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Trophodynamics and stability of regional scale ecosystems in the Northeast Atlantic

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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 database. Multivariate control charts using a Bray–Curtis similarity metric were used to assess whether fluctuations within trophic groupings were within or beyond the 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 the expected limits, although not in 2008 and 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 large marine ecosystem 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: Northeast Atlantic, plankton abundance, plankton community structure, regional ecosystems, trophic indicators.

Introduction

There has been a global increase of ~0.67°C in sea surface temperatures (SSTs) over the past century (Trenberth *et al.*, 2007). However, recent changes in SST have been unprecedented, with large increases over the past 10–15 years compared with the previous two millennia (Philippart *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, http://www.lme.noaa.gov), but 10 of the 18 fastest warming LME's (i.e. those that have increased by >0.60°C) are in the vicinity of the Northeast 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 Northeast Atlantic (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). However, 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 multiscale 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), whereas phytoplankton have been shown to be increasing across the North Atlantic (Leterme *et al.*, 2005) and the North Sea (Edwards *et al.*, 2001; McQuatters-Gallop *et al.*, 2007). At the ocean basin scale (1000–10 000 km), the strongest effects on phytoplankton (Barton *et al.*, 2003; Henson *et al.*, 2009) and zooplankton (Fromentin and Planque, 1996; Planque and Fromentin, 1996) appear to be associated with large-scale multidecadal 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 windstress (Beaugrand, 2004), mixed layer depth (Henson *et al.*, 2009; Reygondeau 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 Northeast Atlantic, and an obvious question to ask is whether regional-scale variability observed for these species is also observed more broadly, for example, within particular trophic levels? This approach is intended to distinguish patterns that are more widely prevalent in North 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 foodweb as outlined in the Marine Strategy Framework Directive (2010/477/EU).

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 Northeast Atlantic. The most numerically dominant species from three trophic assemblages (phytoplankton, herbivorous copepods, and carnivorous zooplankton) were examined in nine predefined ecoregions (McGinty *et al.*, 2011) of the Northeast 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 the 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. As exceptional warming has taken place in the most recent decade, the exercise was repeated using the period 1960–1999 as a baseline, against which the years between 2000 and 2009 were evaluated. The parallel comparisons of control charts across neighbouring ecoregions 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 ecoregions

The study describes changes in the Northeast Atlantic in an area similar in extent to the Celtic Biscay LME, but including offshelf areas (Figure 1). The procedure for defining the ecoregions 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; it is described in McGinty *et al.* (2011) as a finer-scale extension of methods proposed by Longhurst (1998) for defining biogeographic provinces. Briefly, the procedure involved using the level 3 monthly composite images of SeaWiFS Chl *a* (pixel size 9 × 9 km) for the months March–October, 1998–2009. A *k*-means clustering method was first used to cluster the Chl *a* data; thereafter, a cluster dendogram was used to aggregate clusters with >95% similarity. This process resulted in nine clusters, which we equate with ecoregions, that were spatially well-resolved (McGinty *et al.*, 2011). The term ecoregion 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 onshelf ecoregions showed a close affinity with the well-known boundaries of transitional water bodies in the Celtic Sea and Irish Sea, whereas offshelf, the divisions appeared to be more related to the onset of the spring phytoplankton bloom, which occurs later with increasing latitude (Figure 1). Owing to the sparseness of available plankton data, the ecoregion ABN was not used for the current study.

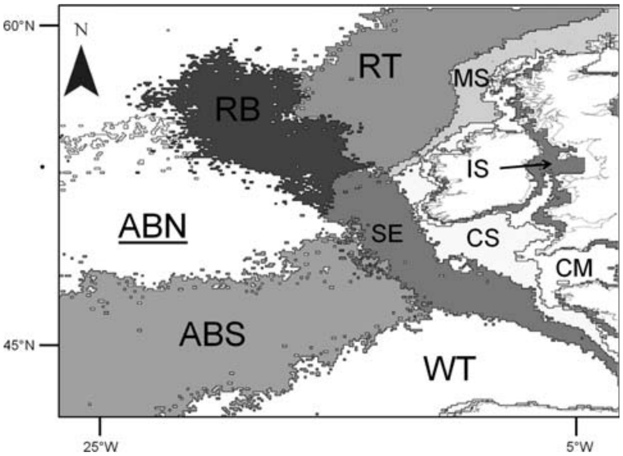

Figure 1. The geographical distribution of the nine ecoregions used in the analyses. These are in clockwise order IS, Irish Sea; CM, Celtic Sea mixed; CS, Celtic Sea stratified; SE, Shelf Edge; WT, Warm Temperate; ABS, Abyssal South; ABN, Abyssal North (not used in analysis); RB, Rockall Bank; RT, Rockall Trough; and MS, Malin Shelf. Ecoregion boundaries are classified based on the temporal clustering of satellite-derived chlorophyll (from SeaWiFS).

Trophic assemblage selection

The plankton data from separate ecoregions 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 indispensible 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 sampled regularly through time, establishing a lower bound limit of 3000 samples (50 years × 12 months × 5 samples) ensured that the maximum number of months in each time-series will be achieved (and caused the exclusion of ecoregion 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 a key trophic link between phytoplankton and carnivorous zooplankton (Williams *et al.*, 1994; Richardson and Schoeman, 2004); and (ii) >100 species of copepod taxa have been differentiated in the CPR database, of which 92.5% of taxa have been identified to the 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, so the selection of trophic indicators was based on the most abundant (for carnivores) or most dominant groups in terms of biomass (phytoplankton and herbivorous copepods). Phytoplankton biomass (Bp) 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 ($Bh_{i,j}$) in a CPR sample was found using the length/wet weight relationship in Equation (1) below, where L is the length of species i obtained from the literature (Richardson *et al.*, 2006) and $x_{i,j}$ the number of individuals for species i in each sample j. Carnivorous zooplankton were quantified using the number of individuals because of the low taxonomic resolution for many of the groups.

$$Bh_{i,j} = (0.08 \times L_i^{2.1})x_{i,j}. \qquad (1)$$

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) characterizes each species' relative importance (RI_i) within a trophic level, where $W_{i,j}$ is the abundance/biomass of species i in sample j, $\text{Max}\left(\sum_{j=1}^{n} W_{i,j}\right)$ the maximum value of individuals/biomass for a species within each trophic assemblage, and F_i the fraction of n samples where species i is present. Equation (2) produces a value between 0 and 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 ecoregion.

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

Within each ecoregion and trophic assemblage, species were ranked by the 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. 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 ecoregion, the species' counts were modelled using a generalized additive model (GAM) to interpolate values subsequently used for the calculation of annual means. GAMs were fitted using a log-link function, using the *mgcv* package within the statistical package R (McGinty *et al.*, 2011). Two models were compared for each species, the first (model 1) modelling the long-term (t, month $1, \ldots, n$, where n is the total number of months in the time-series) and seasonal component (m, $1, \ldots, 12$) separately, and the second (model 2) allowing both terms to interact. The model that 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. Models 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_i the error term.

GAM predictions yielded 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 normalized by subtracting the temporal mean of the species and dividing by the s.d. 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 normalized values were then used for further statistical analysis.

Statistical analysis

Univariate control charts employ a test statistic such as the mean and specify control limits of 2 or 3 s.d. above and below the mean. A system is said to be "out of control" or behaving beyond the 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 ecoregions over the past 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 owing to differences in assemblage structure. To standardize these distances across all trophic communities for display purposes, distances were divided by the value at the 95th percentile so that rescaled differences >1 indicated significance (i.e. assemblages were beyond the expected limits given the baseline set of observations).

Determination of whether an ecoregion was beyond the 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 the expected limits fell within the expected binomial probabilities (see below). Conversely, it was unstable if the number of years a community was beyond the expected limits exceeded that 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/

Table 1. The 32 most important taxa either numerically or as a large contributor to the overall biomass according to Equation (2), for each trophic level, along with the ecoregions where each taxon was the most important (see Figure 1 for explanation of codes) and the biomass/abundance change between the baselines 1960–1999 and 2000–2009 (increase, decrease, or no change).

Taxon	Ecoregions present	Biomass/abundance change between baselines 1960–1999 and 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
Hyperiids	IS CM CS SE WT ABS RB RT	Decrease
Decapods	IS CM CS SE WT	Decrease
Pleuromamma spp.	WT ABS RB RT	Decrease
Candacia spp.	CS SE WT	Decrease
Euchaeta spp.	SE WT	Increase
Corycaeus spp.	SE	Decrease
Herbivorous copepods		
Calanus spp. I–IV	IS CM CS SE WT ABS RB RT MS	Decrease
Acartia spp.	IS CM CS SE WT ABS RB RT MS	Decrease
Paracalanus spp. and small copepods <2 mm	IS CM CS SE WT ABS RB RT	Decrease
Calanus helgolandicus	IS CM CS SE WT ABS MS	Increase
Centropages typicus	CM SE WT ABS	Decrease
Pseudocalanus spp.	CM CS	Decrease
Metridia lucens	RB RT	Decrease
Calanus finmarchicus	RT MS	Decrease
Temora longicornis	IS	Increase
Phytoplankton Dinoflagellates		
Ceratium fusus	IS CS SE WT ABS RB RT MS	Decrease
Ceratium furca	IS CM SE WT ABS RB RT MS	Decrease
Ceratium tripos	CM CS SE RB RT MS	Decrease
Protoperidinium spp.	CM MS	Decrease
Ceratium lineatum	ABS CM	Decrease
Ceratium macroceros	WT	Decrease
Dactyliosolen mediterraneus	RT	Decrease
Diatoms		
Thalassiosira spp.	IS CM CS SE WT ABS RB RT MS	Increase
Hyalochaete spp.	IS CM CS SE WT ABS RB RT	Decrease
Thalassionema nitzschioides	IS CS SE WT ABS RB RT MS	Decrease
Phaeoceros spp.	IS CM CS SE WT ABS MS	Increase
Rhizosolenia alata alata	CM CS SE WT ABS RT	Decrease
Rhizosolenia imbrica shrubsolei	CM CS RB MS	Decrease
Rhizosolenia styliformis	CM RB RT	No Change
Thalassiothrix longissima	ABS RT MS	No Change

biomass across all ecoregions for each trophic assemblage. Spearman's 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 formulated using the FORTRAN program ControlChart developed by Anderson and Thompson (2004).

When calculating the probability of a trophic assemblage for a particular year being within/beyond the 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 the number of times the ecosystem is out of control, and p 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 the abundance of the species present within the trophic assemblage). We therefore examined the change in the standardized abundance between years both within and beyond the expected limits for the two baseline periods, compared the variance around both baseline centroids and the distance between them, and finally related these changes to the changes in abundance at the level of our species or taxa groups.

Results

In all, 32 taxa (Table 1) dominated the ecoregions across all trophic communities according to the ordering procedure in Equation (2). Within each trophic level, two or three species were ubiquitous across almost all ecoregions. The diatom group *Thalassoria* spp. was dominant in all nine ecoregions, and the two most dominant dinoflagellate species (*Ceratium fusus* and *C. furca*) were found in all but one ecoregion. Within the herbivorous copepod group, juvenile *Calanus* spp. I–IV and *Acartia* spp. were found across all ecoregions, and euphausiids and chaetognaths were the most frequently observed carnivorous zooplankton groups across our study area. There were also some species that

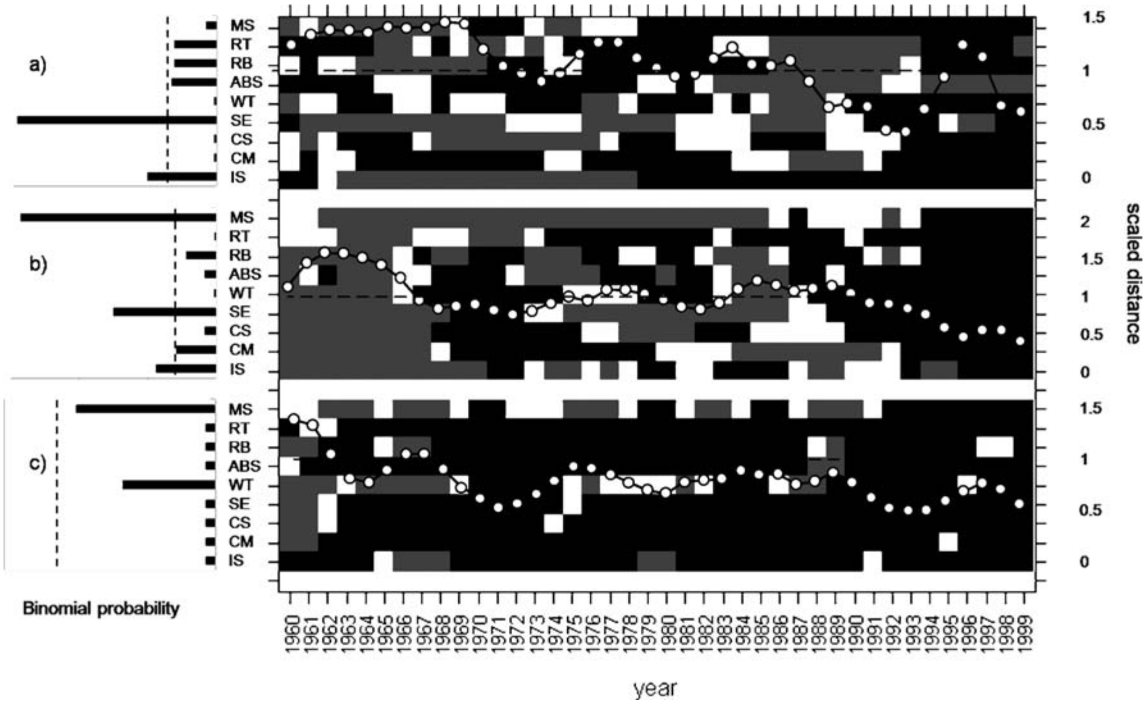

Figure 2. The control chart for each of the trophic communities for all nine ecoregions: (a) phytoplankton, (b) herbivorous copepods, and (c) carnivorous zooplankton for the years 1960 – 1999, using the years 2000 – 2009 as the baseline set of observations. Blue represents cells within the expected limits, yellow represents cells beyond the 90th percentile from the baseline, and red represents cells beyond the 95th percentile from the baseline. The overlaid time-series (white circles and black line) for each trophic level shows the level of control when data are summed across all ecoregions (see axes on the right for scale). Years where the scaled centroid distance is >1 were beyond the expected limits (at the 95th percentile indicated by the dashed line). The columns to the left accompanying each trophic assemblage represent the binomial probability that the number of years beyond the expected limits exceeded the expected amount. Those passing the dashed line are deemed to be significant at the level $p = 0.05$. See Figure 1 for explanation of ecoregion codes.

were endemic to a particular region or group of regions. The temperate species *C. helgolandicus* dominated the regions south of 55°N and the Subpolar species *C. finmarchicus* the two regions north of 55°N, with co-dominance in the region MS. The coastal species *Temora longicornis* was only dominant in the IS region and the predatory copepod *Pleuromamma* spp. only dominant in offshore ecoregions.

The control charts showed contrasting patterns, depending on the baseline period used.

Baseline 2000 – 2009

The phytoplankton community was very stable in all ecoregions (Figure 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 interannual variation at higher trophic levels, and here, the number of years beyond the expected limits exceeded the number we would expect to have arisen through stochastic fluctuations (Figure 2b and c). For example, the number of years beyond the expected limits in both groups was almost half of all the years between 1960 and 1999. For the herbivorous copepods, there was a period between 1960 and 1967 where multiple ecoregions went beyond the expected limits (Figure 2b). This also happened in the carnivorous zooplankton over the same period, although only in certain regions (Figure 2c). Carnivorous zooplankton were beyond the 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 ecoregions (MS, SE, CM, and IS) within the herbivorous copepod community exceeded the number of years beyond the expected limits that one would expect from stochastic processes (Figure 2b). For the carnivorous zooplankton, there were two regions (SE and IS) exceeding such limits (Figure 2c).

To evaluate how well the fluctuations in trophic communities at the regional level reflected the larger LME scale, the summed responses across the study area were compared with those of the individual ecoregions. Correlation coefficients between fluctuations in the trophic level communities and the summed total revealed the varying strengths in this relationship across the ecoregions (Figure 3a). In the phytoplankton community, five ecoregions 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 that were significant in five regions. Overall, although in most instances, regions were positively correlated with the summed total (24/27), only some of these were significant (10/27) and several (3/27) were negatively correlated with the summed total. The latter group were all members of the carnivore community (Figure 3a).

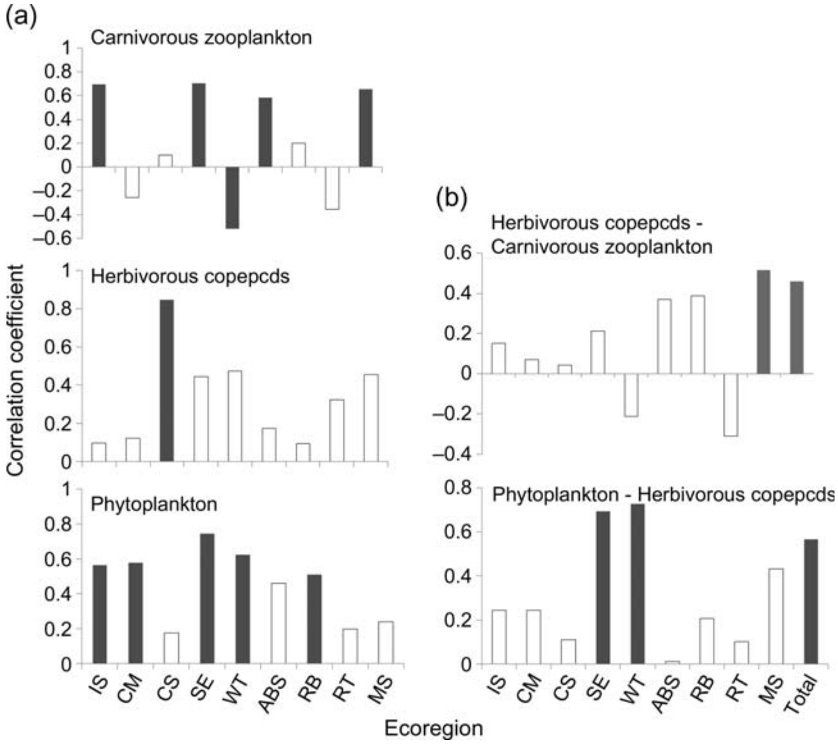

Figure 3. Correlation coefficients (a) between each ecoregion and the summed total and (b) between adjacent trophic levels within each ecoregion with the same procedure applied at the LME scale in the final column, Total. Shaded columns indicate significant correlations where $p < 0.05$ after correcting for temporal autocorrelation. See Figure 1 for explanation of ecoregion codes.

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 (Figure 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 $r_{\mathrm{SE}} = 0.69$, $p = 0.002$; $r_{\mathrm{WT}} = 0.725$, $p = 0.001$; $r_{\mathrm{tot}} = 0.564$, $p = 0.014$). There were two strong positive relationships between herbivorous copepods and carnivorous zooplankton, one in the MS region ($r_{\mathrm{MS}} = 0.515$, $p = 0.034$), and a significant positive relationship at the LME scale ($r_{\mathrm{tot}} = 0.457$, $p = 0.05$).

Baseline 1960–1999

Evaluation of the years 2000–2009 with respect to the baseline 1960–1999 showed that trophic communities underwent a high degree of change in most ecoregions during the latter half of the decade (Figure 4). Despite regional variability within and across trophic levels, there was a general trend post-2005 towards years being beyond the 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 the expected limits, and this dramatic shift was widely observed across all ecoregions.

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 was less evident for phytoplankton (Figure 5a). However, there was a large degree of variance between the years 2007 and 2009 for the phytoplankton community, a pattern also reflected in the control chart (Figure 4).

There was a significant difference between the standardized abundance of species in years that were within the expected limits and those that were beyond the expected limits. For baseline 2000–2009 (Figure 5b), the abundance of species in all trophic levels was significantly greater in years that were beyond the expected limits than years within the expected limits. For the 1960–1999 baseline (Figure 5c), in contrast, the abundances were significantly lower in years beyond the expected limits than for years within the expected limits. This agrees with Table 1, the vast majority of species having shown a marked decrease in abundance between baseline periods. The majority of taxonomic groups showed a significant decrease in abundance over time (25 of 32 taxa). Of the remaining taxa, five showed a significant increase in abundance and 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 (Figure 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 ecoregions (data not shown, for brevity).

Discussion

There is strong evidence to suggest that the regional scale variability observed for trophically important *Calanus* copepods (Beare

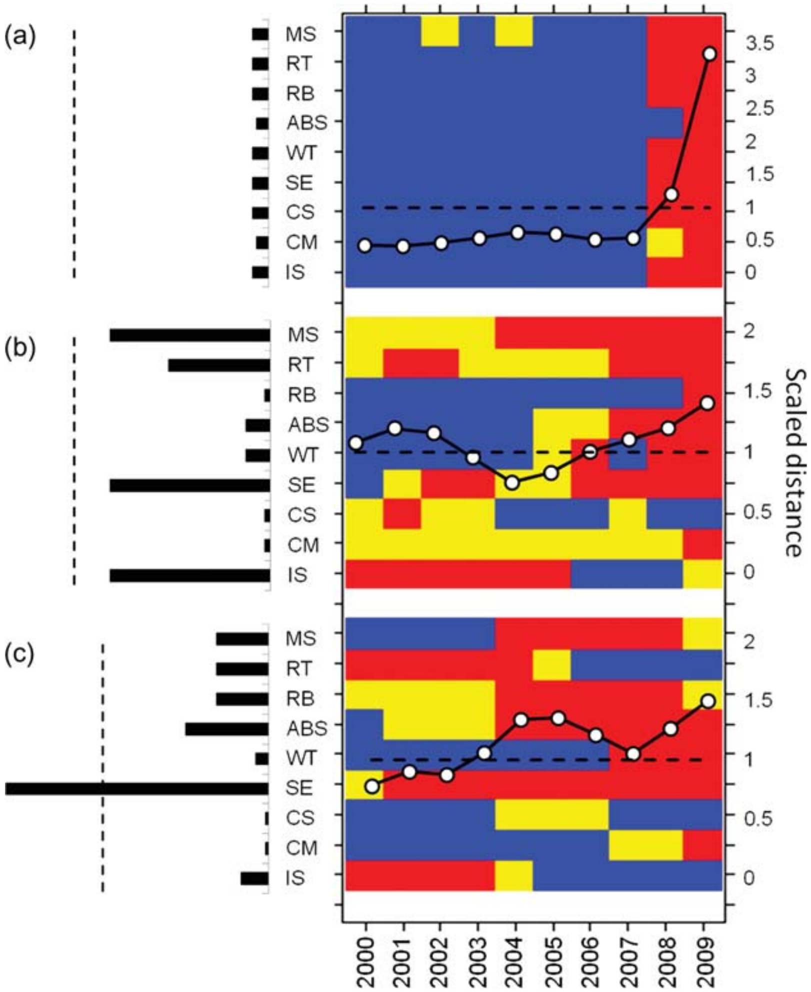

Figure 4. The control chart for each of the trophic communities: (a) phytoplankton, (b) herbivorous copepods, and (c) carnivorous zooplankton for the years 2000 – 2009, using the years 1960 – 1999 as the baseline set of observations for all ecoregions. The legend is the same as described in Figure 2.

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. Often, there was a failure for the regions to follow the patterns of the overall study area (i.e. the scale of 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 basic 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 time-scales. For example, 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, whereas the herbivorous copepod communities were weakly positively correlated with an LME trend, the 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 attributable 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. Eilertsen *et al.*, 1995), which will not vary considerably over our study area. However, drivers that probably operate at regional scales have also been identified.

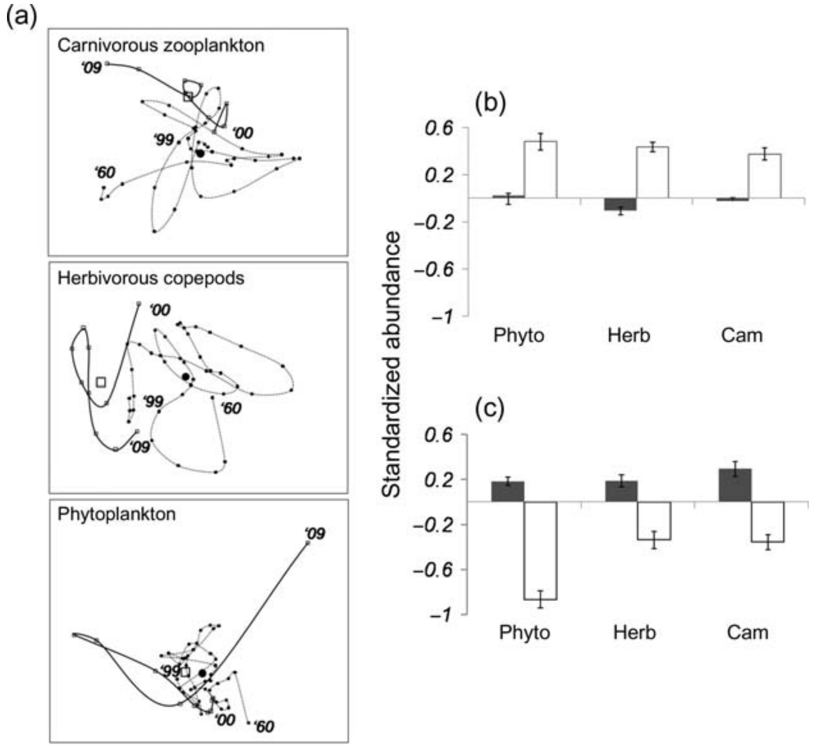

Figure 5. (a) Variability about the baseline centroids (1960 – 1999, large dot; 2000 – 2009, large open square) for each baseline period (1960 – 1999, small dots and stippled line; 2000 – 2009, small open squares and solid line) of each trophic level category: phytoplankton (Phyto), herbivorous copepods (Herb), and carnivorous zooplankton (Carn). Each panel represents a PCA performed on a matrix of the average abundance of species summed across all ecoregions. The centroid represents the arithmetic mean of each year for both baselines. The difference in abundance between years (mean ± s.e.) when trophic communities were within the expected limits (black histograms) compared with years that were beyond the expected limits (white) across all ecoregions for (b) the 2000 – 2009 baseline, and (c) the 1960 – 1999 baseline.

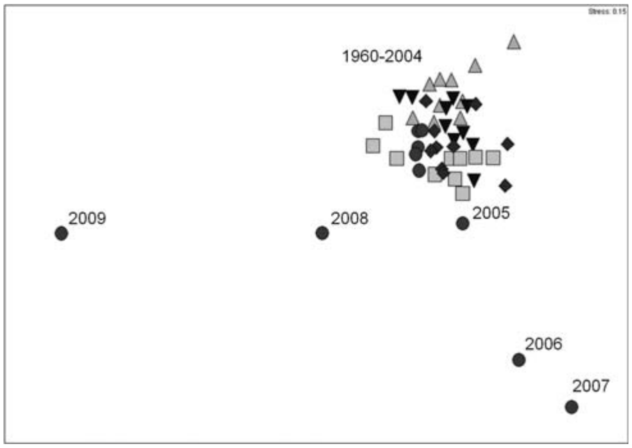

Figure 6. An nMDS plot of the summed numbers of individuals/ biomass of all species from all trophic levels across all ecoregions for the years 1960 – 2009 using the Bray – Curtis similarity measure (grey triangles, 1960s; black inverted triangles, 1970s; black diamonds,1980s; grey squares,1990s; black dots, 2000s).

The effects of variability in SST and windstress also influence phytoplankton dynamics (Edwards *et al.*, 2001). Dutkiewicz *et al.* (2001) modelled the effects of vertical mixing and showed that 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 and Monger, 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 stabilities of regional and large-scale phytoplankton abundances were 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 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. 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 inter-region 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 windfield 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 North 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.*, 2005a, b). Again using *C. finmarchicus* as the model species, Speirs *et al.* (2005a, b) found strong connectivity between centres of distribution in the North Atlantic even when the influence of ocean transport had been factored out.

The most significant changes in trophic communities were in the most recent decade (2000–2009) by comparison with a baseline consisting of the previous four decades. Community similarity for the years 2005–2009, in particular, was drastically altered compared with previous years (Figure 4). Trophic communities were almost universally beyond the expected limits in 2008 and 2009, even for phytoplankton communities, which, in some cases, were more than two scaled 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 the expected limits compared with those that were beyond the expected limits. This translated as a trend for decreased abundance/biomass to be characteristic of years that were beyond the expected limits. Even with 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. Of 32 taxa used in this study, 25 decreased in abundance/biomass within the past decade. With the trophic-wide decreases in species abundance/biomass so evident, the results highlight the exceptional changes that have occured compared with the latter half of the past 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 past century, based on the integration of various proxy and *in situ* measurements of Chl *a* concentration. However, this was subsequently called into question (Mackas, 2011; McQuatters-Gollop *et al.*, 2011; Rykaczewski and Dunne, 2011) based on the possible overestimates of Chl *a* using Secchi disc 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 often over the past 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), although present, were not significant. Rather, such changes were well within the expected stochastic fluctuation. We did uncover some evidence of a possible shift in community structure in the latter half of the past decade, particularly in the years 2008 and 2009 (Figure 4a–c), but it remains to be seen whether this cross-trophic deviation is a temporary effect possibly attributable to the effects of the anomalously cold winters (associated with the 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.

In contrast to phytoplankton, there is general accord about how the long-term changes in zooplankton distribution and abundance have changed in the Northeast Atlantic over the past 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, because these usually contributed no more than 5% towards the total biomass in any 1 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 similar effects 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 (2010/477/EU; Edwards *et al.*, 2010), and research activity is intensifying in this area (e.g. Beaugrand and Kirby, 2010a, b). 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), i.e. 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 an LME scale (Figure 3a), were mostly nonsignificant at regional scales, and for 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 apparently greater stability of phytoplankton compared with 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 the period 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 more-variable sample collection. However, the confidence limits are derived from the data and are based on the 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 component analysis (PCA), where the principal modes of variability are used as univariate measures of community variability. Although there are similarities between PCA and control chart approaches, with similarities among studies depending on the degree of prescreening 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 ecoregion and repeat the control chart analysis, leaving 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 with the preceding decade. We chose a combination of baselines that led to the questions how does the period 2000–2009 differ from the period 1960–1999 and how frequently did conditions typical of 2000–2009 arise in the period 1960–1999? A possibility of using different baseline lengths is that the longer baseline samples more environmental variability (owing to multidecadal patterns of variability), making detection of out-of-control events less likely in the shorter time-series. But 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 (e.g. 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 1950s to negative during much of the 1960s and 1970s, to positive, particularly in the past decade (2000–2009). 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 the expected limits during periods when phytoplankton communities did not appear to be so. The patterns identified suggest that 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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