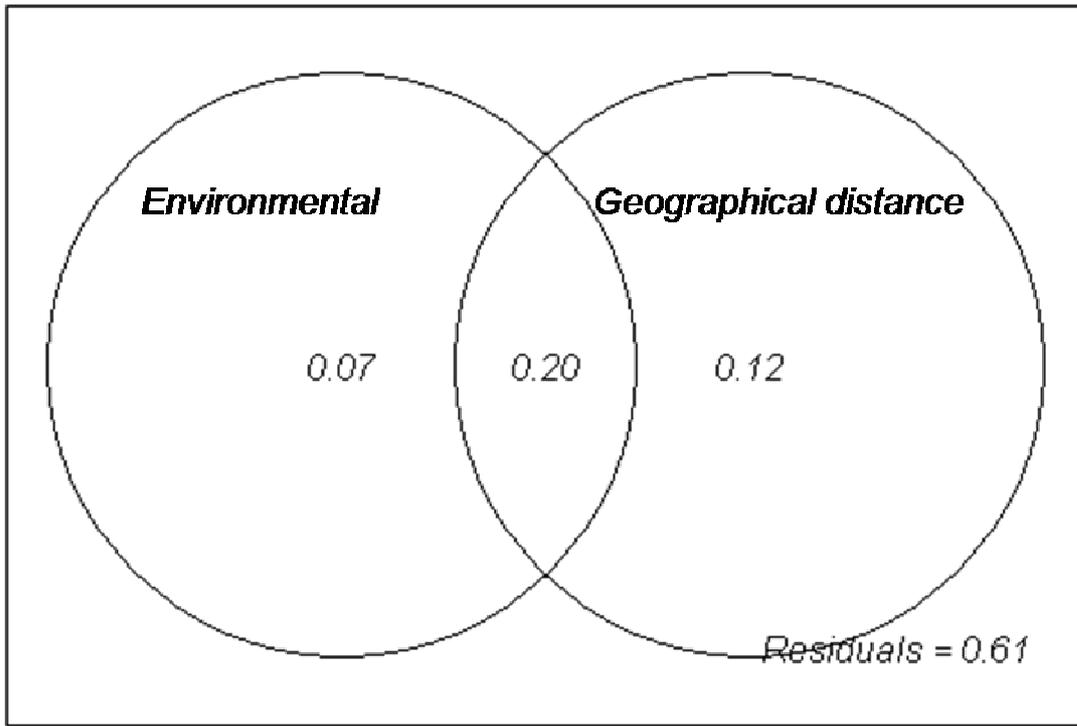


Figure 12



Chapter 6

General Discussion

Discussion

The overall goal of this thesis was to investigate scale processes of both zooplankton and phytoplankton in the N.E Atlantic, linking the broad scale variability with regional and local variability. Initially the problem of identifying the boundaries of the regional ecosystems was solved by utilizing satellite derived *chl-a* data and clustering each 81 km² pixel into clusters with similar spatio-temporal patterns. The resulting “eco regions” provided a number of shelf/oceanic clusters that followed the known hydrodynamics of the area which were described in detail within chapter 2. The work looked to improve on prior methods which tended to aggregate samples in regular polygons (Richardson and Schoeman, 2004) or through interpolation of samples across the ocean basin (e.g. Beaugrand et al., 2003). Our concern was that such techniques fail to consider that the pelagic realm is not homogenous across the N.E. Atlantic because hydrographic boundaries can divide water bodies over short distances such that interpolation or averaging can obscure the dynamics of assemblages.

Fig 1 displays the position of the Celtic Sea LME and biogeochemical provinces with respect to the eco regions defined in this work. The biogeochemical provinces are interesting in that they are largely defined based on remote sensing methodologies, a process in which we utilised in this work. This presents the opportunity of defining regions of varying scales using the same methods allowing a hierarchical classification of regions which would be suitable for analysing in greater detail the scale effects of the interannual and variability of plankton assemblages. Ecosystem typologies such as those described within this work have also become a major research interest in other oceans (Gregg and Bodker, 2007). Defining a suitable method of ocean partitioning to aid in effective management strategies is a worldwide phenomenon and not restricted to problems incurred by the European seas. In many cases regions defined for ocean governance prove to be ineffective due to a spatial mismatch between region and ecosystem that needs management (Crowder et al., 2006). A suggested ocean zoning concept has the potential to alleviate this issue and would greatly benefit from the methods described in this thesis. With the high resolution of remote sensing data, areas can be defined within a pre selected management zone under the same jurisdiction. From there it would be possible to classify regions of particular interest due to the sensitivity of species within an area to changing environmental conditions.

Despite the global responses of the marine ecosystems to increasing SST's there is still a large degree of variability in how species and indeed whole communities are responding to

this change. Different analyses demonstrated (Chapter 2, 3) the interregional heterogeneity in pelagic ecosystems over time. Interactions between large scale climatic variability and local biological and environmental processes have resulted in a mosaic of varying responses across the N.E. Atlantic. The responses of three trophically important copepod species (*Calanus helgolandicus*, *C. finmarchicus* and *Para-Pseudocalanus spp.*) were found to vary across each ecoregion with some regions showing a stronger resistance to the changing climate than others. While there has been considerable expansion of *C. helgolandicus* geographical range in recent years, this species could reach relatively high levels of abundance even towards the southern range limit in the Bay of Biscay (Beaugrand et al., 2003). Niche segregation for each of these species suggests that the thermal range for the warmer water species of *C. helgolandicus* can withstand much higher temperatures than its optimum levels (Helaouet and Beaugrand, 2009).

Species specific responses to climate change are not unknown but a more important question to ask is whether these are isolated cases within a trophic community or are representative of changes at an ecosystem level. The choice to use a measure of ecosystem stability derived from species abundance was selected for two principal reasons. With SST guaranteed to rise over the next 40 years regardless of how humans respond now (Hughes et al., 2003), knowledge of how ecosystems have responded to and will continue to respond to the changing climate needs to be quantified. These holistic approaches are necessary to alter policy and management practices at national and regional levels in order to mitigate against the changing climate (Poloczanska et al., 2007; Richardson, 2008).

In Chapter 3 the long term (1960-1999) and most recent short term (2000-2009) changes to the three trophic communities (phytoplankton, herbivorous copepods and carnivorous zooplankton) in each eco region were quantified. These periods were selected due to sample availability, but do span a recognised period of change in the North Atlantic. Each measure of ecosystem stability requires a baseline set of years to act as a measure in which all other years are assessed by. The most recent decade has seen some of the most profound changes occurring in the marine environment. Thus it serves as a valuable point in which to compare the long and short term changes to each ecosystem communities. This process of “back and forward” evaluation helps alleviate some of the issues involved with shifting baselines (Dayton et al., 1998; Hobday, 2011). Shifting baselines assumes that the current ecosystem state is being compared against a previous original state without anthropogenic interference. However most ecosystems have been disturbed to some degree such that the number of un-

perturbed ecosystems. In addition, it is clear that even 40-50 years may not be sufficient to sample natural variability sufficiently well to define a natural or baseline state for the pelagic system. The Atlantic Multidecadal Oscillation (AMO) is an aperiodic oscillation in SST's of the North Atlantic that go through a 50-88 year cycle (Cannaby and Husrevoglu, 2009). It is thought to arise through a predictable ocean – atmosphere interaction (Cannaby and Husrevoglu, 2009). Although the longest plankton time series only span less than one oscillation of the AMO, studies continue to find relationships between the basin scale oscillations of plankton abundance and the AMO (Martinez et al., 2009; Kane, 2011). The thesis therefore did not seek to compare each ecosystem with an original state - rather to use separate baselines to gain a more rounded picture of stability throughout the AMO oscillation.

As in Chapter 2, the trends over time considered in chapter 3 were both region-specific and specific to the dependent variable used (different species or different trophic groups), especially within the upper zooplankton trophic levels. The relative coherence of the phytoplankton community compared to zooplankton groups was hypothesised as being due to the reduced requirements for phytoplankton growth whereas the added complexity of zooplankton life histories (resting stages, larger vertical migration) increases the spatio-temporal variability for the N.E Atlantic. There have also been suggestions of a switch in the dominant mode of control of zooplankton communities shifting from the accepted bottom up regulation to top down, steadily increasing in its importance since the 1970's (Llope et al., 2011). The highly dynamic regions which occur along the continental shelf edge were found to have the least stable zooplankton communities, significantly shifting beyond the threshold set by the baseline years. One of the principal findings from this research was the trophic wide change in almost all eco regions in the final two years (2008-2009) which corresponds to a dramatic decrease in the trophic level biomass. This may be a latest portent of a long term collapse which has already been seen in the more enclosed seas such as the Barents Sea (Schaber et al., 2011). Possible causes for this change may be due to the historically high negative phases of the NAO winter index which have adversely affected the ecosystem communities the following year (Beaugrand et al., 2002; Lynam et al., 2004; Lynam et al., 2010). Winter NAO encapsulates some of the wind stress, the oceanic currents and SST for the N. Atlantic during the winter months. It could also be the case that this is evidence a more sustained change that will continue over the next few years. Recent observations have hinted at a change in the natural climatic variation (Hunt, 2011) which may perturb the regional

ecosystems in much the same way to develop new ecosystem regimes. It remains to be seen whether either of these cases hold true and it will only be through subsequent measurements over the next few years that will help describe the causes of these anomalous years.

Recently the variability in which the global temperatures, both marine and terrestrial have been examined in order to describe the pace of climate change that species need to track to remain within its thermal niche (Burrows et al., 2011). For the northern temperate latitudes the geographic shift polewards in temperatures were even on land and in the ocean with a velocity of approximately 27.5 km/ decade . However the broad scale coherence between areas begin to fragment at smaller spatial scales which gives rise to a complex mosaic of varying responses with some areas deviating from the simple poleward progression paradigm. This pattern reflects the multifarious responses of the zooplankton species/assemblages within our eco regions. In fact when we also consider that each region experienced a different rate of SST increase over the last 50 years we found that a larger shift in SST did not automatically correspond to the greatest shift in abundance or phenology. Here lies the central tenet from the first two research chapters; that in order to understand how our oceanic ecosystems will be altered by the changing climate we must first identify those regions that are more susceptible to change and uncover why this is so.

The study of zooplankton estuarine dynamics tends to focus on the local hydrographical and environmental characteristics of the area. Many studies cite the sharp gradients in turbidity, salinity and temperature as the main variables which can alter zooplankton populations within an estuary (Lampert et al., 2002; Loyer et al., 2006; Guillard et al., 2008). External forces tend to be restricted to the levels of freshwater flux which is thought to regulate the timing of the phytoplankton bloom in the bay (LeFevre et al., 1995). However a great deal of the variability may be explained by its connection with the waters adjacent to the bay. This is likely given that estuaries are not closed systems but are controlled by both internal and external pressures. Climatic influences on bays and estuaries have received greater attention in recent years owing to the fact that there is greater uncertainty as to how it will alter estuarine ecosystems in the future (Najjar et al, 2010). There is an understanding now that the responses of estuaries to climate change will differ globally owing to the unique physical characteristics of each estuary and the strength of anthropogenic forcing acting upon it (Kemp et al., 2005). However one biological element that appears to have a strong predictive capability on the zooplankton community within a bay or estuary is the zooplankton abundance in adjacent waters. Many of the major bays and estuaries, particularly across

Europe have long term >10 years monitoring of plankton abundance in the areas adjacent to them stretching from the Baltic Sea to the Iberian margin. Subsequent measuring of plankton within the bay could allow accurate predictions to be made regarding the state of the pelagic ecosystem within the estuaries by utilising an external source of biological variability that greatly influences or covaries strongly with dynamics within the estuary.

Finally Chapter five dealt with the structure of the zooplankton community across the Celtic Boundary Front (CBF) during June 2009. This boundary can be seen quite clearly from satellite observations once it forms in mid May. It is also evident in our eco region classification of *chl-a* observations moving from the stratified waters in the CS to the almost permanent mixed waters of the CM and IS regions. This area has been extensively studied regarding its physical structure and primary productivity but there were previously no dedicated zooplankton observations for this area. Our research followed the methodology of grid sampling across the boundary front which has been rigorously employed across frontal regions in the Bay of Biscay and Cantabrian Sea (e.g. Zarauz et al., 2007). The rigid spatial coherence of the clusters and the adherence to either side of the front shows that the CBF is a significant barrier for zooplankton distribution and transport. Biomass was significantly lower in the Irish Sea which is expected. The permanently mixed water column retards phytoplankton development and consequently is reduces the zooplankton biomass in the water column. Evidence of biological hotspots at boundary fronts has been found elsewhere (Berasategui et al., 2000) but the transitional distance between the two water bodies is very narrow and difficult to detect. The elevated productivity was thought to be in a region no greater than 1nm across (Savidge, 1976) at the boundary and even with our high frequency sampling grid we were unable to detect any such biological hotspots. In the context of global oceanography the importance of studying seasonally stable thermohaline fronts contained within LMEs is that they affect productivity both positively and as is the case with the CBF, negatively (Belkin et al., 2009). The ecological significance of investigating regional variability and population links across different spatial scales is recognized but in a management context the results from this thesis also hold a particular importance. Several management strategies have been set out by the European Union in recent years to address ecosystem management of European waters, specifically the Marine Strategy Framework Directive (MSFD). The research initiatives and requirements look for a holistic approach to modelling our seas integrating findings across a range of scales and pelagic ecosystems. The MSFD requires an understanding of economic, ecological, hydrological, and other processes

across many spatial and temporal scales (Apitz, 2005). As such the findings from the chapters 2, 3, and 4 fall under the remit of the MFD. In particular chapter 3 presents a method for evaluating ecosystem health or resilience to continuing pressures which has already been compromised by centuries of anthropogenic disturbance (Jackson et al., 2001).

Another question that needs to be raised is “how” can these eco regions be used in the context of the MFD? While they do provide a more coherent and realistic representation of boundary structure in the oceans compared with standard ICES areas or LMEs, eco regions are not invariant but it is the level of stability that will dictate how they would be used. The original eco regions were defined using data between 1998 and 2009. With the inclusion of 2010 data there was a 93% pixel matchup with all the variability in cluster association occurring within 50nm of any border. The multi-annual variability in clusters is an important consideration that needs to be addressed and before these eco regions can be used to obtain a deeper understanding of how the regions behave.. Different cluster modelling techniques incorporating Bayesian hypothesis testing may provide a better way of modelling these eco regions. This would allow for a more probabilistic measure of pixel associations which would be useful for developing a more flexible model that could handle changes to the eco regions range.

Research development and gaps

The nature of most ecological research is that it follows an iterative approach whereby a pattern is recognised in data, associations are tested and hypotheses are drawn up requiring further data or alternative methods. Although a number of valuable contributions and developments have been made in this thesis (see summary) another important outcome of research studies is that the results should motivate new lines of enquiry that will further elucidate the ecological dynamics of the subject area. Stated below are a few of the possible research developments that arise from the research output from this thesis and current gaps throughout the next section.

Analyses within this thesis address gaps in the knowledge of zooplankton dynamics that were set out by Mackas and Beaugrand (2010). This ranged from assessing different modes of zooplankton variability (abundance and phenology) within regions and making between region comparisons which have been significantly lacking for zooplankton datasets.

Chapter 3 looked at population synchronies of adjacent regions at a local-regional level (cross scale links) but this could perhaps be extrapolated to consider ocean basin connections within other parts of the Atlantic/Pacific oceans where long term plankton data series exist. A nested approach whereby eco regions can be selected within coastal LME's (McGinty et al., 2011), different LME's (Longhurst, 1998) and ocean basins (Atlantic and Pacific Ocean) can all be evaluated in such a way that it is possible to consider multiannual and decadal variability simultaneously across a hierarchy of scales.

While the analyses in these chapters have generally identified how dynamics vary across and between scales, this pattern recognition work generates hypotheses that can be addressed to discover the causes of the observed patterns. One way to approach the origins of pattern would be through the use of a structured population model driven by ocean transport and hydrodynamics. This would help identify connectivity between eco region populations and how the development within one region may affect those in another. With the use of individual based models such as those developed for *Calanus finmarchicus* across the N. Atlantic (Spiers et al, 2005 a,b) it is possible to test the mechanism by which regional differences occur. Switching off the effects of ocean transport at the basin scale resulted in negligible effects to the seasonal development of *C. finmarchicus* (Spiers et al., 2005b), transport is more important in moving stock between the ocean and continental shelf regions (Heath et al., 1999). This was also tested at a regional scale for *C. finmarchicus* populations within the Gulf of Maine (Pershing et al., 2010). By using the relationship between chlorophyll and temperature, realistic estimates of zooplankton interannual variability were made for that area.

Another type of modelling that has been proposed in recent years is the ecological niche model (ENM), which attempts to model the spatial distribution of species not in geographical space but in niche space: characterised by the most prominent environmental variables (Temperature, Bathymetry etc.; Halaouet and Beaugrand, 2009; Lenoir and Beaugrand, 2010). This modelling process can be used in unison with the proposed eco regions as a way to monitor how species are likely to change in a given region under different climate scenarios. This could be used on individual species but could also be applied to multivariate measures of ecosystem health using plankton indices (Beaugrand and Kirby, 2010) or through the use of control charts.

Another possible avenue of research is through investigating the trophic links with fish species in each eco region, specifically contrasting the links made by fish species which are migratory (e.g. Mackerel) and those that remain within a particular area (e.g. Cod). How do non-migratory species respond to years with poor or low zooplankton biomass? Do they shift towards neighbouring regions that may have a larger standing stock? And do migratory fish species respond to zooplankton regional variability by adapting their migratory routes so that they can avail of the strongest zooplankton community?

Finally I believe that the results from the historical time series constructed for Galway Bay between 1973 and 1987 provides evidence of the wide reaching benefits of a regularly monitored station within Galway Bay. With the presence of the Marine Institute at Oranmore and data buoys within the bay, regularly monthly/fortnightly collections can be made in Galway Bay without any added cost to current operations. Within only a few years it could be incorporated into the current network of European shelf sea stations allowing Irish coastal regions to be included in the comparative studies of zooplankton dynamics similar to those that has been conducted in recent years (Bonnet et al., 2005; 2007)

Summary

Listed below is a brief summary of how the research conducted within this thesis will contribute to the further understanding of spatial and temporal dynamics of zooplankton and zooplankton communities.

1. Defining eco regions – One of the initial processes was to evaluate how to define the regional state of the N.E. Atlantic. I used readily available satellite derived chlorophyll data to attempt this. The chlorophyll was used both as a proxy for phytoplankton primary productivity and as a “passive tracer” tracking oceanic and shelf boundaries. The result was a mosaic of regional eco regions that agree with the known hydrodynamics of the area.
2. Regional Forcing at regional scale – Cross eco region comparisons were made between several trophically important copepod species modelling their phenology and long term dynamics over the last 50 years. While the influence of SST affects all species across all eco regions in largely the same way the long-term dynamics vary

considerably across the regions. The broad scale climatic forcing interacts with the local environmental conditions generating a range of responses through time ranging from stochastic fluctuations to steady declines in abundance.

3. The use of control charts to monitor pelagic ecosystem resilience to the changing climate – Control charts are used to determine whether or not a process or system is in a state of statistical control. A multivariate analogue was used on trophic ecosystems within each eco regions to determine just how well communities have responded to the changing climate (i.e. - whether all ecosystems are behaving in the same way or are some more resilient than others to these changes). The zooplankton communities were found to be much more inter-annual variability compared with phytoplankton. Again areas responded differently to each other with some areas being consistently out of control and these tended to be the dynamic regions at the ocean-shelf interface. The use of control charts could be used as a monitoring tool for management practices.
4. Local-Regional links between a coastal inlet and the adjacent regional waters – Using an archived sample set collected within Galway Bay a time series was reconstructed for Galway Bay for the most common copepod species found in the area. This is significant for two reasons. Firstly, there are no multi annual datasets available for zooplankton in Irish waters. Secondly, Galway bay is situated such that the regular CPR tracks form a sampling shadow off the west coast of Ireland at a point of important cross shelf exchange of water masses. Studies within estuarine and coastal ecosystems consider local environmental gradients as the primary source of plankton variability, though much of the variability remains unexplained. One possible explanation is that external influences such as advection and migration patterns from adjacent regions may contribute to the unexplained variability. I found that strong relationships exist between the conspecific populations of a number of taxa within Galway Bay and the surrounding eco regions. Each taxa was also strongly associated with only one eco region suggesting that there are predictable and directional paths taken by plankton populations into coastal areas.
5. Variation at a boundary region – A high frequency sampling grid was established across an eco region boundary between the Celtic and Irish Seas. At this particular boundary we found distinct zooplankton communities on both sides of the boundary. The identified assemblages showed strong cohesiveness and high levels of dissimilarity between each other, which would suggest that the clusters are as a result

of two communities meeting at a discontinuity. Unlike other more stable boundaries there was no presence of an intermediate or transitional group and that this is an example of a sharp ecotone between areas.

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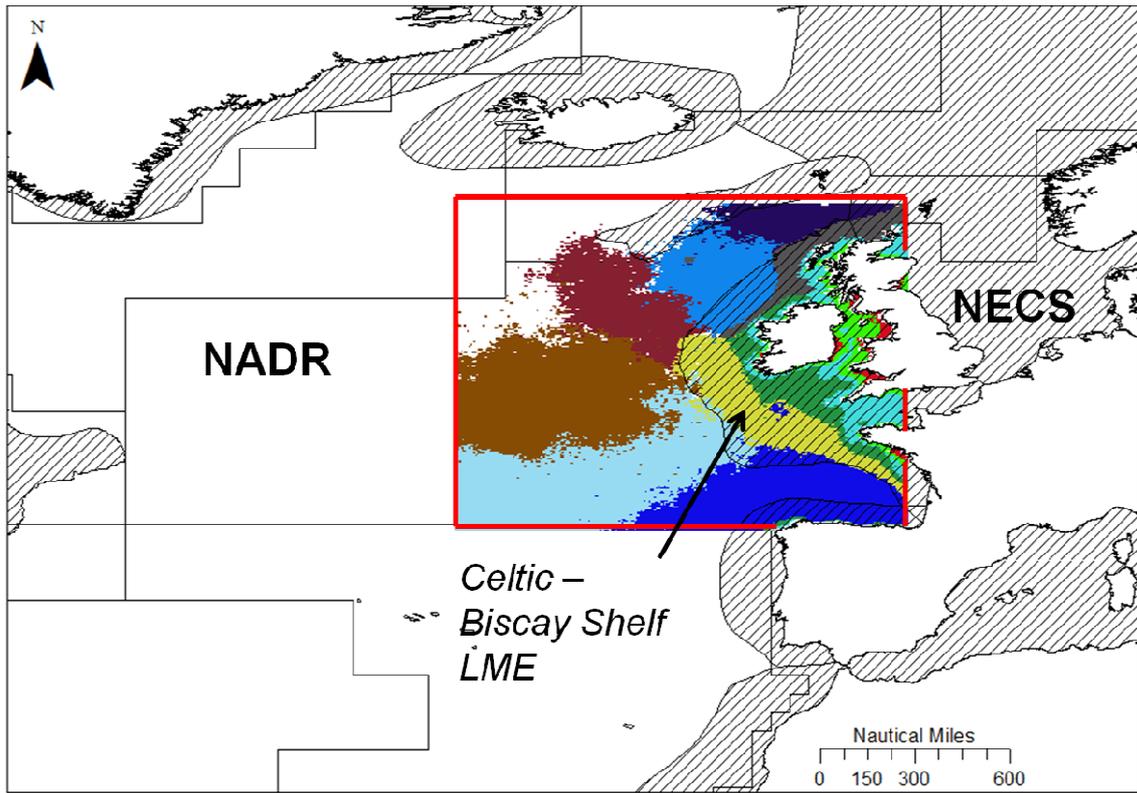
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Figures

Figure 1 The position of the nine eco regions derived from satellite *chl-a* data (methods found in Chapter 2) overlaid on the position of Longhurst's Biogeochemical Provinces (NADR and NECS) and LME's (Celtic – Biscay Shelf LME).

Figure 1.



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