An observational assessment of the influence of mesoscale and submesoscale heterogeneity on ocean biogeochemical reactions

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Abstract

Numerous observations demonstrate that considerable spatial variability exists in components of the marine planktonic ecosystem at the mesoscale and submesoscale (100km -1km). The causes and consequences of physical processes at these scales ('eddy advection') influencing biogeochemistry have received much attention. Less studied, the non-linear nature of most ecological and biogeochemical interactions means that such spatial variability has consequences for regional estimates of processes including primary production and grazing, independent of the physical processes. This effect has been termed 'eddy reactions'. Models remain our most powerful tools for extrapolating hypotheses for biogeochemistry to global scales and to permit future projections. The spatial resolution of most climate and global biogeochemical models means that processes at the mesoscale and submesoscale are poorly resolved. Modelling work has previously suggested that the neglected 'eddy reactions' may be almost as large as the mean field estimates in some cases. This study seeks to quantify the relative size of eddy and mean reactions observationally, using *in situ* and satellite data. For primary production, grazing and zooplankton mortality the eddy reactions are between 7% and 15% of the mean reactions. These should be regarded as preliminary estimates to encourage further observational estimates, and not taken as a justification for ignoring eddy reactions. Compared to modelling estimates, there are inconsistencies in the relative magnitude of eddy reactions and in correlations which are a major control on their magnitude. One possibility is that models exhibit much stronger spatial correlations than are found in reality, effectively amplifying the magnitude of eddy reactions.

1. Introduction

Oceanic plankton play a significant role in the Earth's biogeochemical cycles despite the disparity in size between organism and environment being up to 12 orders of magnitude, from ~1μm cyanobacteria to ~1000km ocean basins. Such a difference in size is not an issue for those seeking to understand the role of plankton in the Earth system provided plankton are distributed uniformly, allowing averages over their vast populations to be used; but they are not. The 'patchiness' of plankton is well-documented at all scales from ocean basins to millimetres. A large scale approach might still be possible if the interactions of plankton with the biogeochemical cycles, through such processes as primary production, were linear in nature. However, ecological interactions are inherently non-linear, with linear interactions being the exception rather than the rule. This leaves those seeking to quantify the global role of plankton with two choices: they can either directly estimate key processes, such as primary production, at each scale, or they can find a way to infer the estimate at a given scale indirectly using an empirical relationship or parameterisation. More specifically, for global biogeochemical models this is a choice of spatial resolution. The choice of the size of a grid-cell in such a model marks the boundary between explicit representation of processes at larger scales and implicit parameterisation of them at smaller scales. The most extreme, but not uncommon, parameterisation is to ignore smaller scales. Although increases in computing power mean that the resolution of models is always improving, Earth system models still poorly resolve features at scales of 100km and smaller. This is unfortunate, as this regime is one where timescales of the physical circulation - that transport, mix and disperse nutrients and plankton - are close to those of the ecological interactions within them, and the literature is increasingly well-stocked with evidence for the significant ways in which eddies, fronts, filaments and their ilk can influence biogeochemistry from local to global scales (e.g. McGillicuddy et al., 2007; Frajka-Williams et al., 2009; Mahadevan et al., 2012, Levy et al., 2012a). There are widely used techniques for representing the influence of sub-gridscale physical processes on the ocean circulation and tracers carried by it (hereafter 'eddy transports') but only preliminary studies (e.g. Wallhead et al., 2013) dealing with what we will call here the 'eddy reaction' terms.

Consider a process, such as primary production or the grazing of phytoplankton by zooplankton. One can go to any spot in the ocean and measure these processes by whatever method is favoured. But how does one go about estimating their average values for a larger area, *A*? Ideally, one makes many measurements across *A* and averages them for the estimate, i.e. for primary production, $PP_{ideal}=<PP_i>$, where angle brackets denote an average over all the observations, *i*, in *A*. Satellites allow such estimates to be made near globally for PP. However, most other planktonic processes, including grazing, are much more sparsely sampled and thus models remain a key tool in extrapolating the cumulative effect of processes to global scales, aside from their importance in predicting how biogeochemistry and ecosystems may change with time. In a model, processes are estimated from the local abundance of controlling factors e.g. *PP* is estimated as a function of nutrient (*N)* and phytoplankton (*P)* abundances. However, a model with spatial resolution of size *A* can only use average values of *N* and *P* in *A* as it has no information at smaller scales. It therefore has to estimate *PP* as $PP_{mean}=PP(<N>,<P>)$. The difference, $PP_{eddy}=PP_{ideal}-PP_{mean}$, is what we refer to as the eddy reaction; it is the consequence of ignoring non-linear biogeochemical interactions at scales smaller than *A*. Only if the relationship between *N* and *P* in setting *PP* is linear will PP_{eddy} be zero. A fuller explanation can be found in Lévy and Martin (2013).

To understand the impact of eddy reactions on global biogeochemistry the simplest question to start with is: how large is PP_{eddy} compared to PP_{mean}? More pragmatically, are the eddy reaction terms small enough to ignore? Although some of the many observational examples of increased phytoplankton abundance or primary production associated, for example, with eddies, fronts or filaments, have already been mentioned, these have generally been attributed to the influence of physics rather than to biological interactions.

The significance of eddy reactions can be tackled using a model by running it at a range of resolutions (e.g. Mahadevan and Archer, 2000; Lévy et al., 2009, Lévy et al., 2012) but such studies have tended to attribute differences to eddy transports. Nevertheless, in a recent modelling study (Lévy and Martin, 2013) the eddy reaction terms were separated from eddy transport terms. It was found that eddy reaction terms had a small influence from the perspective of nutrients and biogeochemistry. For biology, however, the eddy reactions had a significant impact on organism abundances. This suggests an intriguingly ambivalent role of eddy reactions. The necessary next step is to assess whether the model estimates of the eddy reaction terms are accurate. This study therefore uses a combination of satellite and *in situ* observational data to quantify eddy reactions and their magnitude relative to those at larger scales.

2. Data

2.1 *In situ* data

All of the *in situ* data used in this study were collected using the SeaSoar undulating vehicle. This flexible platform is towed behind a vessel, typically at a speed of 8.5 kts. Controllable wings allow it to perform alternating dives and ascents between the surface and depths of up to 400m, providing saw-tooth vertical sections of water properties. At the above ship speed there is a profile roughly every 3-4km. In addition to standard hydrographic parameters, and of more direct relevance to this study, the vehicle was equipped with a fluorometer (as a proxy for phytoplankton biomass, e.g. Allen et al. 2005 and cruises D227 and D321 described below), the NOC developed SUV-6 nitrate sensor (cruise D321, Pidcock et al, 2010) and/or an Optical Plankton Counter (OPC) which can be used to estimate zooplankton abundance (cruise D227, Srokosz et al., 2003). Surface values are not used because there is evidence of quenching affecting fluorescence measurements on D321 above 25m. Details can be found in van Gennip (2014). Data are therefore taken between 25-35m depth for all cruises for consistency. We keep as close as possible to the surface given that one motivation is to use satellite data which only represents phytoplankton abundance in near-surface waters. Repeating our analysis for greater or lesser depths does not significantly change our results. It should be noted that the *Chl a* and zooplankton biomass values reported are estimated using the manufacturer's calibration; they have not been calibrated against direct samples. However, as such calibrations are generally linear, this does not affect any of the results as we are interested in the relative sizes of eddy and mean reactions.

Data from two cruises are used. The locations are shown in Figure 1. All cruises were carried out by the UK research vessel RRS Discovery in the North Atlantic. The relative positions of observations within each survey are shown in Figure 2c (cruise D321) and Figure 3c (cruise D227). The spatial surveys typically cover an area ~150km x 150km and so the data allow us to quantify the eddy reactions at the mesoscale and smaller.

Cruise D321 (Allen, 2008) simultaneously mapped nitrate and phytoplankton using the SUV-6 and fluorometer mounted on the SeaSoar vehicle respectively. The SUV-6 nitrate data was calibrated against bottle samples collected from CTD casts (Pidcock et al., 2010). The fluorescence data was uncalibrated but we assume a linear relationship between fluorescence and phytoplankton biomass. The cruise was carried out in the sub-polar Northeast Atlantic from 24 July to 23 August 2007, performing a survey of 130km x130km that took 5.3 days in the vicinity of the historical Ocean Weather Station India site at 59^{o}N 19^{o}W. There are 4329 datapoints because ungridded data are used here to preserve as much variability as possible. Nitrate concentrations were typically 2-10 mmol N m^{-3} and consequently not limiting (Eppley et al., 1969). Sarmiento et al. (2004) identifies the region where D321 took place as being in the subpolar biome. Zooplankton data are not available.

Cruise D227 was centred on 47.5^{o}N 18^{o}W spanning the period 19 April to 13 May 1997 (Srokosz, 1997). We use data from two surveys covering the periods 1-3 May and 10-13 May respectively. The first covered an area roughly 50km x 50km whilst the second covered a larger area of approximately 150km x 150km. Note that the spatial resolution along transects was the same for both surveys because it is set by the speed of the vessel and the depth of profiling by SeaSoar. Orthogonal to transects, the resolution was however increased with smaller transect spacing for the smaller survey. An optical plankton counter (OPC) was used to measure zooplankton abundance, specifically their biovolume (cm^3 m^{-3}). Because of the processing necessary for OPC data, the zooplankton abundance estimates have been gridded into 8m deep bins (Morrison et al., 1998). For consistency, the *Chl a* estimates from the fluorometer are binned the same way. A consequence is that there are fewer datapoints (162 and 296) for D227 compared to D321 where it has been possible to use ungridded data. Note, however, that the along-track horizontal resolution for D227 is identical to that for D321. The area surveyed by D227 is within the region identified by Sarmiento et al. (2004) as the transition zone between subpolar and subtropical gyres. Nitrate data are not available.

2.2 Satellite data

We use '4km' resolution, 8 day composite, Level 3 Aqua MODIS ocean colour data for the decade 2003-2012 inclusive. Data were downloaded directly from the NASA OceanColor website: http://oceandata.sci.gsfc.nasa.gov. We focus on the North Atlantic for comparison to the modelling study of Lévy and Martin (2013). Note that although the data are referred to as 4km resolution, the data pixels are equally sized in degrees not kilometres. (Note that we use the word 'pixel' to refer to the size of the box which each satellite datum represents, rather than the resolution of the raw satellite data.) The angular size is 0.0417° corresponding to a size of 4.7km at the Equator. The longitudinal size of the pixel will decrease with increasing latitude. It was decided to use the original pixels for calculations, rather than ones recalculated to be of equal size, for the following reasons: first, the Rossby deformation length decreases in the same manner as pixel size with latitude so if it is assumed that much of the spatial variability results from mesoscale dynamics, then the pixel size is tracking the size of the dominant physical processes; second, to maintain the same size of pixels in kilometres would involve either interpolation (risking modifying the variability we seek to quantify) and/or use of a different number of pixels for each calculation (which makes a comparison of pixels at different latitudes less statistically robust).

For each pixel in a given satellite image, we identify the 27 x 27 = 729 pixels (corresponding to 126km meridional distance, of similar size to the surveys in Section 2.1.4) in a box centred upon it. These data are used to calculate the coefficient of variation, the value of which is then prescribed to the centre pixel. The calculation excludes gaps in data e.g. due to clouds. For each pixel we therefore produce a time series of the coefficient of variation at 8 day resolution for the decade 2003-2012 in the 1.13° x 1.13° area surrounding it. The impact of geographical coverage changing seasonally with day length is discussed in Section 3.2. Each of these time-series is then used to calculate the mean and standard deviation coefficient of variation for each pixel over the decade. This gives a global map of phytoplankton's coefficient of variation.

3. Methodology

It should be stressed that the emphasis is on examining the relative size of eddy reaction (ER) and mean reaction (MR) terms using observational data. For reasons already given, the interactions we explore are as represented in models. However, no suite of observations can give the full knowledge of a system provided by a model. For that reason it is necessary to focus on the few interactions for which there are sufficient data at the necessary spatial resolution to quantify eddy reactions at scales smaller than 100km. Even so, it should be noted that the data available (see Sections 2.1.4 and 2.2.2) have a resolution of a few kilometres so we will still miss effects due to variability at sub-kilometre scales.

We use two complementary approaches to assess the significance of eddy reactions. The first uses *in situ* data where either phytoplankton and nitrate, or phytoplankton and zooplankton, have been simultaneously mapped at a suitable horizontal resolution. While these data are ideal for estimating eddy reactions associated with primary production and grazing (Equations 2-4 below) such datasets are nevertheless local in both space and time, covering typically 150km x 150km over a period of just

4-6 weeks. Satellites provide data at the necessary spatial resolution on a near global scale almost weekly, but only for phytoplankton, via the proxy of chlorophyll. Our second approach, therefore, uses ocean colour data to explore how significant eddy reaction terms may be on broader space and time scales. More generally, because the satellite data are limited to surface values, this study focuses on the surface waters of the ocean.

3.1 ER/MR as a function of correlations and coefficients of variation

The case of a simple non-linear interaction, where a rate, Z, involving two fields, X and Y, is given by $Z=\alpha XY$ provides a useful insight into what controls the magnitude of ER/MR.

For a chosen area we can write

$$\langle Z\rangle = \alpha\langle X\rangle\langle Y\rangle + \alpha\langle X'Y'\rangle$$

where angled brackets denote an average over the area. For every observation within the area, $X'=X-\langle X\rangle$ and $Y'=Y-\langle Y\rangle$ are the observations relative to the average, effectively the fluctuations about it. The first term on the right hand side of the equation is the mean interaction (MR), whilst the second is the eddy reaction (ER). We are therefore interested in the ratio of these two terms. More specifically, the relative magnitude of the eddy reaction to the mean reaction is

$$R = \frac{\langle X'Y'\rangle}{\langle X\rangle\langle Y\rangle}$$

This can be rewritten as

$$R = \left(\frac{\langle X'Y'\rangle}{\sqrt{\langle X'^2\rangle}\sqrt{\langle Y'^2\rangle}}\right)\left(\frac{\sqrt{\langle X'^2\rangle}}{\langle X\rangle}\right)\left(\frac{\sqrt{\langle Y'^2\rangle}}{\langle Y\rangle}\right) = \frac{ER}{MR} \qquad (1)$$

The first term on the right hand side is the correlation coefficient and cannot be larger in magnitude than 1. The second and third terms are the coefficients of variation for X and Y respectively. The coefficient of variation is a widely used statistic to represent the variability of a field. Hence, the relative magnitude of the eddy reaction to the mean reaction is controlled by the degree of spatial variability in the two interacting fields and by the strength of the spatial correlation between them.

3.2 Eddy reactions from *in situ* data only

The observations of nitrate, phytoplankton and zooplankton available for *in situ* estimates have been introduced in Section 2.1. We can regard each cruise survey as providing information inside one model 'grid-cell'. The eddy reactions are estimated both using abundances averaged over the survey area (to give mean reactions) and averaging over the interactions calculated at each data-point (an estimate of the 'true' value). The eddy reaction is the difference between these two.

3.2.1 Primary production

Following a standard modelling approach (including Lévy and Martin 2013) we represent nitrate control of primary production, *PP*, as

$$PP = \mu_P \left(\frac{N}{k_N + N}\right) P \qquad (2)$$

where μ_P is the phytoplankton maximum growth rate, k_N is the half-saturation constant for nitrate (*N*) uptake and *P* is the phytoplankton concentration. For simplicity we assume that light is uniform across an area of ~150kmx150km and ignore its effect for now (but see Discussion). The focus is on surface *PP*. We are interested in the size of the eddy reaction relative to the mean field estimate of Equation 2. Therefore, we do not need to know the maximum growth rate for which we have no direct information. It cancels when we take the ratio. Similarly, assuming a linear conversion from units of fluorescence (as recorded by the fluorometer) to carbon or chlorophyll we do not need to worry about the units of *P*. We have no knowledge of k_N for the given datasets and so for simplicity, and for consistency with Lévy and Martin (2013), we take a value of 0.7 mmol N m^{-3} as baseline but explore the consequences of using values either side of it.

3.2.2 Grazing

The representation of grazing is also a simple one, with grazing, *GR*, given by

$$GR = \mu_Z \left(\frac{P}{k_P + P}\right) Z \qquad (3)$$

where μ_Z is the maximum grazing rate, k_P is the half-saturation constant and *P* and *Z* are the phytoplankton and zooplankton concentrations respectively. Once again this form is widely used in modelling studies, including Lévy and Martin (2013). We have had to ignore the feeding of zooplankton on other resources, such as detritus, for lack of data. While we can ignore the maximum grazing rate, μ_Z, and units of *Z*, because of our focus on the relative size of eddy and mean reactions, we do need to put a value on k_P. We choose a baseline value of 1 mmol m^{-3} to be consistent with Lévy and Martin (2013), converting this into units of mg Chl m^{-3} by multiplying by a conversion factor of 1.6 mg Chl (mmol N)$^{-1}$ to be consistent with the data units. Once again, we explore a range of values on either side of this, which also implicitly accounts for uncertainty in the conversion factor.

3.2.3 Zooplankton 'mortality'

The 'mortality' term for zooplankton in biogeochemical models is, from a practical perspective, a closure term representing the effect on zooplankton of higher trophic levels not represented by the model. For the sake of simplicity, these unrepresented organisms are often assumed to vary proportionally in abundance with zooplankton such that zooplankton mortality, *ZM*, is defined as

$$ZM = m_Z Z^2 \qquad (4)$$

Fortunately we do not need to know the value of the parameter m_Z, once again because we are comparing the relative size of eddy and mean reactions. This is a parameterisation frequently used in models (including Levy and Martin, 2013) and it shares a similar non-linearity to the above representations of primary production and grazing.

3.3 Eddy reactions from satellite and *in situ* data

The major advantage of satellite data is that we have global coverage at scales of a few kilometres updated on a near-weekly frequency. The disadvantage is that we only have reliable data for phytoplankton. Furthermore, because of frequent cloud cover it is necessary to use 8 day composites which may additionally smooth out variability (this is addressed in the Discussion). Consequently, the satellite may not accurately resolve features smaller than 20km. However, it is still possible to explore the potential significance of eddy reactions even given these limitations. In particular, starting with Equation 1 and making assumptions about the correlations and CVs, or combining the satellite and *in situ* estimates, gives the potential to calculate the temporal and spatial variability of ER/MR in a way that is not possible using the *in situ* data alone.

We first focus on the primary production term (Equation 2) but simplify it. When nitrate abundance is significantly in excess of the half saturation constant, Equation 2 is approximately $PP=\mu_P P$. This is linear and in any situations where this is a good approximation the eddy reaction will be negligible. In the other extreme, where nitrate concentrations are less than k_N, the primary production equation is approximated by

$$PP_{sat} = \left(\frac{\mu_P}{k_N}\right) NP \qquad (5)$$

This represents the most non-linear case of Equation 2. If the eddy reaction is not significant relative to the mean reaction in this case, it will not be in any case. Equation 5 is of the same form as that used to derive Equation 1 and so we can use Equation 1 to estimate ER/MR. To proceed we first assume that correlation coefficient is unity, which means that any estimate of ER/MR is an upper bound. Unfortunately, we cannot quantify the nitrate coefficient of variation from satellite data. However, if we assume that it takes a value of one then we can put a rough upper bound on the size of *R* (an issue returned to in the Discussion), and hence on the significance of eddy reactions relative to mean ones. We can also use the estimate of the coefficient of variation for nitrate calculated using the *in situ* data (Section 3.1.1).). Therefore, in making the ER/MR estimates the key factor becomes the coefficient of variation of the phytoplankton obtained from the satellite data.

A similar approach can be used to put an upper limit on the relative size of the eddy reaction for grazing since in the most non-linear case of scarce phytoplankton Equation 3 reduces to

$$GR_{sat} = \left(\frac{\mu_Z}{k_P}\right) PZ \qquad (6)$$

4. Results

4.1 ER/MR from *in situ* data only

4.1.1 Primary production

The abundances of phytoplankton and nitrate within the survey area of D321 are shown in Figure 2a and Figure 2b respectively. They are shown plotted against cumulative distance travelled as a simple way of showing all the data on one plot. The period of the survey (5.3 days) was chosen to make the survey as synoptic as possible. Note that although the distance in Figs. 2a and 2b extends to several hundred kilometres, all data were obtained in the same ~130km x 130km box (Figure 2c). Although coverage of the region is intermittent, due to technical issues with SeaSoar (Figure 2c), it is still apparent that there is considerable spatial variability in the distributions of both phytoplankton and nitrate (Table 1); their abundances vary by 10 and 5 fold and their coefficients of variation (mean divided by standard deviation) are 0.31 and 0.36, respectively. Comparison of Figs. 2a and 2b suggests that there is no strong correlation between phytoplankton and nitrate (see also Figure 2d), which is borne out by the correlation coefficient of -0.31. The correlation between phytoplankton and the nutrient limitation term in Equation 2, $N/(k_N+N)$, varies monotonically from -0.37 when k_N equals zero to -0.34 when k_N equals 10 mmolN m^{-3} (not shown). We use Equation 2 to calculate MR using the spatially averaged fields for the survey. We also average Equation 2 evaluated at all data points in the survey. The difference gives ER. This is repeated for values of k_N spanning from zero, through the baseline value of 0.5 mmolN m^{-3}, to a maximum of 10 mmolN m^{-3}. The largest value is chosen to be just larger than the maximum concentration of nitrate seen on D321. As previously stated (Section 2.1.4), nitrate was not limiting during the cruise but the upper limit for k_N was chosen as a simple proxy to explore the effect on ER/MR if it had been. Figure 2e shows the relative size of the eddy reaction to the mean reaction, ER/MR, as a function of k_N. ER/MR varies with k_N but is always negative. We discuss the absolute value, |ER/MR|, to avoid confusion. This varies between 0, when k_N is zero, and a maximum value just below 0.05, when k_N is 6 mmolN m^{-3}. The reason why there is a maximum in absolute value is because at larger k_N the magnitude of the eddy reaction decreases as the correlation between *P* and the nitrate limitation term decreases (see above), whilst as k_N tends to zero the nutrient limitation term becomes increasingly close to a value of one resulting in primary production becoming increasingly linear and, hence, in the eddy reaction decreasing towards zero. Even at the maximum, ER is only 5% of the magnitude of MR.

4.1.2 Grazing

Cruise D227 provided an opportunity to examine the relative size of the eddy reaction term to the mean reaction on two scales. Figure 3 shows data from 2 spatial surveys. The first survey covered an area approximately 50km across whilst the second mapped an area roughly 150km across. As the sampling interval along transect is set by the range of depths covered by SeaSoar and the speed of the ship which were the same for both surveys, the main difference in resolution comes from the reduced spacing between the transects which comprise the survey (Figure 3c). Figure 3a and Figure 3b show data from both surveys in full against distance travelled on each survey. As for D321 there is considerable spatial variability (Table 1).

In the first, smaller survey phytoplankton abundance varies over 0.9-1.9 mg Chl m^{-3} with a mean of 1.36 mg Chl m^{-3} and coefficient of variation of 0.16. Zooplankton abundance varies over 0.1-0.6 cm^3

m^{-3} with mean 0.33 cm^3 m^{-3} but with more marked variability, indicated by a coefficient of variation of 0.38. The correlation coefficient for phytoplankton and zooplankton is -0.47 (Figure 3d). The correlation coefficient for zooplankton and the phytoplankton limitation term in Equation 3, $P/(k_P+P)$, varies between -0.42 when k_P is zero to -0.45 when k_P is 10 mg Chl m^{-3} (not shown). The relative size of the eddy reaction to the mean reaction, ER/MR, is always negative, as for primary production. The magnitude is seen to reach its highest value, 0.027, when k_P is 10 mg Chl m^{-3}, decreasing at an increasing rate as k_P decreases, to be zero when k_P is zero (Figure 3e). The eddy reaction is never more than 3% of the magnitude of the mean reaction.

During the second, larger survey phytoplankton fluctuate over a smaller range from 0.6-1.1 mg Chl m^{-3} with mean 0.72 mg Chl m^{-3} and a coefficient of variation of 0.11. Similarly, zooplankton variability is now constrained within the range 0.2 to 0.5 cm^3 m^{-3} with 0.38 cm^3 m^{-3} mean and a coefficient of variation (0.15) that is comparable to that of phytoplankton. Phytoplankton and zooplankton have a correlation coefficient of -0.56 (Figure 3d). The correlation between the phytoplankton limitation term and zooplankton changes from -0.52 to -0.56 as k_P increases from 0 to 10 mg Chl m^{-3} (not shown). EL/MR is even smaller in magnitude than for the first survey with a maximum of 0.01 at k_P, otherwise sharing the convergence on zero as k_P tends to zero. This means that the eddy reaction is at most 1 % of the mean reaction.

There is an indication of a significant temporal change over the 7 days between the two surveys (Figs. 3a, 3b and 3d). The mean chlorophyll concentration decreases by 0.64 mg Chl m^{-3} whilst the mean zooplankton abundance increases by 0.05 cm^3 m^{-3}. For both phytoplankton and zooplankton the coefficients of variation decrease, by 0.05 and 0.23 respectively. Of particular relevance, ER/MR is threefold lower for the second survey compared to the first. This is unlikely to be due to the different sizes of survey area. The larger survey has a smaller ER/MR than the smaller survey even though statistically it should sample a similar range of values if there is no change in time. Furthermore, although the smaller survey has more closely spaced transects than the larger survey, the highest resolution is still along-track which is the same for both surveys. The indication therefore is that the changes in ER/MR are associated with temporal change, an aspect addressed in more detail through the satellite analysis below (Section 3.2).

4.1.3 Zooplankton 'mortality'

As for grazing, for zooplankton mortality we have two surveys at different scales courtesy of D227. The variability in the zooplankton abundance has already been described in the previous section. Given the form of the closure term representing mortality (Equation 4), the variables involved are perfectly correlated since they are both *Z.* Despite this, the eddy reaction is still less than 15% of the mean reaction; ER/MR is 0.14 and 0.02 for the first and second survey respectively.

4.2 ER/MR from satellite and *in situ* data

As described in Section 3.3, we can only use the satellite data directly to estimate an upper bound on ER/MR. More specifically, for the purposes of this section we assume that nitrate and zooplankton are both perfectly correlated with phytoplankton and both have CV equal to 1. The CV of phytoplankton estimated from satellite data is therefore our estimate of ER/MR. We return to these assumptions in the Discussion.

For the satellite data, the median coefficient of variation (CV) over the years 2003-2012 (Figure 4b) shows less large scale structure than the annual chlorophyll distributions (Figure 4a - note the log scale). In particular there is a much weaker demarcation in CV between the subpolar and subtropical gyres with the main contrast provided by higher values associated with persistent open ocean fronts and mesoscale variability associated with boundary upwelling. Over the entire North Atlantic, for the 10 years analysed, the median coefficient of variation is 0.18 but the distribution is very skewed; the mean value is 0.28, and the standard deviation is 0.35. Just 12% of locations exhibit a mean coefficient of variation greater than 0.5 at some time, but 4% manage to exceed 1 (Figure 4c). The range of values taken by the median CV across a year (0.14 to 0.24 – not shown) is low.

Despite the weaker geographical variability in annual median compared to phytoplankton abundance, Figure 5 shows that the coefficient of variation nevertheless exhibits geographical variability in the seasonal cycle. In the subpolar gyre there is an increase across the spring and summer, with values in the open ocean in excess of 0.4. This period of raised values begins in March but is most pronounced between April and August with a weaker signal into September. However, there is also a seasonal signal apparent in the subtropical gyre, across the basin from 15°-35°N, if of smaller magnitude. Here the period of raised values is concentrated between May and September but extending more weakly into April and October.

The seasonal variation of CV can be seen more clearly in Figure 6 which shows median CV versus latitude for each month. For reference, the annual median value of the coefficient of variation at each latitude is shown in Figure 6 (red line). The median is used rather than the mean because of the skew mentioned above. Broadly speaking, south of 40°N the annual median is ~0.2, taking a higher value of ~0.25 further north. Because satellite coverage is limited during the winter, the annual estimates of coefficient of variation north of 50°N will be biased by only using data from March to September. Figure 6 therefore also shows the coefficient of variation versus latitude when only data from April to September (inclusive) are used (green line). The values in the south do increase relative to those found using data from the whole year, but the change is far from sufficient to make up the difference between north and south values. For the monthly estimates (black) the largest values occur between 65°-80°N, where a peak either side of a minimum at around 75°N develops over the course of May and June, reaching a maximum of ~0.6 during June. Another seasonal peak develops from April to June between 40°N and 55°N, this time reaching a maximum of just over 0.4 in May. Between 20°N and 35°N, there is a more persistent peak from May to September but reaching a maximum of only ~0.3 in July. Finally there is a sharp peak from 5°N to 10°N that is present for just August and September but reaches 0.4.

5. Discussion

5.1 Relative size of eddy and mean reactions

It has only been possible to estimate eddy reaction terms fully directly using *in situ* data, because satellite sensors cannot yet quantify components of the ecosystem other than phytoplankton at the necessary spatial resolution for this study. Using widely used parameterisations of nitrate uptake by phytoplankton as a proxy for primary production (Equation 2) and of grazing of phytoplankton by zooplankton (Equation 3) the eddy reaction (ER) estimates using *in situ* data are never more than 5% of the mean reaction (MR). For the typical closure term used to represent zooplankton mortality to higher organisms in models ER/MR is less than 15%. The difference in magnitude between ER/MR for zooplankton mortality and the estimates for primary production and grazing is predominantly due to the strength of the correlation involved. For reactions involving phytoplankton and zooplankton or phytoplankton and nitrate the correlation is between 0.3 and 0.5 in magnitude. For 'mortality', however, the relevant correlation is for zooplankton with itself i.e. 1. It should be noted that the motivation for the form of the closure term is that the unrepresented predator of zooplankton is assumed to be proportional in abundance to zooplankton. In practice the correlation is unlikely to be so tight and so the estimate of ER/MR for mortality is likely an over-estimate. The importance of the correlation in setting the magnitude of the eddy reaction is returned to in Section 5.3.

The limited data and the assumptions underlying the method of calculating the eddy reaction may both influence the estimates. First, cruise D321 took place in a location and time of year where nitrate was not limiting. This should still give a reasonable estimate for ER/MR for such scenarios. However, it may not be an accurate estimate of ER/MR for regions where nitrate is limiting even though nitrate was artificially made to be limiting by increasing the half-saturation constant for uptake. The reason for the potential inaccuracy is once again one of correlations. The correlation between nitrate and phytoplankton in a nitrate rich environment may be different to that in a nitrate limited environment. In particular, one might expect a stronger correlation under nutrient limitation which would increase the size of ER/MR, all other things being equal. There is therefore a clear requirement to repeat this exercise using data from an oligotrophic environment. It is also the case that the correlation between two fields may change with time, particularly over a seasonal cycle. Once again taking the example of nitrate and phytoplankton, in early spring correlations may be weak as nitrate is not limiting but this may change as nitrate is drawn down by phytoplankton growth. The net impact of the multiple eddy reactions affecting a particular field will also vary seasonally. As the different reactions involved may have different patterns of seasonal variation, the net impact need not necessarily vary seasonally in a way which correlates with the magnitude of individual eddy reactions (e.g. Lévy and Martin, 2013). It is the net effect which influences the field's dynamics.

Second, it has been assumed that primary production and grazing are relatively simple functions of just two variables: phytoplankton and nitrate or zooplankton and phytoplankton. In practice, even in a standard biogeochemical model, primary production will also be a function of light and abundance of other nutrients, such as ammonium, whilst zooplankton will be feeding on detritus and possibly other zooplankton and bacteria. When multiple nutrient or food resources support primary production and grazing, respectively, then to first order the contributions from use of different resources to the total are additive. Each contribution could therefore be considered independently, if data were available. As before, the size of ER/MR in each case will be a function of how much the additional resources vary spatially and the strength of their correlation to the consumer. However, there are instances where a greater degree of non-linearity can occur. An example is including spatial variability of light in calculating primary production. As a rather simple example, light control of primary production can be included in a manner similar to nitrate limitation such that Equation 2 becomes

$$PP = \mu_P \left(\frac{I}{k_I + I}\right)\left(\frac{N}{k_N + N}\right)P$$

where I is irradiance and k_I the associated half-saturation constant. In the case where both light and nitrate are limiting this becomes $PP = (\mu_P/k_I k_N)INP$ and an analysis similar to that in Section 3.1 produces a variant on Equation 1 which now has four contributions from eddy reactions: three from the eddy reaction involving each pairing of I, N and P and a fourth from a reaction involving all three. In the absence of *a priori* information to suggest otherwise, taking the three new terms involving light to be of similar magnitude to the eddy reaction just involving nitrate and phytoplankton, then the total eddy reaction term could quadruple. Variations in mixed layer depth, such as those associated with mesoscale and submesoscale physical features, can introduce significant spatial variability into the average light experienced by phytoplankton within the surface mixed layer because of the exponential decay of light with depth. If phytoplankton concentrations are also correlated with such physical features (e.g. D'Ovidio et al., 2010), then the additional contributions to ER involving light could be significant. A similar argument applies to models that use multiplicative multiple nutrient limitation rather than assuming that only the most-limiting resource affects a process.

Although the satellite data analysis does not allow us to calculate the full eddy reaction directly, Equation 1 nevertheless demonstrates that a rough upper limit can be put on the relative size of eddy to mean reactions. In the extreme case where fields are assumed to be perfectly correlated and nitrate and zooplankton to have CV equal to 1, then ER/MR for primary production and grazing is less than 0.6 which is the upper limit for the phytoplankton CV from the satellite data (Figure 6). Note that the highest values occur at higher latitudes where nutrient is less likely to be limiting and so ER/MR for PP may be much smaller as a consequence. Regardless, if estimates of correlations and CVs for nitrate and zooplankton from *in situ* data are used then estimates decrease by a factor of 5 (grazing) and 9 (primary production). A comparison of ER/MR estimated using the latter method (satellite for phytoplankton CV and *in situ* for all else) to the entirely *in situ* estimates still shows the latter to be lower (Table 2) despite both approaches using *in situ* data to estimate nitrate and zooplankton CVs and correlations to phytoplankton. Therefore, the discrepancy comes from a lower

CV for phytoplankton *in situ* relative to the satellite estimate. Specifically, the CV for phytoplankton *in situ* is fourfold and twofold smaller for D227 (0.11-0.16) and D321 (0.3), respectively, than the value of 0.6 that is the upper limit derived from satellite data.

Cruise D321 took place in July and August of 2007 in the vicinity of 59°N 19°W. Figure 7 shows that, for this period and latitude, the *in situ* estimate of the coefficient of variation for phytoplankton (0.31) is consistent with that seen in the satellite data for the period 2003-2012. In particular there is a good match for the year of the cruise, 2007. There is clearly considerable inter-annual variability however.

Cruise D227 took place earlier in the year (April and May of 1997) and further south (47°N-49°N). Here the *in situ* estimates of coefficient of variation for phytoplankton (0.11 and 0.16) are generally lower than the satellite estimates for the same months (the medians are upwards of 0.2). Unfortunately, satellite data are not available to coincide with cruise D227. Compared to the marked inter-annual variability in the data available, the *in situ* estimate is consistently below the 25% quartile. Nevertheless, it is not possible to rule out a match between satellite and *in situ* estimates for D227. Alternatively, given the variability visible in Figure 7, both within a given month and across a year, chance cannot be ruled out as an explanation of the seemingly good agreement between satellite and *in situ* estimates for D321. This further reinforces the need for more data to quantify better the relationship between *in situ* and satellite estimates. Both gliders and bio-Argo floats are promising in this regard, particularly with the development of ultraviolet based nitrate sensors (e.g. Pidcock et al., 2010; Evans et al., 2013).

In summary, while there is still uncertainty regarding whether satellite colour data over-estimates the CV for phytoplankton, the *in situ* data available for correlations and CVs for nitrate and zooplankton nevertheless make a strong case for an estimate of ER/MR based solely on satellite data being a potentially significant over-estimate.

5.2 Consistency with modelling

In the modelling study of Lévy and Martin (2013) the eddy reaction for grazing was between 5% and 10% in magnitude of the mean reaction. While this is substantially lower than the upper limit calculated only from satellite data (whose caveats are discussed above) it is consistent with the direct estimate of the eddy grazing from *in situ* data and from satellite data using the *in situ* correlation and CV for zooplankton. It should be noted, however, that the correlation between phytoplankton and zooplankton though small (<0.05) was positive in Lévy and Martin (2013, their Figure 6) in contrast to the larger negative correlations found here in observations.

For primary production (more specifically nitrate uptake), in the model of Lévy and Martin (2013) the ratio of eddy to mean reactions varies between 5% and 20% over the year (with peaks in April and November) in the subpolar regions and between 10% (March/April) to 45% (September/October) in the subtropics. This is significantly larger than the observational estimates presented here (Table 2). The question of why ER/MR for nitrate uptake should be so much larger in the model is best tackled by examining the components of the eddy reaction.

It is possible that the model has a stronger correlation between fields than is observed in reality. This may arise due to the model being a deterministic one based on interactions between a small number of variables, rather than the complicated web of interactions in the real ecosystem. To provide a stronger test of how well models may be capturing correlations between fields we can look at how the correlation varies with depth. Figure 8 shows the vertical profile of correlations between nitrate (N) and phytoplankton (P) and between phytoplankton and zooplankton (Z). The N-P correlation is almost always negative, just breaking into positive values at 30m with peaks in magnitude either side of this at 20 and 50m. This is remarkably similar in shape to the depth profile seen in Figure 6 of Lévy and Martin (2013), though note that their figure shows only the cross-product which needs to be normalised by the size of the P and Z fields to give the correlation. In our study, the P-Z correlation changes sign for both surveys around 30m depth, being positive below where, for the large survey at least, it can reach values near one i.e. a perfect correlation. The reason for this high correlation at depth is the presence of an internal wave. P and Z are more uniform on, but vary strongly across, density surfaces. The undulations in the depth of density surfaces at 75m associated with the wave are projecting a trend of phytoplankton and zooplankton with depth on to the 75m surface. Nevertheless, the shape of our correlation-depth profile is the opposite of that seen in the Lévy and Martin (2013) model (their Figure 6). One possible reason for the discrepancy is that the model has a single variable for all zooplankton whereas the observations focus on a restricted range of organism sizes. The Optical Plankton Counter used to measure zooplankton abundance in this study allows biomass in different size-classes to be estimated. In this study we have used the size class of <500μm, assuming that the smaller zooplankton will be those most likely to be consuming the phytoplankton. If other size classes are used (500-1000 μm, 1000-2000 μm) or if the sum of all zooplankton in these groups are used then the results are the same. In summary, for N-P the model and observations have a similarly shaped vertical profile but seem to disagree on magnitude, while for P-Z the magnitudes match better but there is a disagreement in profile shapes. Clearly more work is needed to resolve this difference but it is worth noting that although they are from the rather different setting of a shelf sea, there are nevertheless some previous observations to support a hypothesis that deterministic models may over-estimate correlations (Martin et al., 2008).

Another possibility to consider is that model or observations may be biased in their estimate of CV. If the model is over-estimating or the satellite estimates are under-estimating then the two may yet be reconciled. It is not clear why the model would be over-estimating the CV. There will always be processes that cannot be resolved in a model yet are capable of generating spatial structure e.g. mixed layer eddies are below the resolution of the Lévy and Martin (2013) model. Models also have an inevitable degree of numerical diffusion that will reduce spatial gradients. Hence, it is more likely that the model is under-estimating the CV. The alternative is that the observational estimates are under-estimates. The satellite images used for analysis are 8 day composites. The reason for this is because cloud cover is rarely small enough to permit sufficiently clear single images. To assess the impact of such compositing, we have managed to find a sequence of 8 consecutive daily images. Details can be found in Supplementary Information. If the CV is calculated for each daily image, the median CV across the 8 days is 0.18. If the images are combined as they would be to form an 8-day composite, the resulting image has a CV of 0.12, only 66% of the median CV of daily images. Unfortunately, there are very few instances where such an analysis can be done and so this can only illustrate the potential impact of using 8 day composites. Nevertheless, it demonstrates that when looking at features at scales of 100km and smaller, 8 day composites may significantly blur structure and lead to under-estimates of CV. However, if satellite estimates of phytoplankton CV are under-estimates this weakens the match between in situ and satellite estimates discussed above.

Before leaving the topic of comparing model results to observations it is worth noting that in the Lévy and Martin (2013) model study, eddy reaction terms for ammonium uptake and zooplankton feeding on detritus are the largest ones but for these we have no data at the necessary scales.

5.3 Broader implications

An unfortunate consequence of inevitably not having observational estimates for all processes within the ecosystem is that it is not possible to assess the cumulative effect of the eddy reactions from observational data. In Lévy and Martin (2013) it was demonstrated that the eddy reactions can both augment and cancel each other, such that cumulatively eddy reactions are small compared to other fluxes for nitrate but significant for phytoplankton, despite nitrate uptake affecting both. It should be noted, however, that even if the cumulative eddy reactions are small this does not mean that their effect is trivial. In the Lévy and Martin (2013) study the eddy reactions were simply diagnosed from a higher resolution model. It is possible that, though small, the eddy reactions nevertheless feedback to affect the mean state of the system, in the same way that small scale physics have been shown to do (Lévy et al., 2012).

Taking an alternative perspective, the possibility that models may have stronger correlations between phytoplankton, nutrients, zooplankton etc than in reality may indicate that eddy reactions are a problem of a model's own making. For reasons of computational limitations and concerns over an absence of data to constrain much of the ecosystem, many global biogeochemical models reduce the plankton ecosystem to a very small number of components, describing the interactions between them using deterministic differential equations. While the presence of chaotic behaviour cannot be ruled out, the very design of global biogeochemical models may predispose them to exhibit strong local correlations. One way to test this would be to explore the strength of spatial correlations found in models of different ecological complexity. If using a simpler biogeochemical model does turn out to increase the relative magnitude of eddy reactions this potentially poses a dilemma for climate modellers who typically use both simplified biology and coarse spatial resolution. Additionally, if the problem is one of their own making, there is the question of whether they should even seek to represent eddy reactions because they may arise from a phenomenon at smaller scales that is not significant in reality. This is relevant to recent suggestions that biogeochemistry could be run at coarser scales than the physical circulation in global and climate models (Lévy et al., 2012).

6. Conclusions

An analysis of *in situ* and satellite observational data has provided estimates of eddy reactions for primary production, grazing and zooplankton 'mortality' that are less than 7%, 12% and 15% of the mean reaction terms respectively. Given issues surrounding the use of satellite data and the limited amount of *in situ* data these should be regarded as preliminary estimates and by no means a robust basis for ignoring eddy reactions. Comparison to results of a previous modelling study show some consistency in magnitude (but not sign) for grazing, but reveal a substantially different reaction relative to the mean one for primary production. The discrepancy may arise from underestimates of coefficients of variation from satellite data or from a difference in the strength of correlations. The latter raises the possibility that biogeochemical models may exhibit stronger correlations between fields than are found in reality with implications for the impact of sub-gridscale processes on their behaviour.

Acknowledgements

The MODIS Aqua Level 3, 4km, 8-day Chlorophyll a data were obtained from the NASA Ocean Color website, http://oceandata.sci.gsfc.nasa.gov. We are indebted to the Captain and crew of RRS Discovery. All cruise data are freely available from the British Oceanographic Data Centre (www.bodc.ac.uk). Several of the authors (APM, SvG, MAS, SCP) were supported by NERC National Capability funding.

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Tables

Table 1: Summary of *in situ* data

	survey											
	D321				D227 small				D227 large			
	mean	range	CV	Corr	mean	range	CV	Corr	mean	range	CV	Corr
N (mmol N m^{-3})	3.5	1.4-9.8	0.36	-0.31								
P (mg Chl m^{-3})	0.24	0.0-0.6	0.31		1.4	0.9-1.9	0.16	-0.47	0.72	0.6-1.1	0.11	-0.56
Z (cm^3 m^{-3})					0.33	0.1-0.6	0.38		0.38	0.2-0.5	0.15	

Table 2: Comparison of estimates for ER/MR using *in situ* data alone, satellite data for phytoplankton CV in conjunction with *in situ* estimates for correlation coefficients and CV for nitrate and zooplankton and the modelling study of Lévy and Martin (2013)

	Primary production	Grazing
in situ	0.04	0.01, 0.03
Satellite + *in situ*	0.07	0.12
Model – Lévy & Martin (2013)	0.2-0.45	0.05-0.1

Figure captions:

Figure 1: Locations for *in situ* data: circle, cruise D227; triangle, cruise D321.

Figure 2: Analysis of relative magnitudes of eddy and mean reaction terms for primary production (Equation 1) using data from cruise D321: (a) Chl a data shown against distance travelled (km), (b) nitrate data shown against distance travelled, (c) positions of observations, (d) scatterplot of Chl a and nitrate observations and (e) relative size of eddy reaction (ER) and mean reaction (MR) terms for a range of values for nitrate half-saturation, k_N.

Figure 3: Analysis of relative magnitudes of eddy and mean reaction terms for zooplankton grazing (Equation 2) using data from cruise D227. Results from analysing two spatial surveys are shown, the first (red) from 1-3 May 1997, the second (black) from 10-13 May 1997: (a) Chl a data shown against distance travelled (km), (b) zooplankton abundance data shown against distance, (c) positions of observations, (d) scatterplot of Chl a and zooplankton observations and (e) relative size of eddy reaction (ER) and mean reaction (MR) terms for a range of values for phytoplankton half-saturation, k_P.

Figure 4: For the years 2003-2012: (a) average daily phytoplankton abundance (Chl a mg m^{-3}), (b) median coefficient of variation for phytoplankton abundance in an area 1.13° x 1.13° centred on each pixel and (c) cumulative distribution for CV including estimates every 8 days for each pixel for this period. Data are from the MODIS Aqua satellite - see Acknowledgements.

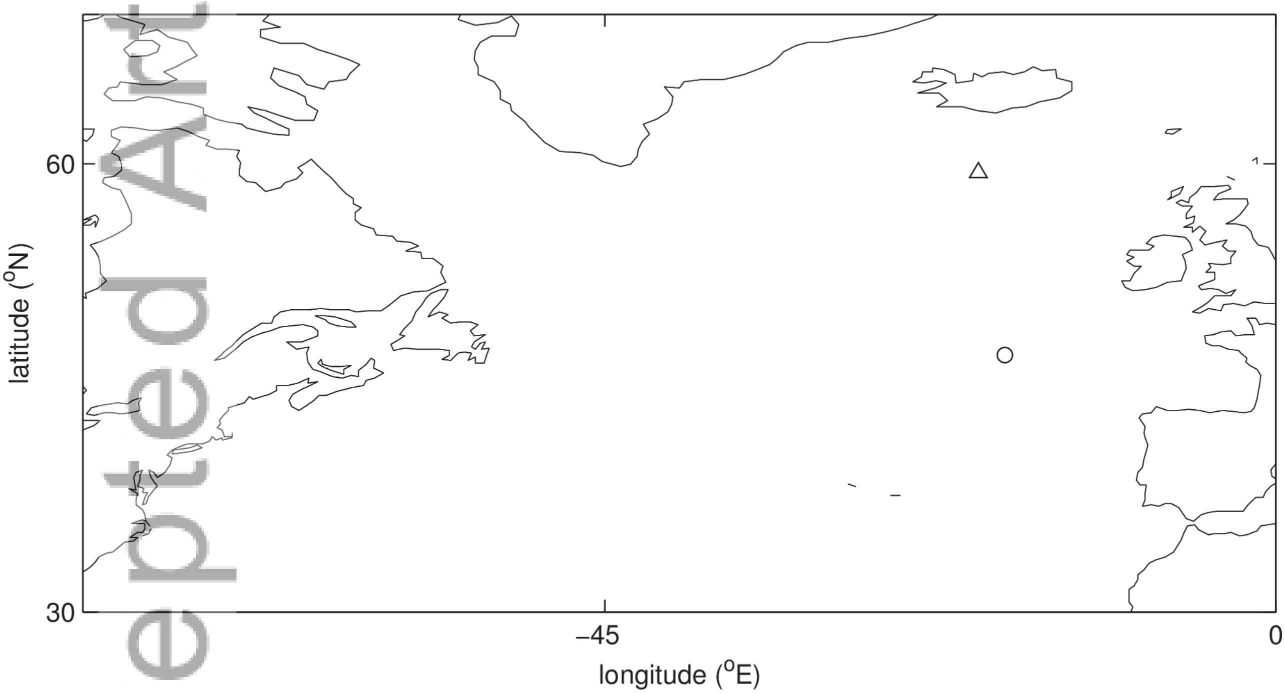
Figure 5: Monthly climatology of median coefficient of variation for Chlorophyll a for the years 2003-2012. Each pixel value is calculated using data in a box of side 1.1° centred upon it – see 2.2.2. Data are from the MODIS Aqua satellite - see Acknowledgements.

Figure 6: Median coefficient of variation for Chlorophyll a at each latitude and each month (black line). The median coefficient using data from the whole year is also shown in each panel (red line).

The green line shows estimates using data restricted to March to September. Data are from the MODIS Aqua satellite - see Acknowledgements.

Figure 7: Box plot of coefficient of variation (CV) in 130km x 130km region centred on (a) 59N 19W for cruise D321 and (b) 47.5N 18W for cruise D227 for the years 2003-2012. For each year, the boxplot uses all estimates from July and August for D321 and April and May for D227, to match the period of the cruises. The centre line is the median, the box top and bottom are the 75% and 25% quartile limits, the whiskers denote the extent of 1.5xIQR either side of the box, where IQR is the interquartile range, and points outside the whiskers are marked individually as outliers. Each boxplot uses 5103 and 5832 datapoints for D321 and D227 respectively.

Figure 8: Variation of correlation with depth between nitrate and phytoplankton from cruise D321 (top) and between phytoplankton and zooplankton from cruise D227 for small (middle) and large (bottom) surveys. Note that the vertical resolution is greater than the 10m interval (25—35m) used elsewhere.



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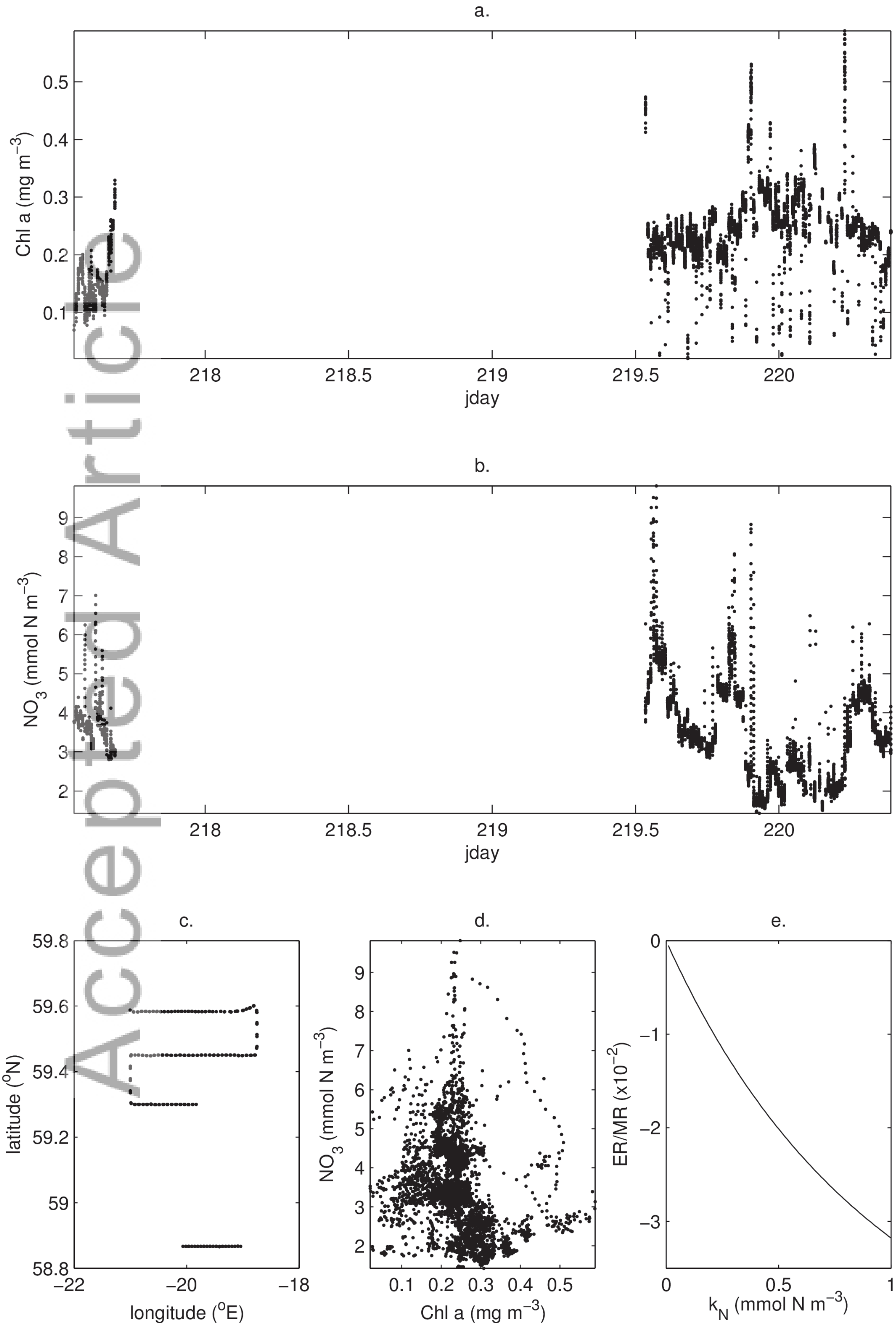

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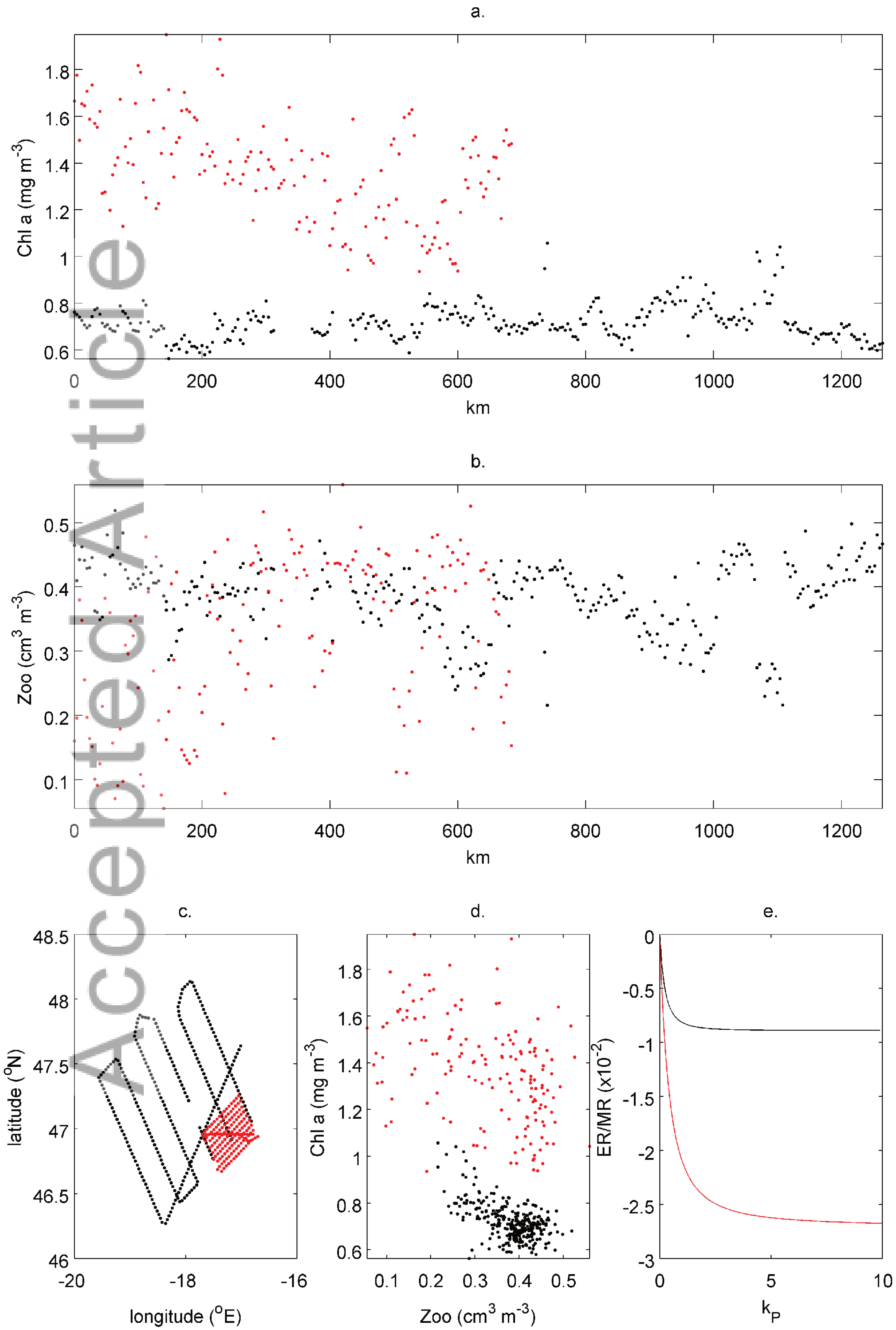

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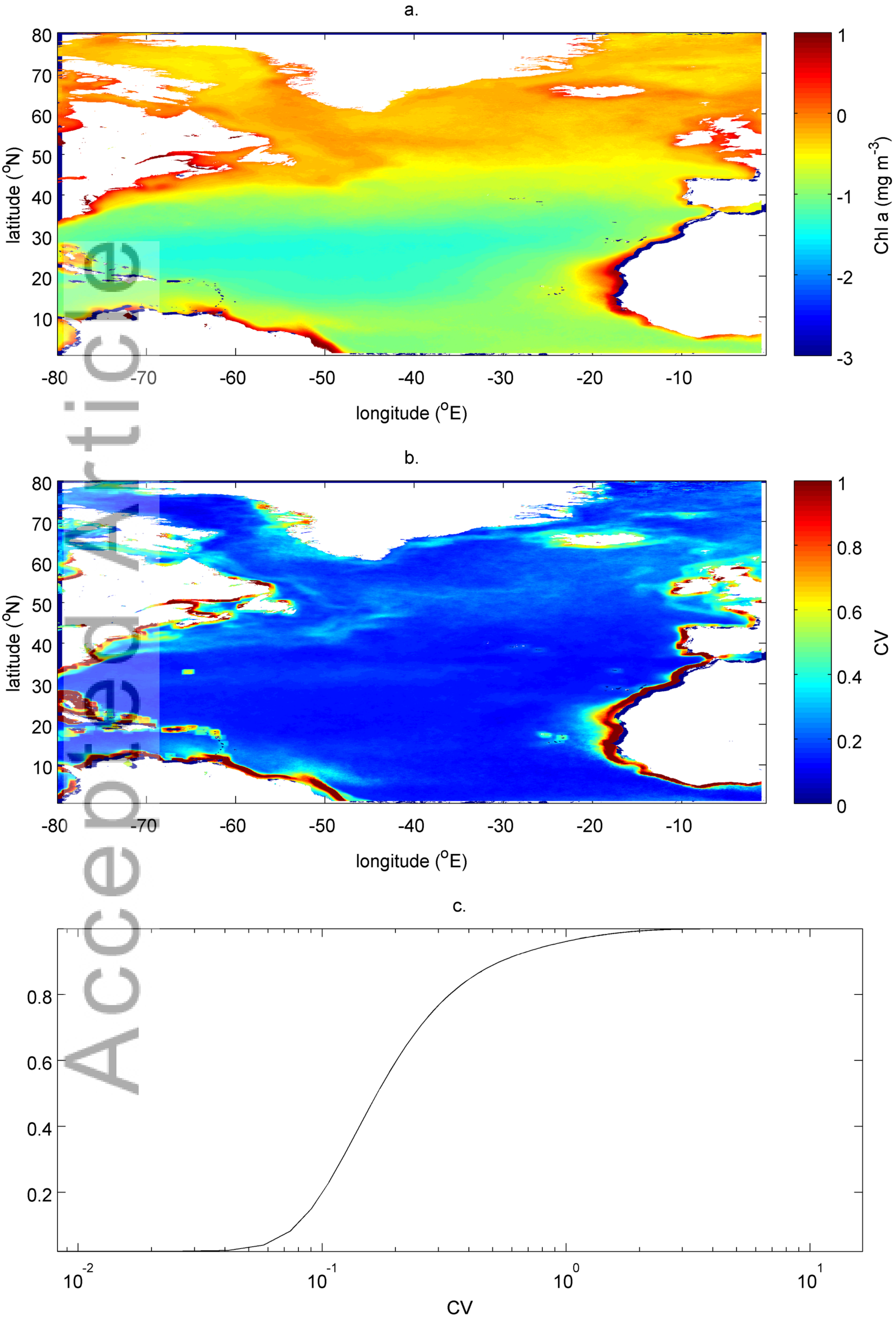

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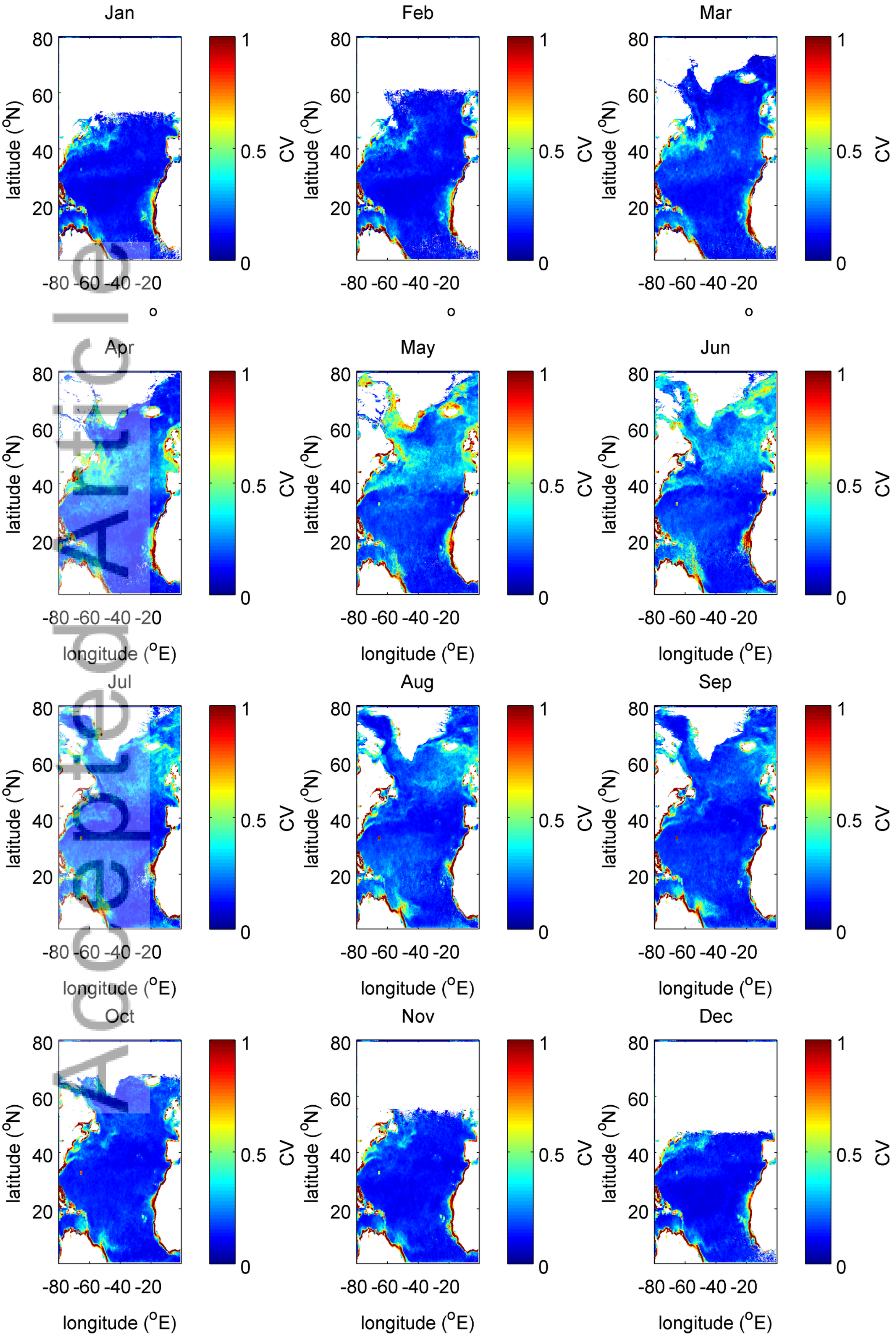

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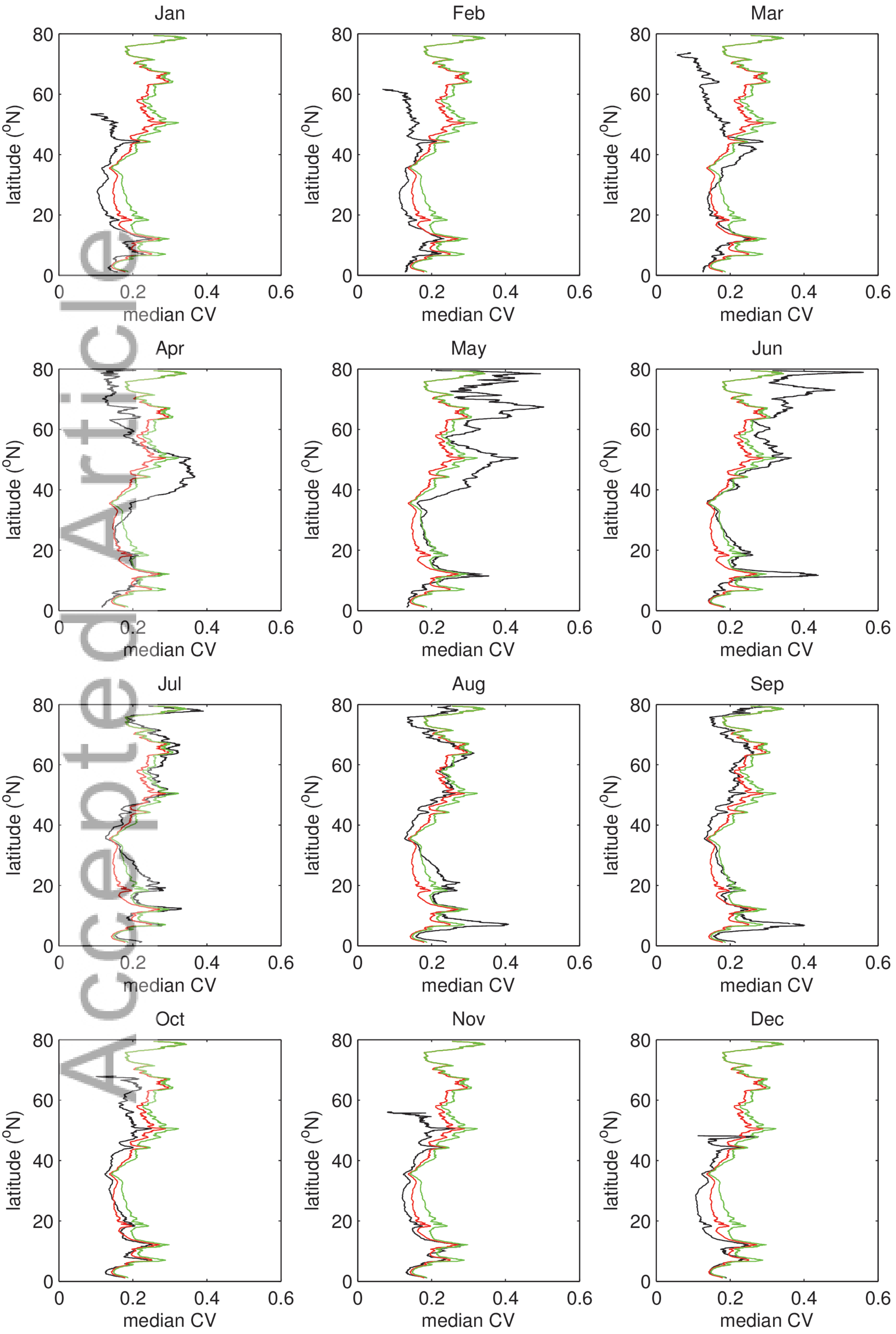

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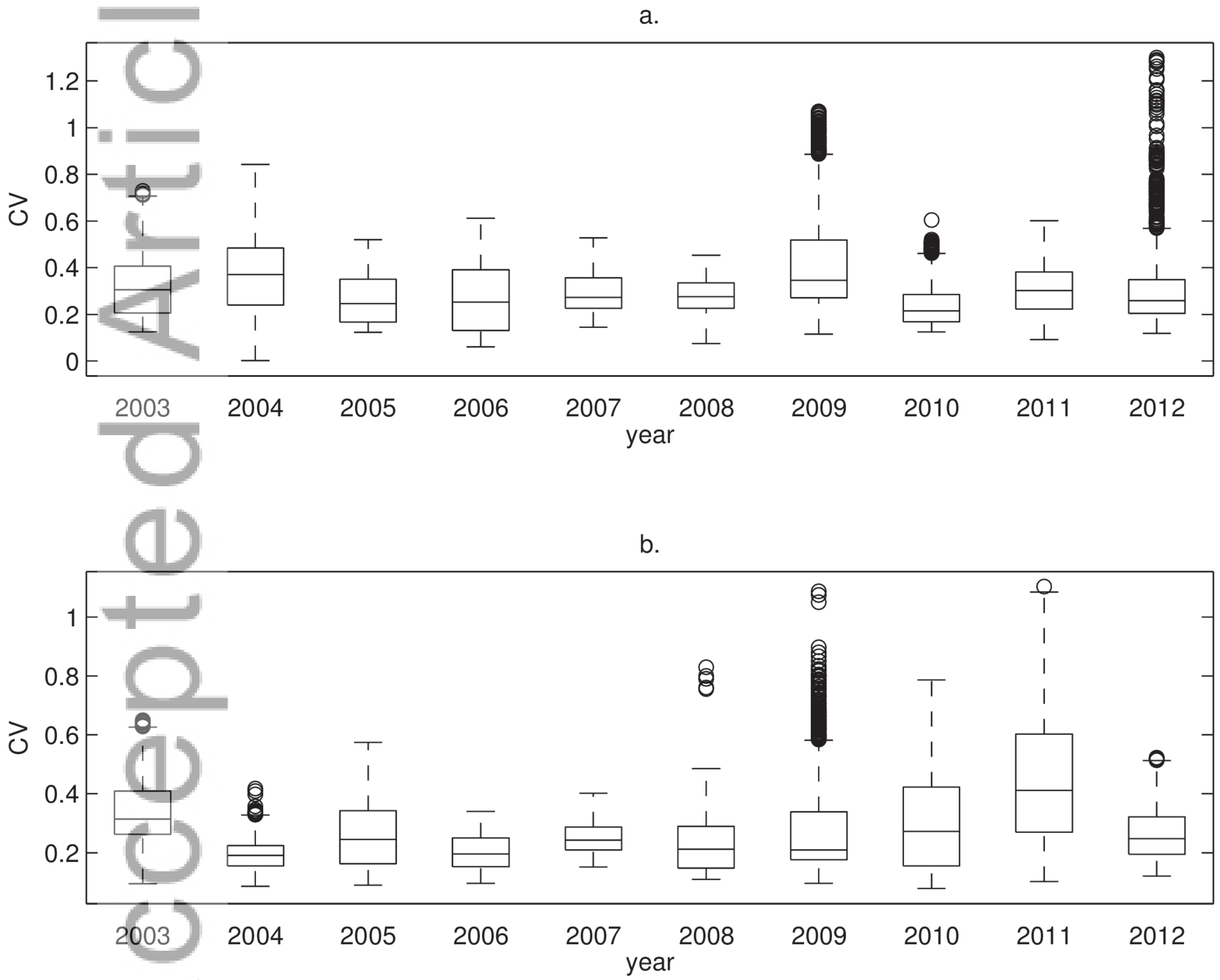

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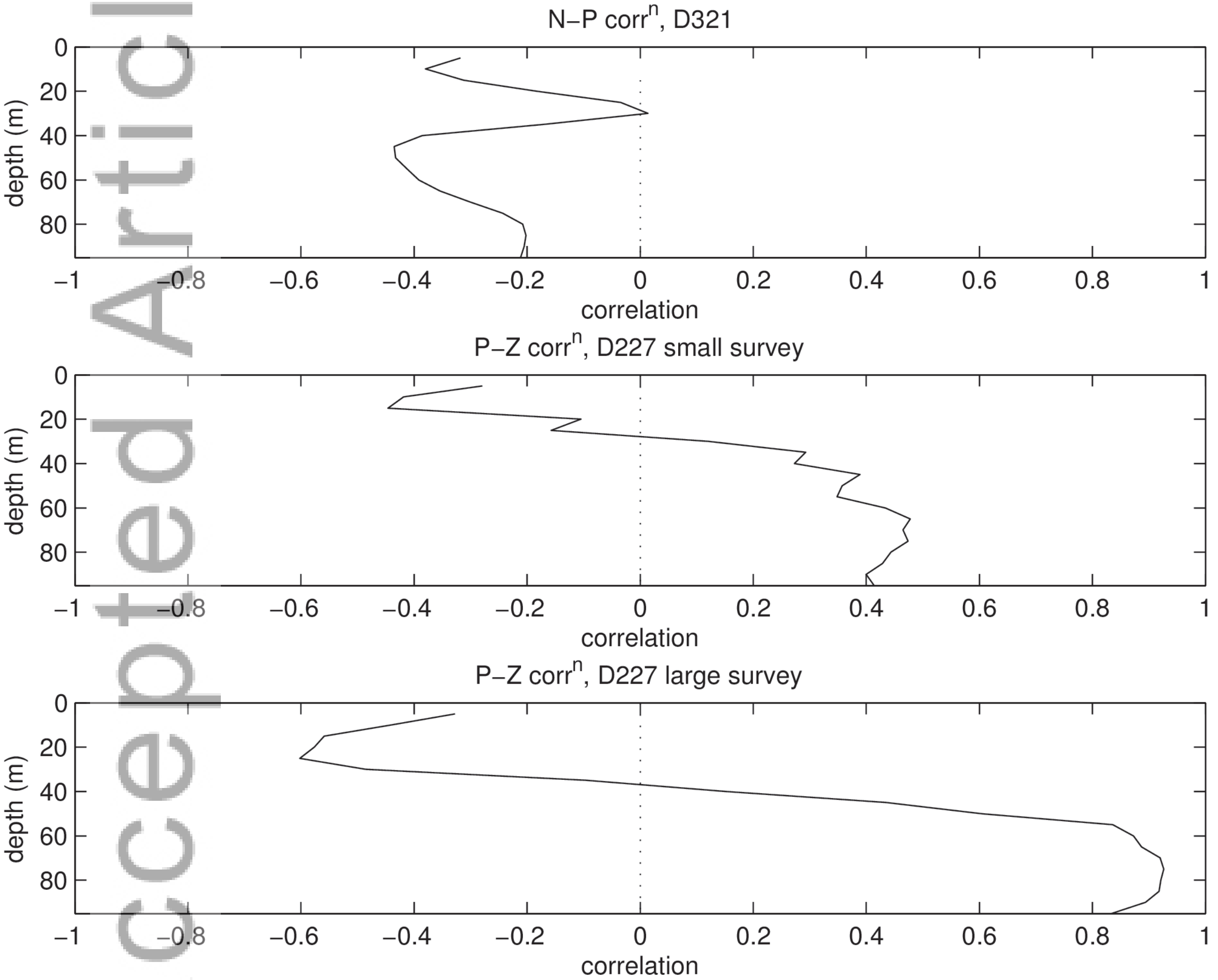

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