

# Imprint of Southern Ocean mesoscale eddies on chlorophyll

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**Abstract.** Although mesoscale ocean eddies are ubiquitous in the Southern Ocean, their average spatial and seasonal association with phytoplankton has not been quantified systematically yet. To this end, we identify over 100,000 mesoscale eddies with diameters of 50 km and more in the Southern Ocean and determine the associated phytoplankton biomass anomalies using satellite-based chlorophyll-a (Chl) as a proxy. The mean Chl anomalies,  $\delta\text{Chl}$ , associated with these eddies, comprising the upper echelon of the oceanic mesoscale, exceed  $\pm 10\%$  over wide regions. The structure of these anomalies is largely zonal, with cyclonic, thermocline lifted, eddies having positive anomalies in the subtropical waters north of the Antarctic Circumpolar Current (ACC) and negative anomalies along its main flow path. The pattern is similar, but reversed for anticyclonic, thermocline deepened eddies. The seasonality of  $\delta\text{Chl}$  is weak in subtropical waters, but pronounced along the ACC, featuring a seasonal sign switch. The spatial structure and seasonality of the mesoscale  $\delta\text{Chl}$  can be explained largely by lateral advection, especially local eddy-*stirring*. A prominent exception is the ACC region in winter, where  $\delta\text{Chl}$  is consistent with a modulation of phytoplankton light exposure caused by an eddy-induced modification of the mixed layer depth. The clear impact of mesoscale eddies on phytoplankton may implicate a downstream effect on Southern Ocean biogeochemical properties, such as mode water nutrient contents.

## 1 Introduction

Phytoplankton account for roughly half of global primary production (Field et al., 1998). They form the base of the oceanic food web (e.g., Pomeroy, 1974) and drive the ocean's biological pump, i.e., one of the Earth's largest biogeochemical cycles with major implications for atmospheric  $\text{CO}_2$  and climate (Sarmiento and Gruber, 2006; Falkowski, 2012). Yet, our understanding of the processes controlling their spatio-temporal variations is limited, particularly at the oceanic submesoscale to mesoscale, that is at scales of the order of 0.1 to 100 km (e.g., reviews by Lévy, 2008; McGillicuddy Jr., 2016; Mahadevan, 2016). We here focus on mesoscale eddies, i.e., the vortices with diameters of 50 km or more, and thus leave out the submesoscale variations. This choice is largely driven by the spatial resolution of the data we employ, but it is also motivated by the fact that mesoscale eddies have been shown to dominate the ocean's kinetic energy spectrum (Stammer, 1997; Chelton et al., 2011b), and affect phytoplankton in a major way (Lévy, 2008; McGillicuddy Jr., 2016). In comparison, the contribution of the submesoscale to the variance in kinetic energy is smaller, and its role for phytoplankton variability, although potentially large (Mahadevan,

2016) is not well characterized. In contrast, mesoscale eddies have been recognized to be among the most important drivers for the spatio-temporal variance of phytoplankton (e.g., Doney et al., 2003; Glover et al., 2018) as has been noted already from the analyses of some of the very first ocean color satellite images of chlorophyll (Chl), a proxy for phytoplankton biomass (Gower et al., 1980). Despite decades of work since this discovery, the mechanisms governing the interaction of phytoplankton with mesoscale eddies remain poorly understood, even though there is a broad consensus that different sets of mechanisms dominate in different regions and at different times, and that the different polarity of the mesoscale eddies tends to induce signals of opposite sign (Denman and Gargett, 1995; Lévy, 2008; McGillicuddy Jr., 2016).

Lateral advection arising from local *stirring* of eddies has been argued to be a major driver globally. The argument is based on the observed correlation of the magnitude of eddy-associated Chl anomalies,  $\delta\text{Chl}$ , and the larger-scale Chl gradient ambient to eddies (Doney et al., 2003; Uz and Yoder, 2004; Chelton et al., 2011a; O'Brien et al., 2013). Further, it has been suggested that advection of Chl by eddies via *trapping*, i.e., the enclosing and dragging along of waters, causes  $\delta\text{Chl}$  (Gaube et al., 2014), particularly in boundary current regions characterized by steep zonal Chl gradients. Numerous other potential mechanisms through which eddies affect phytoplankton have been identified (e.g., Bracco et al., 2000; McGillicuddy Jr. et al., 2007; D'Ovidio et al., 2010; Siegel et al., 2011; Gaube et al., 2013, 2014; Dufois et al., 2016; Gruber et al., 2011), including vertical and lateral advection of nutrients, restratification and vertical mixing, and providing spatial niches through isolation of waters. These mechanisms modulate the phytoplankton's light exposure, their nutrient availability or their grazing pressure, i.e., they affect their net balance between growth and decay. Thus, in contrast to the physical mechanisms of *stirring* and *trapping* where phytoplankton is merely passively being advected, these mechanisms create eddy-associated phytoplankton biomass anomalies by altering their biogeochemical rates.

In the Southern Ocean, an area of light and iron limitation of phytoplankton (Boyd, 2002; Venables and Meredith, 2009), with distinct Chl heterogeneity (Comiso et al., 1993), and abundant with eddies (e.g., Frenger et al., 2015), individual eddies have been found to modulate Chl through many of the above processes (e.g., Strass et al., 2002; Ansong et al., 2010; Lehahn et al., 2011; Kahru et al., 2007). Here, we aim (i) to provide a reference estimate of the average seasonal Chl anomalies associated with mesoscale eddies in the different regions of the Southern Ocean, distinguishing anticyclones and cyclones, and (ii) to discuss the mechanisms likely causing the observed average imprint. Previous studies have used eddy kinetic energy as a proxy for eddy activity rather than sea level anomalies (SLA), which does not allow a distinction by polarity of eddies (Comiso et al., 1993; Doney et al., 2003), did not focus on the Southern Ocean (Chelton et al., 2011a; Gaube et al., 2014), or lacked a discussion of the seasonality of the relationship. We show here that the imprint of cyclones and anticyclones on Chl mostly is of opposite sign, largely zonal, and features a substantial seasonality along the ACC. Our results indicate that most of this mesoscale imprint can be explained by advection of Chl by the eddies.

Our approach is to identify individual eddies based on satellite estimates of SLA and combine those with satellite estimates of Chl (Chelton et al., 2011a; Gaube et al., 2014). We discuss possible mechanisms playing a role based on large-scale Chl gradients (Doney et al., 2003; Chelton et al., 2011a; Gaube et al., 2014) and the local shape of the average imprint of eddies on Chl (Chelton et al., 2011a; Gaube et al., 2014; Siegel et al., 2011).

## 2 Methods and data

We first introduce our analysis framework before describing the methods and data sources. This permits us to explain the approaches we use to assess the potential mechanisms explaining the  $\delta\text{Chl}$  associated with Southern Ocean mesoscale eddies.

### 2.1 Analysis framework

5 Fundamentally, mesoscale eddies can lead to local phytoplankton biomass anomalies through either advective processes, i.e., the spatial reshaping of existing gradients, or through biogeochemical fluxes and transformations that lead to anomalous growth or losses of biomass. In the following, we present these potential mechanisms in more detail, and how we estimate their importance.

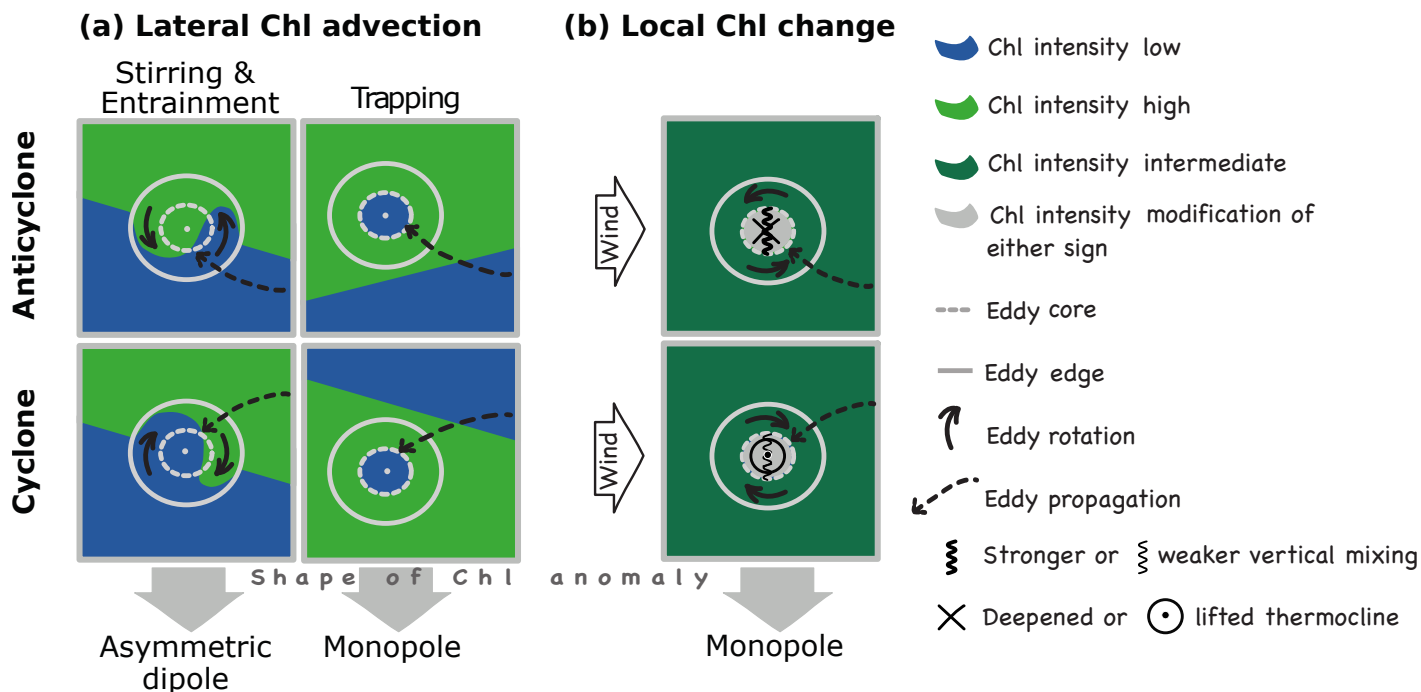
#### 2.1.1 Causes of $\delta\text{Chl}$ by advective processes

10 Mesoscale eddies may cause  $\delta\text{Chl}$  as they laterally move waters, i.e., horizontally advect waters including their Chl characteristics. This mechanism may lead to  $\delta\text{Chl}$  if (i) a lateral Chl gradient is present that is sufficiently steep at the spatial scale of the eddy-induced advection (Gaube et al., 2014), and (ii) the time scale of advection matches the time scale of phytoplankton biomass changes (Abraham, 1998). This time scale is order of days to weeks, possibly months, with the lower boundary representing roughly the reactivity time scale of phytoplankton biomass governed largely by the growth rate of the phytoplankton,  
15 and the upper boundary the potential sustenance of phytoplankton biomass via recycling of nutrients within the mixed layer. Concerning the spatial scale of advection by eddies, we distinguish two effects, that we have labelled *stirring* and *trapping*, respectively.

*Stirring* (Siegel et al., 2008; Chelton et al., 2011a; Gaube et al., 2014; McGillicuddy Jr., 2016) refers to the local distortion of a large-scale Chl gradient due to the rotation of an eddy, as illustrated in Fig. 1a (left column, with black arrows indicating  
20 the eddy rotation and associated advection). The turnover time scale associated with the rotation of eddies is order of days to a few weeks, which matches the time scales of phytoplankton reactivity. The spatial scale of *stirring* is given by the spatial extent of an eddy and is somewhat larger than the eddy core, as defined based on the Okubo-Weiss parameter (Frenger et al., 2015), that is several tens to several hundreds of kilometers.

Next to *stirring*, eddies advect material properties due to their intrinsic lateral propagation (Fig. 1a, right column). We refer  
25 to the ability of eddies to transport fluid along their propagation pathway in their core as *trapping* (e.g., Flierl, 1981; Gaube et al., 2014; McGillicuddy Jr., 2016). The upper time scale of *trapping* is given by the typical lifespan of Southern Ocean eddies, which is weeks to months (Frenger et al., 2015), i.e. it may match the longer time scale of phytoplankton biomass changes. Propagation speeds are small (an order of magnitude smaller than rotational speeds) which implies that the majority of eddies tends to die before they can propagate far. Thus, the fraction of very long-lived eddies that propagate over distances  
30 exceeding a few hundred kilometers is small (Frenger et al., 2015).

A necessary condition for *trapping* to happen is that the eddies' swirl velocity is larger than their propagation speed (Flierl, 1981), a condition generally met for mid- to high-latitude eddies (Chelton et al., 2011b). Indeed, observations of eddies carrying



**Figure 1. Schematic illustrating the mechanisms of how eddies may impact chlorophyll (Chl),** distinguished by anticyclones (top row) and cyclones (bottom row), for the southern hemisphere; **a** shows the effects of advection (lateral displacements) of Chl due to the eddies' rotational speed (*stirring*, left column) and lateral propagation (*trapping*, right column); *trapping* and *stirring* can cause  $\delta\text{Chl}$  of either sign, depending on environmental Chl gradients; **b** shows multiple potential effects eddies may have on Chl by affecting biogeochemical processes. The local shape of  $\delta\text{Chl}$  is anticipated to look different depending on the mechanism active, i.e. a monopole  $\delta\text{Chl}$  is expected for all eddy-effects except for *stirring* where an asymmetric dipole is expected (Figure inspired by Siegel et al. 2011, Figure 1).

the signature of their origin in their cores support the *trapping* effect (Bernard et al., 2007; Ansoerge et al., 2010; Lehahn et al., 2011), as does the modeling study by Early et al. (2011). Even though the *trapping* is never perfect (Beron-Vera et al., 2013; Haller, 2015), we expect eddies to be able to drag along some entrained waters for some time, hence displacing these waters for some distance as they propagate. This may be sufficient to displace waters from e.g., the south to the north of an ACC front along an intense Chl gradient, leading to  $\delta\text{Chl}$  through (permeable) *trapping*.

### 2.1.2 Causes of $\delta\text{Chl}$ by local biogeochemical processes

Mesoscale eddies affect the biogeochemical/physical properties that control the local rates of growth and loss of phytoplankton (biogeochemical rates) in their interior through many mechanisms. These include, e.g., the stimulation of phytoplankton growth through enhanced nutrient concentrations or increased average light levels, or the modification of predator-prey encounter rates, affecting the mortality of phytoplankton (Fig. 1b). Even though these effects have been analyzed and discussed for decades (see review by McGillicuddy Jr., 2016), their overall impact on productivity continues to be an issue of debate. The canonical

lifelong vertical pumping of nutrients by thermocline lifted cyclones (Falkowski et al., 1991, indicated as black circle in Fig. 1b) has been challenged to be a major player (Oschlies, 2002; Gaube et al., 2014), and multiple other mechanisms have been proposed how eddies may affect phytoplankton biomass. These include a modification of vertical mixing through changes of stratification (wiggly lines in Fig. 1b) and eddy current-wind interactions causing thermocline displacements (eddy swirl currents and winds are indicated as black and thick white arrows in Fig. 1b), resulting in modifications of nutrient supply and light exposure of phytoplankton (e.g., Llido, 2005; McGillicuddy Jr. et al., 2007; Mahadevan et al., 2008; Siegel et al., 2011; Xiu et al., 2011; Lehahn et al., 2011; Boyd et al., 2012; Mahadevan et al., 2012; Dufois et al., 2016). The prevailing lack of data of temporally sufficiently highly resolved subsurface observations hampers a systematic large-scale observationally-based assessment of the role of effects of mesoscale eddies on the local biogeochemical processes.

### 10 2.1.3 Assessing mechanisms causing $\delta\text{Chl}$

We employ two sets of approaches to assess the mechanisms causing  $\delta\text{Chl}$ . In the first we diagnose whether the environmental conditions are met for supporting a major contribution of a particular set of mechanisms. Namely, we assess if lateral Chl gradients sufficiently support advective effects of eddies to explain  $\delta\text{Chl}$  (see Sect. 2.3 for technical detail).

In the second set we diagnose the shape of  $\delta\text{Chl}$  associated with eddies as this spatial signature tends to differ between the two major sets of processes, i.e., the advective process *stirring* and biogeochemical rates (Siegel et al., 2011). Eddies that stir are anticipated to have a dipole shaped  $\delta\text{Chl}$  (Fig. 1a, left column), as they distort the underlying gradient field, with the rotation of the eddy determining the orientation of the dipole. In contrast, most mechanisms associated with modifications of the biogeochemical rates cause a monopole shape, irrespective of polarity (Fig. 1b). This is a consequence of the mesoscale  $\delta\text{Chl}$  tending to be caused by anomalies in the nutrient supply or light availability, which are altered inside eddies in a radially symmetric manner. The advective *trapping* mechanisms tend to also cause a monopole shape of  $\delta\text{Chl}$  (Fig. 1a, right column), but rate-based mechanisms can be distinguished from *trapping* for instance by their history, or their tendency to trap the anomalies very tightly in the inner domain of the eddy (McGillicuddy Jr., 2016). Rate-based mechanisms presumably play a role in regions and seasons where the potential for advective effects is insufficient to explain the observed eddy-induced  $\delta\text{Chl}$ . Here we diagnose these as a residual.

Some complexity is added to the interpretation of the spatial pattern by the fact that the dipole shape arising from *stirring* tends to be asymmetric (Fig. 1a). Such an asymmetry was suggested by Chelton et al. (2011a) to arise from the westward propagation of eddies and the leading (mostly western) side of an eddy affecting upstream unperturbed waters, resulting in a larger anomaly at the leading compared to the trailing side of an eddy, with the latter stirring already perturbed waters. Also, the eddy may entrain some of the westward upstream waters into its core, labeled here lateral entrainment or permeable *trapping* (Hausmann and Czaja, 2012; Frenger et al., 2015). Indeed, averaged over an eddy's core, *stirring* will only cause a net anomaly if the dipole associated with *stirring* is asymmetric. It is not obvious how to quantify this effect. Independent of the dipole asymmetry, we will qualitatively discuss the potential maximum  $\delta\text{Chl}$  induced by *stirring* (see Sect. 2.4 for technical detail). We note that advection by an ambient larger-scale flow does not affect the *stirring* mechanism. For instance,

the eastward Antarctic circumpolar flow in the Southern Ocean makes eddies propagate eastward in an Eulerian sense, while still propagating westward in a Lagrangian sense relative to the ACC and ambient Chl.

## 2.2 Data

To assess the relationship between ocean eddies and Chl anomalies, we use the data set of Southern Ocean eddies and their characteristics as derived and described in detail in Frenger et al. (2015). The data set contains more than 1'000'000 snapshots of mesoscale eddies identified in weekly maps of Aviso SLA and defined based on the Okubo-Weiss parameter. Eddies with positive and negative SLA are defined as anticyclones and cyclones, respectively. We consider here only eddies tracked in the region 30°S to 65°S over at least three weeks in the time period between 1997 and 2010, i.e., the operation time period of the SeaWiFS satellite-based sensor. The resolution capacity of Aviso SLA allows for the analysis of the larger mesoscale eddies with minimum diameters of about 50 km at 65°S and 100 km at 30°S (Chelton et al., 2011b; Frenger et al., 2015).

For Chl we use the ESA GlobColour Project product (<http://www.globcolour.info>, case-1 waters) which merges several sensors according to Maritorena and Siegel (2005), with a spatial and temporal resolution of 0.25° and one day, respectively. We choose a merged product for Chl as the merging on average doubles the spatial coverage of the daily data in the Southern Ocean (Maritorena et al., 2010). Of the three available sensors, i.e., SeaWiFS (SeaStar), MODIS (Aqua) and MERIS (Envisat), SeaWiFS generally features the best spatio-temporal coverage, but its contribution drops below 40% in high latitudes and partly in the western ocean basins of the Southern Hemisphere. For these areas after 2002, SeaWiFS data were complemented with MODIS as well as MERIS data. We average the Chl data to weekly fields to match the temporal resolution of the eddy dataset. The combined eddy Chl-dataset is publicly available at <http://dx.doi.org/10.3929/ethz-b-000238826>.

To examine the  $\delta\text{Chl}$  of eddies, we compare the Chl averaged over their core to background fields of Chl. For the latter, a monthly climatology of Chl proved not to be appropriate due to high spatio-temporal variability of Chl unrelated to eddies. Hence, we obtain the background fields the following way: we apply a moving spatio-temporal Gaussian filter (Weierstrass transform, spatial filter similar to e.g., Siegel et al. 2008, with  $2\sigma$  of 10 boxes/ $\sim$ 200 km at 45°S, 8 boxes/ $\sim$ 200 km and 1 week in longitudinal, latitudinal and temporal dimensions, respectively) to each of the weekly Chl fields. We then subtract the result from the original fields to produce  $\delta\text{Chl}$  fields. The  $\delta\text{Chl}$  fields are not sensitive to the selected  $\sigma$ . The choice of a rather small spatiotemporal filter makes  $\delta\text{Chl}$  amplitudes smaller compared to if a larger filter is chosen, producing a conservative estimate of  $\delta\text{Chl}$ . In order to generate spatial maps of  $\delta\text{Chl}$ , we averaged all eddy associated anomalies of the respective eddy polarity into  $5^\circ \times 3^\circ$  longitude/latitude boxes.

Prior to our analysis we log-transform Chl, due to Chl being lognormally distributed (Campbell, 1995). We frequently give  $\delta\text{Chl}$  in percentage difference relative to the background Chl as

$$\delta\text{Chl} = \left[ \exp \left( \log(\text{Chl}_e) - \log(\text{Chl}_{bg}) \right) - 1 \right] \times 100 = \left( \frac{\text{Chl}_e}{\text{Chl}_{bg}} - 1 \right) \times 100$$

with subscripts e and bg denoting *eddy* and *background*, respectively. Where we show absolute  $\delta\text{Chl}$  on a logarithmic scale, we use the base 10 logarithm.

Regarding geographical, that is spatial, analyses, we use on the one hand the positions of the main ACC fronts (Polar Front, PF, and Subantarctic Front, SAF) as determined by Sallée et al. (2008). On the other hand, we make use of a climatology of sea surface height (SSH) contours (Maximenko et al., 2009), which are representative of the long-term geostrophic flow in the area. The mean positions of the PF and SAF align approximately with the mean SSH contours of -40 cm and -80 cm, respectively.

5 We select the -20 cm SSH contour to separate waters of the southern subtropical gyres to the north of the ACC, referred to as subtropical waters from waters in the "ACC influence area", referred to as ACC waters. This choice is based on both, a tendency for net eastward propagation of eddies south of this contour (Frenger et al., 2015) indicating advection by the ACC mean flow, and a seasonal sign switch of  $\delta\text{Chl}$ , which will be addressed later in the paper. Waters south of the PF/-80 cm SSH we refer to as Antarctic waters. Finally, we use mixed layer depths derived from Argo floats, available at <http://www.locean-ipsl.upmc.fr>

10 (<https://doi.org/10.17882/42182>).

### 2.3 Analysis of environmental Chl conditions

Using the data presented in the previous section, we calculate a monthly Chl climatology. Based on this climatology, we derive the *potential*  $\delta\text{Chl}$  ( $\hat{\delta}\text{Chl}$ ) eddies may induce due to lateral advection (Fig. 1a): In order to assess the  $\hat{\delta}\text{Chl}$  emerging from *stirring* in the Southern Ocean, we compute the climatological meridional Chl gradient at the spatial scale of individual

15 eddies, here taken as two eddy radii ( $\hat{\delta}\text{Chl}_{\text{stir}}$ ). To assess the  $\hat{\delta}\text{Chl}$  emerging from *trapping*, we estimate the Chl variation along individual eddies' pathways by computing the difference of the climatological Chl at the very location of an eddy and at the location of its origin ( $\hat{\delta}\text{Chl}_{\text{trap}}$ ). We use for this difference the climatological Chl at the month of the very location of the eddy to consider the effects of the seasonal Chl variations, assuming that potentially trapped Chl would seasonally covary with the Chl at the place of the eddy's origin.

### 20 2.4 Analysis of the shape of $\delta\text{Chl}$

We compute the composite spatial pattern of Chl and  $\delta\text{Chl}$  associated with mesoscale eddies the same way as was done by Frenger et al. (2015) for sea surface temperatures: We extract a squared subregion for each individual eddy from the weekly maps of SLA and Chl, centered at the eddy's center. The side lengths of the subregion are 10 eddy radii each, implying an implicit scaling according to the eddy size. We rotate the Chl snapshots according to the ambient Chl gradient and average

25 them over all eddies to produce the eddy composite. Note that the estimate of the magnitudes of the dipole and the average ambient Chl gradient (see below) tend to be slightly weaker without rotation. Nevertheless, as averages are taken over regimes of largely similar orientation of the ambient Chl gradient (see Discussion Sect. 4), our conclusions do not depend on whether we rotate the snapshots or not.

Further, we decompose the composite spatial pattern  $\delta\text{Chl}$  into a monopole (MP) and dipole (DP) component by first constructing the monopole by computing radial averages of  $\delta\text{Chl}$  around the eddy's center, i.e.,  $\delta\text{Chl}(r)_{\text{MP}} = \overline{\delta\text{Chl}(r)}$ , where  $r$  is

30 the distance from the eddy's center. In the second step, we calculate  $\delta\text{Chl}_{\text{DP}}$  as a residual, i.e., by differencing the monopole pattern from the total signal. Even though this residual approach captures in the dipole structure any non-monopole pattern, experience has shown that the  $\delta\text{Chl}_{\text{DP}}$  typically feature dipoles (Frenger et al., 2015). In the final step, we quantify the ampli-

tudes of the monopoles and the dipoles, assess the contribution of the two components to the spatial variance of the total signal based on the sum of variances ( $\text{var}$ ), i.e.  $\text{var}(\delta\text{Chl}) = \text{var}(\delta\text{Chl}_{\text{MP}}) + \text{var}(\delta\text{Chl}_{\text{DP}})$ , and compute the local Chl gradient at the scale of two eddy radii, as an estimate of the potential maximum contribution of *stirring* to  $\delta\text{Chl}$ .

## 2.5 Handling of measurement error and data gaps

5 An individual eddy  $\delta\text{Chl}$  signal may be undetectable even with in-situ measurements (Siegel et al., 2011), and it may be easily smaller than the error of the satellite retrieved Chl. The significance of our results, which we test based on t-tests, arises from the very large number of analyzed eddies, which totals about 600'000 eddy snapshots across the entire Southern Ocean. This is substantially smaller than our original data set, largely due to the missing Chl data arising from frequent cloud cover in the Southern Ocean. For 33 % of the eddies identified by SLA, the corresponding Chl data was entirely missing, and for 75 %  
10 of eddies at least part of the data was missing. The average missing data over eddies due to cloud cover only (leaving aside missing data due to the polar night) increase from 18 % at 30°S to 63% at 65°S. Anticyclones exhibit a higher percentage of data gaps than cyclones (48 % versus 42 % averaged over the Southern Ocean), which can be explained by the impact of their sea surface temperature anomalies on cloud cover (Park et al., 2006; Small et al., 2008; Frenger et al., 2013).

## 3 Results

### 15 3.1 Imprint of mesoscale eddies on Chl

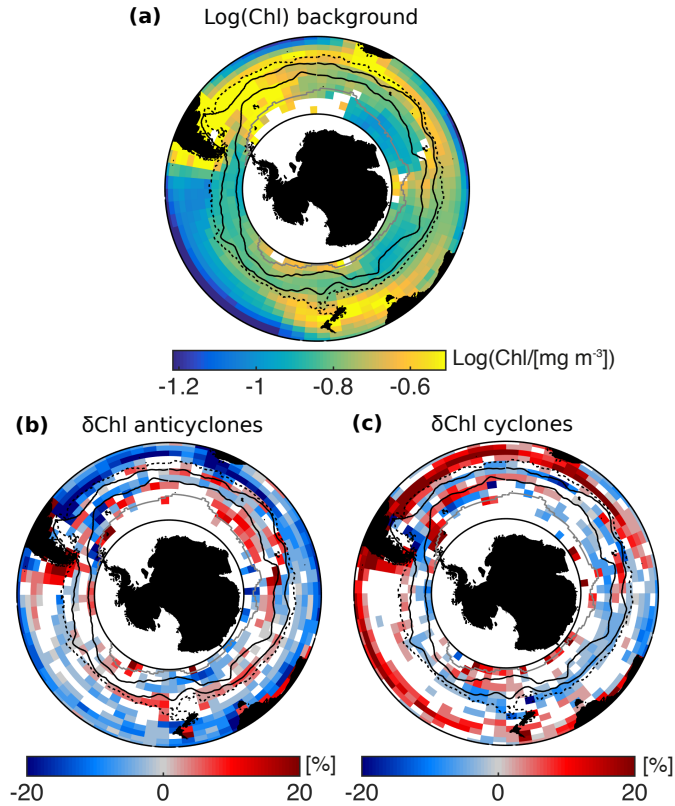
#### 3.1.1 Mean imprint

Averaged across the entire Southern Ocean and all seasons, we detect a significant, although small, mean imprint of mesoscale eddies on Chl (Supplementary Figure S1) for both anticyclonic (warm-core, high SLA, and deepened thermocline) and cyclonic (cold-core, low SLA, and lifted thermocline) eddies. The overall mean  $\delta\text{Chl}$  associated with anticyclones is -4 %, while that  
20 for cyclones is of even smaller magnitude, i.e., +1 %. Though small, both anomalies are actually statistically significant ( $p < 0.05$ ). The distributions around these means are very broad, however, with many anticyclones and cyclones having both, positive or negative  $\delta\text{Chl}$ , depending on the region and time of the year. The long tails of the distributions, corroborated by visual inspection of the individual  $\delta\text{Chl}$  of eddies, suggest anomalies that are substantially larger than the mean. Thus, it appears that by averaging the signals in time and space, a substantial amount of information is lost. As a consequence, it is  
25 more insightful to disentangle the signals and to examine the regional and seasonal variation of  $\delta\text{Chl}$ .

#### 3.1.2 Spatial variability of imprint

The maps of the annual mean imprint of cyclonic and anticyclonic eddies on Chl clearly support this hypothesis of a strong regional cancellation effect (Fig. 2). First, the regional mean signal associated with eddies is indeed much larger than suggested by the mean  $\delta\text{Chl}$  across the entire Southern Ocean. In fact, around a quarter of the analyzed grid cells have absolute  $\delta\text{Chl}$  larger  
30 than 10 %, with the mean absolute  $\delta\text{Chl}$  exceeding several tens of percent in a substantial number of grid cells (Fig. 2b,c).





**Figure 2. Spatial distribution of chlorophyll anomalies ( $\delta\text{Chl}$ ) associated with eddies; a** Logarithm (base 10) of climatological Chl for reference, and mean  $\delta\text{Chl}$  of **b** anticyclones and **c** cyclones;  $\delta\text{Chl}$  is the average of anomalies of eddies existing at least 3 weeks in  $5^\circ \times 3^\circ$  longitude-latitude-grid boxes; white boxes indicate insufficient data (less than three data points) or anomalies insignificantly different from zero (t-test,  $p=0.05$ ); solid black lines mark the main branches of the ACC (Subantarctic and Polar fronts); the dashed black line denotes the -20 cm SSH contour and the solid gray line the northernmost extension of sea-ice cover.

Second, the signals associated with mesoscale eddies of either polarity vary in sign across the different regions with regions of strong enhancements bordering regions with strong reductions (see also Figure 1 in Gaube et al. 2014). In the broadest sense, the pattern is zonal in nature, reflecting the zonal nature of the climatological Chl distribution (Fig. 2a).

For anticyclones,  $\delta\text{Chl}$  is clearly negative in subtropical waters, i.e., the waters north of the SSH = -20 cm, and in the regions around the western boundary currents (Fig. 2b). These prevailing negative  $\delta\text{Chl}$  is contrasted by mostly positive  $\delta\text{Chl}$  along the ACC. Cyclones have a largely similar spatial pattern, but of opposite sign (Fig. 2c): prevailing positive  $\delta\text{Chl}$  in subtropical waters are mirrored by a band of negative, yet weaker anomalies along the ACC. South of the ACC, in Antarctic waters, the pattern of  $\delta\text{Chl}$  is spotty for anticyclones as well as cyclones, with anticyclones and cyclones featuring average positive and negative  $\delta\text{Chl}$ , respectively. In summary, SLA and  $\delta\text{Chl}$  are largely negatively correlated in subtropical waters north of the ACC, and positively correlated along the ACC.

A few exceptions break this mostly zonal picture for Chl (Ardyna et al., 2017), and also for  $\delta\text{Chl}$ . An exceptional area of negative  $\delta\text{Chl}$  for cyclones in the subtropical waters of the eastern Indian Ocean disrupts the zonal band of largely positive anomalies. Also,  $\delta\text{Chl}$  in coastal/shelf areas often are distinct from open-ocean  $\delta\text{Chl}$ . A clear signal emerges south of the Australian and west of the South-American coasts, west of New Zealand, and more subtly, east of the Kerguelen Islands and the Drake Passage (see also Sokolov and Rintoul 2007; D'Ovidio et al. 2015), where  $\delta\text{Chl}$  tends to be positive for both anticyclones and cyclones.

### 3.1.3 Seasonality of imprint

The pronounced zonal bands of  $\delta\text{Chl}$  for mesoscale anticyclones and cyclones persist over the year, but tend to migrate meridionally (Fig. 3a-d, middle/right columns), thereby following the pronounced seasonality of Chl (Fig. 3a-d, left column; Thomalla et al. 2011; Sallée et al. 2015; Ardyna et al. 2017). The seasonality of  $\delta\text{Chl}$  is larger along the ACC and in Antarctic waters compared to subtropical waters. In the subtropical gyres,  $\delta\text{Chl}$  of anticyclones and cyclones are negative and positive, respectively, i.e., SLA and  $\delta\text{Chl}$  are negatively correlated all year round. Here,  $\delta\text{Chl}$  shows a weak peak in austral summer when climatological Chl is smallest (Fig. 3c). In the ACC regions and in Antarctic waters, a striking feature is the seasonal change in the sign of  $\delta\text{Chl}$  for both cyclones and anticyclones (Fig. 3b-d).

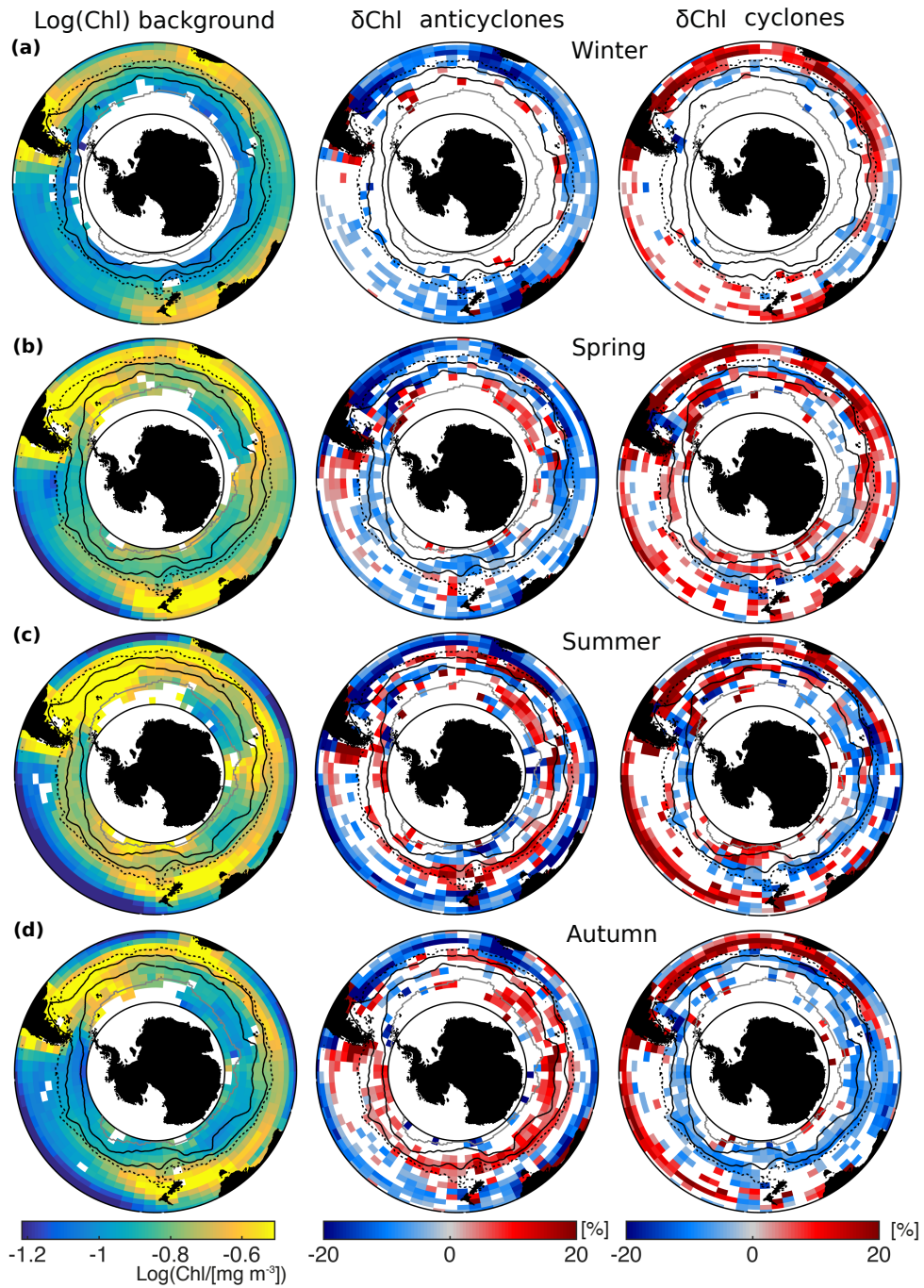
This becomes even more evident when inspecting the zonally averaged Chl and  $\delta\text{Chl}$  as a function of season and SSH, i.e., plotted in the form of a Hovmoeller diagram (Fig. 4). Along the ACC, anticyclones exhibit negative  $\delta\text{Chl}$  in winter to spring concurrent with deep mixed layers, followed by positive  $\delta\text{Chl}$  in summer to autumn (Fig. 4b). Cyclonic  $\delta\text{Chl}$  patterns are opposite, featuring negative  $\delta\text{Chl}$  in summer to autumn, with close to zero to positive  $\delta\text{Chl}$  in winter to spring (Fig. 4c). This implies that SLA and  $\delta\text{Chl}$  are positively correlated summer to autumn, followed by a negative correlation in winter to spring. The sign switch of the correlations shows a seasonal lag towards Antarctic waters, with positive correlations prevailing autumn to winter, and negative correlations prevailing spring to summer, resulting in the aforementioned apparent southward migration of the sign switch of the seasonality of  $\delta\text{Chl}$  over the course of the year.

## 3.2 Causes for the imprint

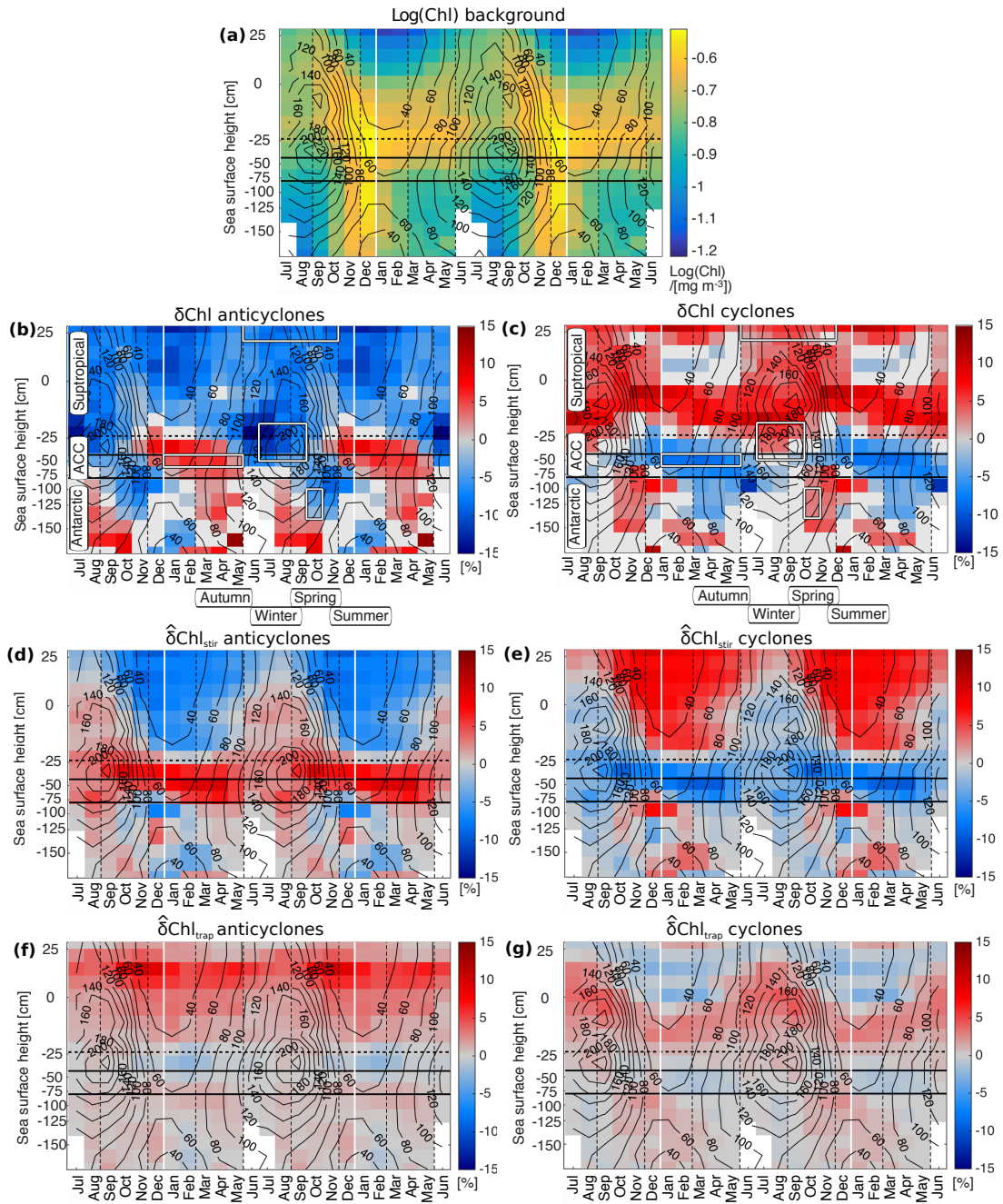
### 3.2.1 Advection

To assess the contribution of advective mechanisms to the observed  $\delta\text{Chl}$ , we contrast it with the potential of eddies to cause  $\delta\text{Chl}$  through Chl advection, that is with the potentials  $\hat{\delta\text{Chl}}_{\text{stir}}$  associated with *stirring* and  $\hat{\delta\text{Chl}}_{\text{trap}}$ , associated with *trapping* (Figures 4d-g, Method Sect. 2.3). The closer the observed  $\delta\text{Chl}$  is to these potentials, the more important the respective processes would be in causing this signal.

In the northern domain, i.e., in subtropical waters, the sign of  $\hat{\delta\text{Chl}}_{\text{stir}}$  tends to agree with  $\delta\text{Chl}$  throughout the year for both anticyclones and cyclones (Figures 4b-e). So does the seasonal variation of the magnitude of  $\hat{\delta\text{Chl}}_{\text{stir}}$ , with the largest magnitudes found in summer to autumn. Also the regional variations match, such as a weaker  $\hat{\delta\text{Chl}}_{\text{stir}}$  and  $\delta\text{Chl}$  in the Pacific



**Figure 3. Seasonality of chlorophyll anomalies ( $\delta\text{Chl}$ ) associated with eddies; Austral a winter (JJA), b spring (SON), c summer (DJF) and d autumn (MAM) for anticyclones (middle) and cyclones (right); The logarithm (base 10) of climatological Chl is shown for reference (left). Otherwise as Fig. 2.**



**Figure 4. Seasonality of chlorophyll anomalies ( $\delta Chl$ ) associated with eddies, and potential of eddies to cause  $\delta Chl$  through lateral advection, i.e.,  $\hat{\delta}Chl_{stir}$  for stirring and  $\hat{\delta}Chl_{trap}$  for trapping. **a** Base 10 logarithm of climatological Chl for reference; **b,c**  $\delta Chl$  related to anticyclones and cyclones, respectively; **d,e** advective potentials (Method Sect. 2.3) due to *stirring* by anticyclones and cyclones, respectively; **f,g**, advective potentials due to *trapping* by anticyclones and cyclones, respectively. In **a**,  $\delta Chl$  is the mean of all eddies existing at least 3 weeks binned in monthly sea surface height (SSH) bins so that boxes roughly are of equal area; In all subpanels, values that are not significant (t-test,  $p > 0.05$ ) are colored in light gray, insufficient data (less than three data points) in white; solid black lines mark the ACC (approximate positions of the Subantarctic and Polar fronts); the horizontal dashed black line denotes the -20 cm SSH contour, the vertical dashed lines mark the seasons; solid black contours show averaged mixed layer depths in meters; note that the seasonal cycle is shown repeatedly to highlight cyclic patterns.**

sector compared to the Atlantic and Indian Ocean sectors (Fig. 3, middle/right columns and Supplementary Figure S2, left column).

Also, along the ACC and its northern flank in summer to autumn,  $\hat{\delta}\text{Chl}_{\text{stir}}$  and  $\delta\text{Chl}$  agree in sign, and are of the same order of magnitude. Finally, along the southern ACC and in Antarctic waters,  $\hat{\delta}\text{Chl}_{\text{stir}}$  mirrors the seasonal sign switch of  $\delta\text{Chl}$ , and the apparent seasonal southward migration of the zonal bands of  $\delta\text{Chl}$  (Figures 3 and 4b-e). Thus, it appears that *stirring* can already explain a good fraction of the observed  $\delta\text{Chl}$  (i) in subtropical waters outside of those characterized by winter deep mixed layers, (ii) along the ACC and its northern flank in summer to autumn, and (iii) south of the ACC.

The reason underlying the strong potential of *stirring* is the presence of strong average ambient gradients of Chl. For instance: Averaged over mesoscale eddies in northern subtropical waters in winter to spring (Method Sect. 2.4), the absolute gradient of Chl at scales of two eddy radii is 7 % for both anticyclones and cyclones, compared to the absolute maximum  $\delta\text{Chl}$  of 10 % and 9 %, respectively (Fig. 5a, see numbers at the bottoms of left two panels). A similar correspondence is found along the ACC and its northern flank in summer to autumn (Fig. 6a), and in Antarctic waters in spring (Fig. 5b), supporting that *stirring* alone may largely explain the observed  $\delta\text{Chl}$  (Fig. 6a; anticyclones: gradient of 9 % and maximum  $\delta\text{Chl}$  of 5 %; cyclones: gradient of 9 % and maximum  $\delta\text{Chl}$  of 11 %; and Fig. 5b; anticyclones: gradient of 5 % and maximum  $\delta\text{Chl}$  of 6 %; cyclones: gradient of 5 % and maximum  $\delta\text{Chl}$  of 5 %).

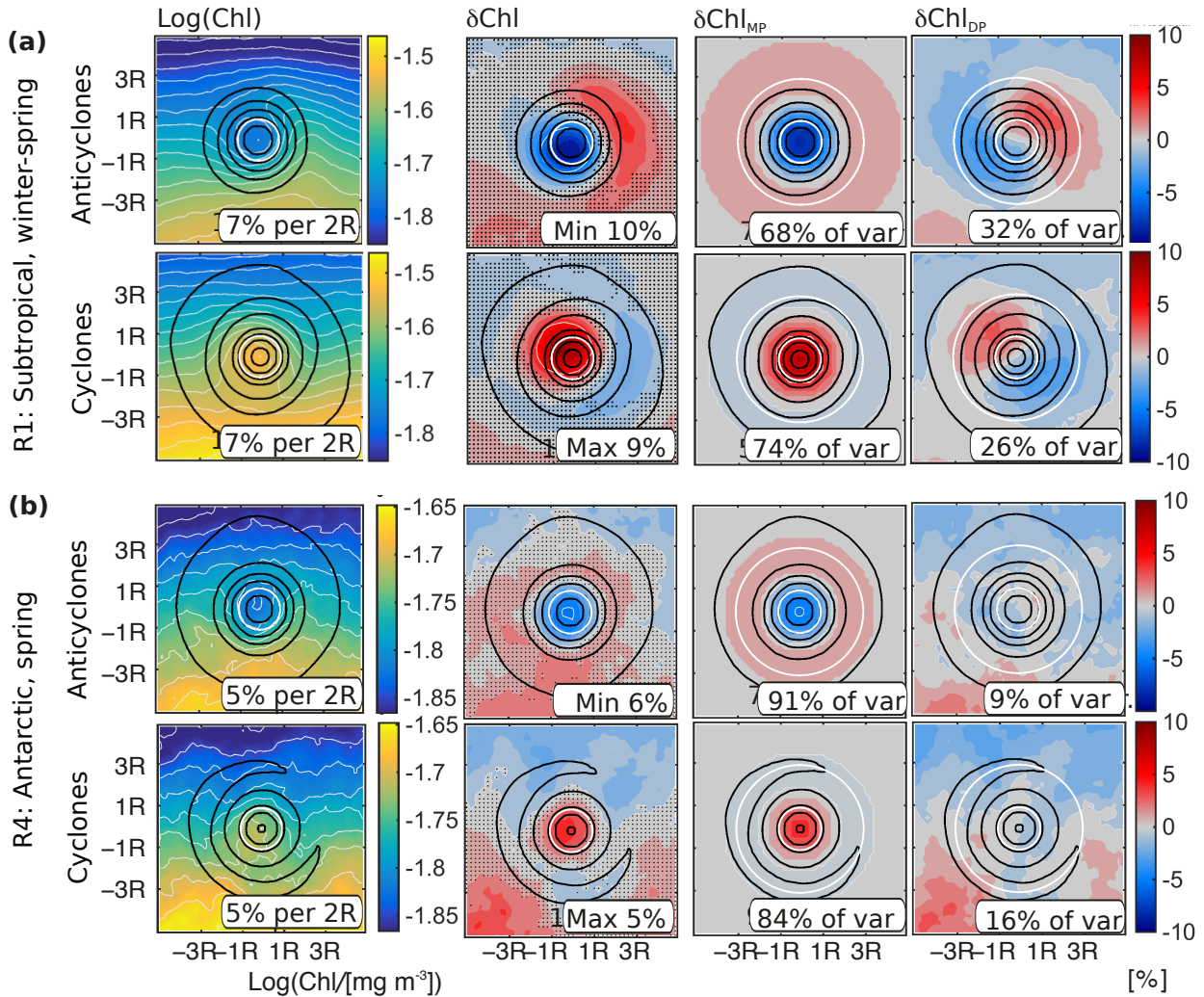
The advective potential for the other lateral advective mechanism, i.e., *trapping*,  $\hat{\delta}\text{Chl}_{\text{trap}}$ , partly counteracts and partly enhances  $\hat{\delta}\text{Chl}_{\text{stir}}$  (Figures 4d-g). For instance, for cyclones along the ACC in summer to autumn, *trapping* possibly contributes to a  $\delta\text{Chl}$  (11 %) signal that is slightly larger than the Chl gradient at two eddy radii (9 %), and the contribution of the variance of the monopole is increased compared to anticyclones (Fig. 6a, 96 % versus 87 %). Yet, overall the trapping potential  $\hat{\delta}\text{Chl}_{\text{trap}}$  is weak compared to  $\delta\text{Chl}$  (Fig. 4b,c,f,g), and outweighed by  $\hat{\delta}\text{Chl}_{\text{stir}}$ .

### 3.2.2 Local biogeochemical rates

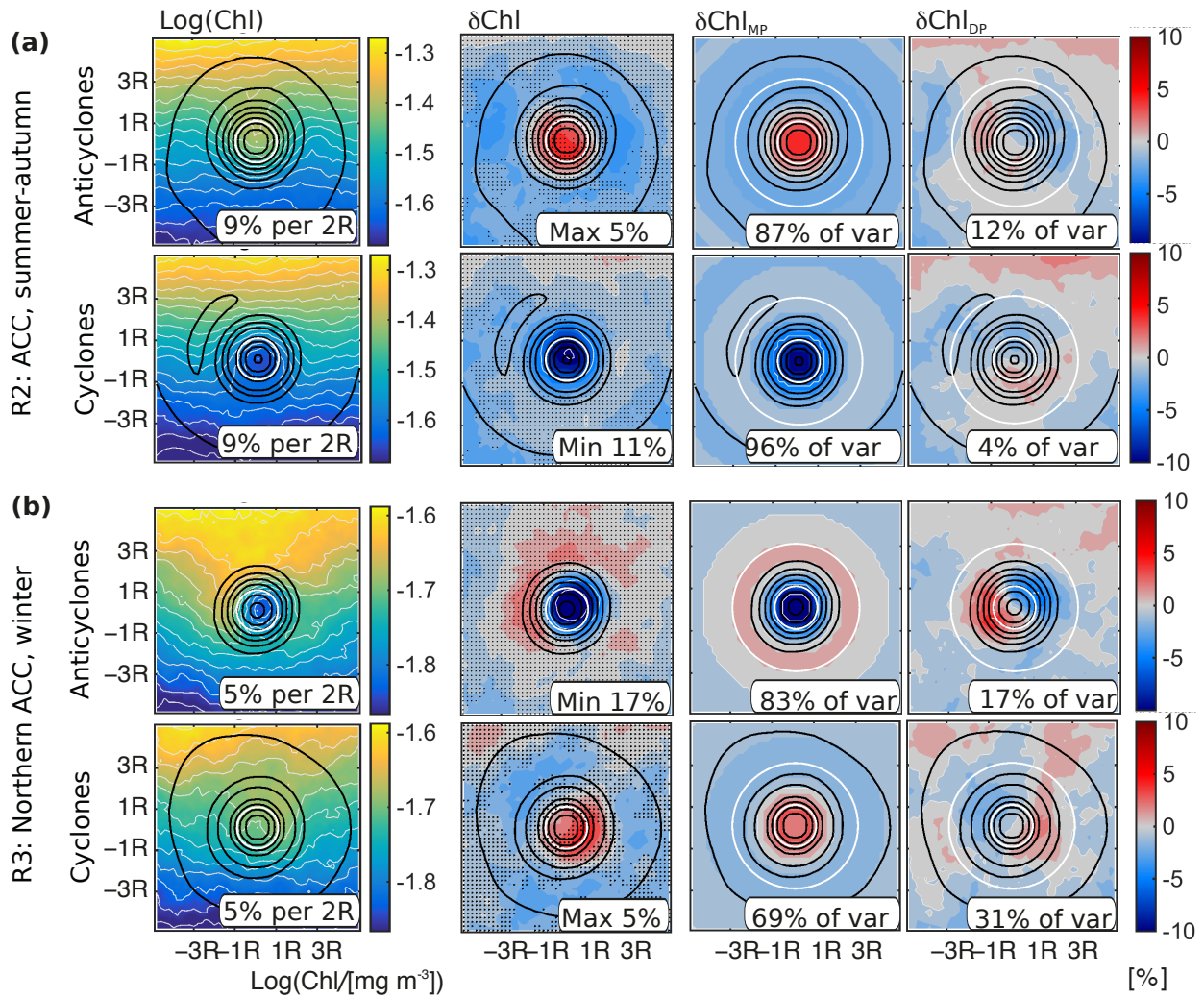
Even though advective processes and particularly *stirring* appear to be the dominant driver for the mesoscale eddy-associated Chl anomalies, there are nevertheless a few places where the magnitudes of the potentials for advective effects are too weak compared to the observed  $\delta\text{Chl}$  or of opposite sign. These are the places where variations in the local growth and loss processes, i.e., variations in the local biogeochemical rates may be the dominant driver.

The most prominent instance is found along the northern ACC, a region associated with the seasonal sign switch of  $\delta\text{Chl}$  (Figures 4b-g, blue boxes in Fig. 7a). Here, anticyclones switch to negative  $\delta\text{Chl}$  in the presence of deep mixed layers, whereas both  $\hat{\delta}\text{Chl}_{\text{stir}}$  and  $\hat{\delta}\text{Chl}_{\text{trap}}$  suggest positive  $\delta\text{Chl}$ . The shape of the local imprint of anticyclones in the respective region and season (Fig. 6b) indicates that indeed, the lateral Chl gradient at the scale of eddies (5 %) is small compared to the maximum absolute amplitude of  $\delta\text{Chl}$  (17 %). Further, the decomposition of the local shape of  $\delta\text{Chl}$  into a monopole and a dipole suggests that *stirring* (dipole) supports an anomaly of the opposite sign compared to the observed  $\delta\text{Chl}$ , consistent with Fig. 4d. Given that *trapping* would cause also a weak anomaly of the opposite sign (Fig. 4f), we hypothesize that eddy-induced changes in the biogeochemical rates are responsible for the negative  $\delta\text{Chl}$  in winter and spring in the northern ACC.

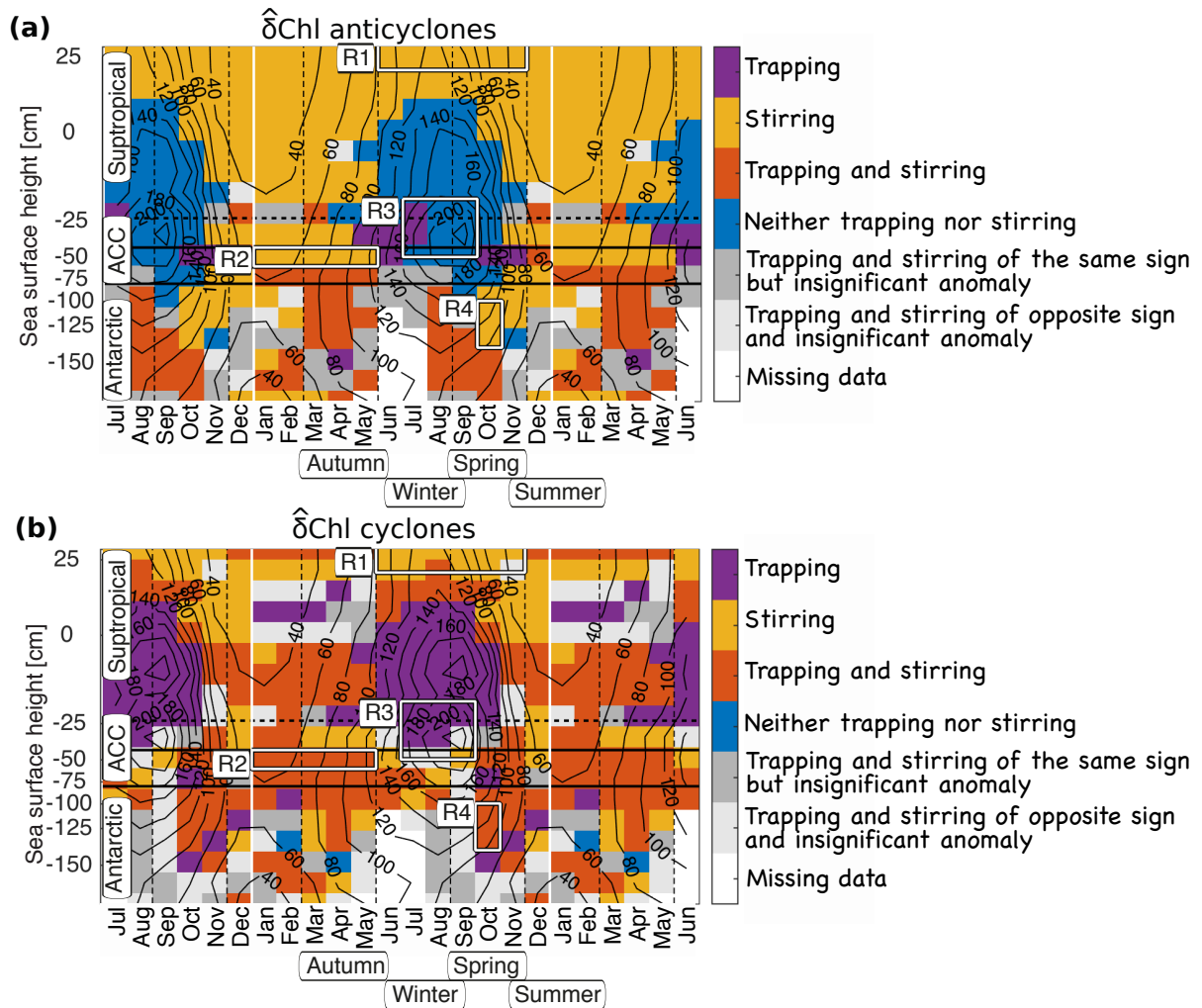
Similarly, the sign switch of  $\delta\text{Chl}$  of cyclones in the same region cannot be explained based on  $\hat{\delta}\text{Chl}_{\text{stir}}$  (Fig. 4e). The local



**Figure 5. Attribution of stirring/trapping components** of mesoscale eddy associated Chl; **a** Chl and  $\delta\text{Chl}$  in region R1 (SSH larger 10 cm, June to November) and **b** in region R4 (SSH -140 to -100 cm, October), indicated as white boxes in Figures 4b,c and 7. Within each subpanel, the top rows show the results for the anticyclones, and the bottom rows for the cyclones. The left column shows the logarithm (base 10) of Chl, the middle left the  $\delta\text{Chl}$  (stippling marks insignificant anomalies), the middle right one the monopole component, MP, and the right one the residual component (approximately the dipole component, DP) (see text for details and cartoon in Fig. 1). The sea level anomaly contours are shown in black (0.05 spacing, normalized before averaging); the inner and outer white circles indicate the eddy core and area used for the computation of the contribution to the variance of  $\delta\text{Chl}$  of the monopole and the dipole, respectively; text in panels denotes (left) the meridional Chl gradient at two eddy radii, (second left) the maximum or minimum of the anomaly, (second right and right) the contribution to the variance of the anomaly pattern of the monopole and dipole, respectively; before averaging, the individual eddy snapshots are rotated according to the ambient instantaneous Chl gradient.



**Figure 6. Attribution of stirring/trapping components;** same as Fig. 5 but for **a** the region R2 (SSH -60 to -40 cm, January to May) and **b** for region R3 (SSH -50 to -15 cm, July to September). The regions are indicated with boxes in Fig. 7.



**Figure 7. Hovmoeller diagram of the likely processes controlling the chlorophyll anomalies ( $\delta\text{Chl}$ ) in a anticyclones and b cyclones:** *stirring* (yellow), *trapping* (purple), a combination of the two (red) or neither of the two (blue), with the latter often interpreted to be the consequence of changes in the local growth or losses (biogeochemical rates). A region is colored if the sign of the potential effect is the same as the observed one, and if  $\delta\text{Chl}$  is significant. See text for details; white boxes indicate regions R1 to R4 used for composite Figures 5/6. The data were binned in monthly sea-surface height bins.



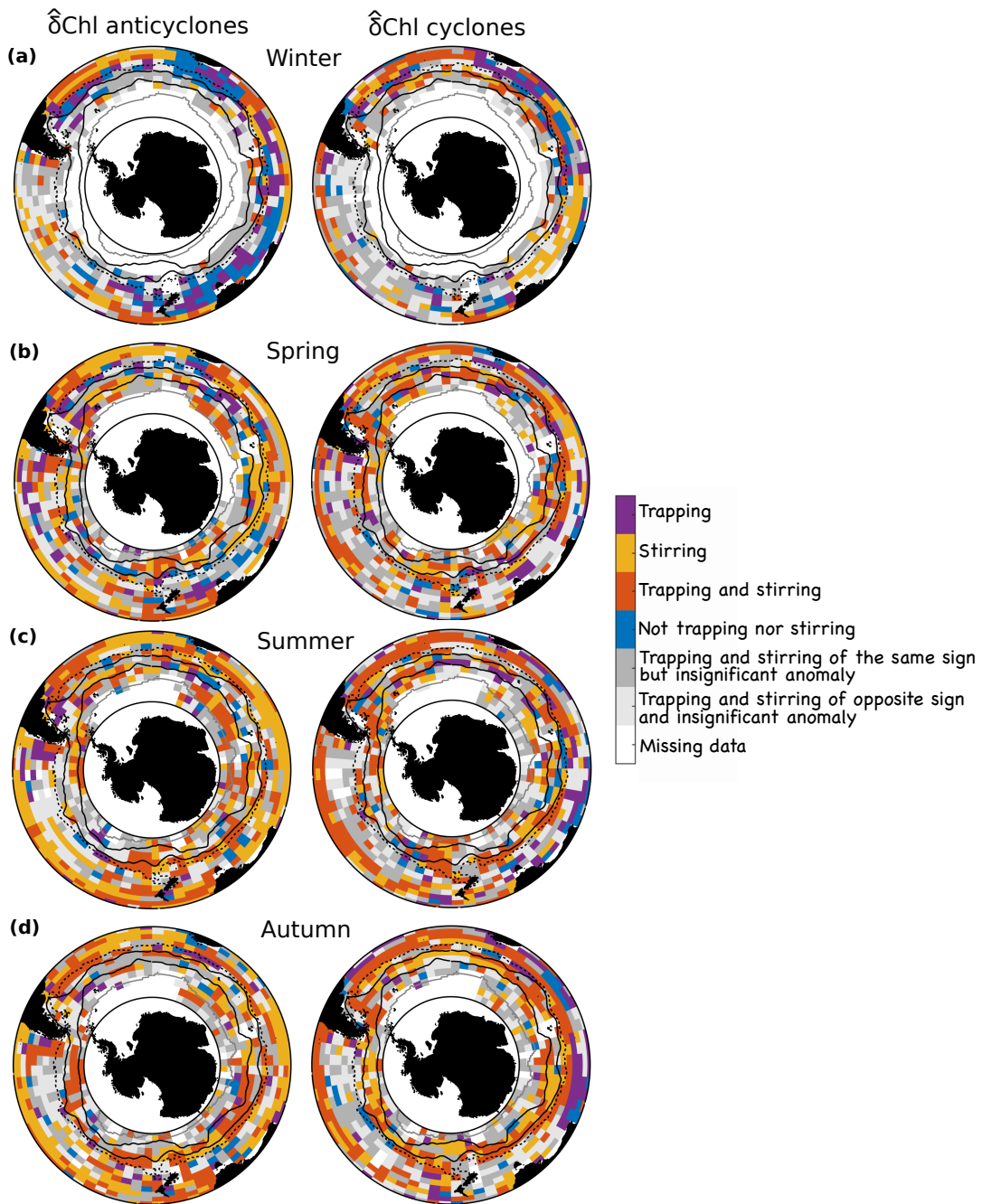


Figure 8. Maps of the distribution of the likely processes controlling the chlorophyll anomalies ( $\delta\text{Chl}$ ) for austral a winter, b spring, c summer and d autumn for anticyclones (left) and cyclones (right). The method and legend is the same as used in figure 7. Otherwise as Fig. 2.

shape of Chl corroborates that also for cyclones *stirring* of the average ambient Chl gradient induces an anomaly of the opposite sign (Fig. 6b). In contrast to  $\hat{\delta}\text{Chl}_{\text{stir}}$ ,  $\hat{\delta}\text{Chl}_{\text{trap}}$  for cyclones is of the same sign as  $\delta\text{Chl}$  (Fig. 4g), indicating a potential contribution of *trapping* to positive  $\delta\text{Chl}$  under deep mixed layers. Yet, as noted in the previous paragraph, the magnitude of  $\hat{\delta}\text{Chl}_{\text{trap}}$  is small, hence the contribution by *trapping* is limited. Further, *trapping* is not of the same sign as  $\delta\text{Chl}$  for cyclones  
5 everywhere in the region either (see blue boxes Fig. 8a,b, right column). Hence, the likely explanation for the  $\delta\text{Chl}$  in cyclones in regions with deep winter mixed layers is that eddies also modify the local biogeochemical rates.

Effects of eddies on biogeochemical rates also may play a role in other regions or seasons. For instance, the magnitudes of  $\hat{\delta}\text{Chl}_{\text{stir}}$  and  $\hat{\delta}\text{Chl}_{\text{trap}}$  appear too weak to explain  $\delta\text{Chl}$  in subtropical waters in winter and spring (Figures 4d-g/5a). Further, closed Chl contours are associated with the eddy cores that cannot origin from local lateral entrainment associated with *stirring*  
10 (Figures 5/6, left columns). Also the generally weak potential  $\hat{\delta}\text{Chl}_{\text{trap}}$  fails to explain the closed Chl contours and the associated strong monopole component of  $\delta\text{Chl}$  that contributes about 70 to 100% to the variability of the  $\delta\text{Chl}$  shape (Figures 4f,g/5/6). Both of these points support that effects on biogeochemical rates enhance the  $\delta\text{Chl}$  monopole.

#### 4 Discussion and synthesis

The zonal pattern of the  $\delta\text{Chl}$  identified here for the Southern Ocean is similar to that described by Gaube et al. (2014) across  
15 the world's oceans. Analogous to the results of our analyses, they also found spatial variations in the sign of  $\delta\text{Chl}$  associated with either cyclonic and anticyclonic eddies. Yet, there are also substantial differences, especially along the ACC, where, e.g., the  $\delta\text{Chl}$  is more widespread and more intense than previously acknowledged. Further, the seasonal variations in the Southern Ocean appear to be stronger than elsewhere (Gaube et al., 2014), except, perhaps, for the eastern Indian Ocean and the South China Sea (Gaube et al., 2013; Guo et al., 2017). Possibly, the underappreciated  $\delta\text{Chl}$  along the ACC is due to previous  
20 conflation of seasonal anomalies of opposite sign, resulting in a much weaker annual signal. To our knowledge, such seasonal changes in the sign of  $\delta\text{Chl}$  in a particular region have not been reported before. Hence, the strong seasonality with a seasonal change in the sign of  $\delta\text{Chl}$  along the ACC and south of the ACC appears to be rather specific to the Southern Ocean.

The spatiotemporal variability of  $\delta\text{Chl}$  may not be that surprising in hindsight, given that the same mechanism, e.g., advection can lead to either positive or negative signs for the same polarity depending on the sign of the lateral gradient. In addition,  
25 several mechanisms may be involved simultaneously, so that small differences in their relative importance can lead to substantial differences in the net sign of the response (Siegel et al., 2011; Gaube et al., 2014; McGillicuddy Jr., 2016). Nevertheless, we have demonstrated that most of the eddy induced signatures of  $\delta\text{Chl}$  in the Southern Ocean are likely due to *stirring*, a mechanism that has been shown to control  $\delta\text{Chl}$  in the low to mid-latitude ocean as well (Chelton et al., 2011a). *Stirring* is an effective mechanism for eddies to cause  $\delta\text{Chl}$  as eddy rotation is omnidirectional and thus necessarily perpendicular to the  
30 ambient Chl isolines. This fact combined with the steep meridional Chl gradients in the Southern Ocean favor *stirring* as the driving mechanism for  $\delta\text{Chl}$ . *Stirring* in such an environment of meridional Chl gradients supports Chl anomalies of a banded, zonal structure, similar in pattern and magnitude to the actual observed  $\delta\text{Chl}$ , in most regions and seasons. *Stirring* is also favored compared to *trapping* by the fact that the majority of the eddies are relatively short lived and also have low transla-

tional speeds, such that the average eddy does not get far during its lifetime. This means that the eddy is much more likely to efficiently stir the environmental gradient due to its rotation than to move great distances up or down the gradient.

Next to *stirring*, our work elucidated also the importance of the other processes, namely *trapping* and changes in biogeochemical rates, in certain regions and at certain times. This leads to a relatively complex mosaic of dominance across space and time in the Southern Ocean (Fig. 7). This synthesis figure reveals that *stirring* as the sole mechanism is limited to the subtropical waters outside of regions with deep winter mixed layers, and for anticyclones along the northern ACC in summer to autumn (Fig. 7, yellow). Our results suggest that *trapping* contributes to  $\delta\text{Chl}$  for anticyclones along the southern ACC in summer to autumn and in Antarctic waters in autumn and spring. It also adds to the  $\delta\text{Chl}$  of cyclones in most regions and seasons, except for parts of the subtropical waters (see also Fig. 8a, south and southwest of Australia). Yet, the magnitude of the potential of *trapping* is generally small, with the exception, perhaps, of a few specific regions, such as the eastern boundary currents, and those to the southeast of the Kerguelen Islands, and in the Drake Passage (Supplementary Figure S3, see also Gaube et al., 2014). In these regions, eddies tend to move down intense zonal Chl gradients (Supplementary Figure S2, right column), carrying their high initial Chl with them. This tends to result in positive  $\delta\text{Chl}$  year round for both anticyclones and cyclones (Fig. 3). An additional possible explanation is the offshore advection of iron trapped in the nearshore region by eddies that fuels extra growth in the offshore waters, as suggested e.g., for Haida eddies in the North Pacific (Xiu et al., 2011), or for eddies passing the Kerguelen Plateau (D'Ovidio et al., 2015).

The weaker role of *trapping* relative to *stirring* can be explained by the inherently westward propagation of mesoscale eddies, meaning a propagation largely along Chl isolines, as zonal Chl gradients typically are much smaller than meridional Chl gradients. An additional reason is the aforementioned short propagation distance of an average eddy. Moreover, the efficiency of *trapping* is often also reduced owing to the trapped waters from the eddies' origins being diluted along their pathways (Beron-Vera et al., 2013; Wang et al., 2015; Haller, 2015). This dilution effect may help to explain also the puzzling observation that despite *stirring* being the dominant process overall, the spatial structure of the  $\delta\text{Chl}$  within the eddies is much more monopole than dipole (Figures 5,6). This can be resolved by hypothesizing that the lateral entrainment weakens the dipole component of the  $\delta\text{Chl}$  generated by stirring, while strengthening the monopole component (see illustration in Fig. 1a).

The clearest case for a substantial contribution of changes in biogeochemical rates on  $\delta\text{Chl}$  was found for the northern ACC region during winter and spring, when the mixed layers are deep (Fig. 7, blue), and correlations of Chl and SLA are negative. The associated negative  $\delta\text{Chl}$  of anticyclones is consistent with the mechanism of an amplification of the prevailing light limitation in the deep mixed layers (Boyd, 2002; Moore and Abbott, 2002; Venables and Meredith, 2009; Fauchereau et al., 2011): As a result of their suppressing the thermoclines, anticyclones tend to deepen the mixed layer depths by several tens of meters, especially in winter (Song et al., 2015; Hausmann et al., 2017; Dufois et al., 2016). Hence, phytoplankton within the mixed layer will be exposed to reduced mean light levels in anticyclones as compared to ambient waters, leading to lower Chl levels. The opposite is the case for cyclones.

In the same region in summer to autumn, the weak trapping potential, the pronounced monopole-shape of  $\delta\text{Chl}$  and the closed Chl contours suggest that the  $\delta\text{Chl}$  is at least partly caused by the effects of eddies on the local biogeochemical rates. Here, the positive correlations of SLA and  $\delta\text{Chl}$  could arise due to eddy-induced modifications of the prevailing iron limitation.

Anticyclones could reduce the iron limitation and lead to positive  $\delta\text{Chl}$  owing to their being more weakly stratified, leading to intensified vertical mixing in the high wind conditions of the Southern Ocean, bringing more iron from below to the surface. Vice-versa, the iron limitation could be enhanced by cyclones owing to their weaker vertical mixing (Dufois et al., 2016; Song et al., 2018). Hypothetically, an alleviation of grazing pressure due to reduced predator-prey encounter rates in deepened mixed layers in anticyclones could further favor positive  $\delta\text{Chl}$ , and more shallow mixed layers could increase grazing pressure for cyclones. Thus, we argue that along the northern ACC, the seasonal sign switch of  $\delta\text{Chl}$  could be explained by varying degrees of light and iron limitation and grazing pressure over the course of the year (Smetacek et al., 2004; Carranza and Gille, 2015; Le Quéré et al., 2016).

Finally, along the southern ACC and in Antarctic waters in autumn to spring, the potentials of *stirring* and *trapping* often-times are of the same sign. However,  $\delta\text{Chl}$  associated with eddies is insignificant in these waters in many places (dark gray regions, Fig. 7). Presumably, these situations arise because the eddy effects on the local biogeochemical rates may almost perfectly cancel the advective effects.

Our analysis is constrained to the surface ocean, hence three caveats need to be kept in mind: (i) one potential issue are non-homogeneous vertical Chl profiles, e.g., the presence of unrecognized subsurface Chl maxima. But subsurface Chl maxima presumably are not prominent in our area of study (Sallée et al., 2015), as wind speeds are high and mixed layers deep, promoting well-mixed Chl levels over the upper ocean; further, surface and mixed layer depth integrated analyses provide similar results in terms of SLA-Chl correlations (based on model simulations, Hajoon Song, pers. comm.), supporting the assumption that an analysis of surface Chl is representative for the total Chl in the water column. (ii) modification of mixed layer depths by eddies may result in a surface Chl concentration modification due to a dilution effect. Especially in winter to spring, when the mixed layers are deep, we cannot exclude that this effect contributes to the observed  $\delta\text{Chl}$ . Yet as noted in (i), surface and mixed layer depth integrated analyses provide similar results in a model simulation. (iii) Potential effects of eddies on phytoplankton growth presumably occur mostly in the lower euphotic zone and may thus be expressed more weakly at the surface (McGillicuddy Jr. et al., 2007; Siegel et al., 2011). We therefore note that because our study is based on ocean surface data it may underestimate the total effect of mesoscale eddies on biogeochemical rates.

Furthermore, we may underestimate the overall effect of mesoscale eddies on Chl also because of additional effects of mesoscale eddies that are not considered in our analysis. Such effects include the impact of smaller mesoscale features, and of submesoscale processes near the edges of eddies (Woods, 1988; Strass, 1992; Martin et al., 2002; Lévy, 2003; Klein and Lapeyre, 2009; Siegel et al., 2011), e.g., eddy-jet interactions and associated horizontal shear-induced patches of up- and downwelling. Such features are included in our analysis only insofar as they have rectified effects on the larger mesoscale Chl patterns resolved by the data we use. Another effect we do not consider is non-local stirring (D'Ovidio et al., 2015), the contribution of eddies to lateral dispersion outside the eddies' cores in interaction with the ambient flow. This effect, for instance, shapes iron plumes downstream of shelves along the ACC, thus preconditioning Chl blooms (Ardyna et al., 2017). Therefore, we note that the overall effect of mesoscale eddies on biogeochemical rates may be larger than suggested by our analysis of the mesoscale, local imprint of eddies on Chl. Finally, we note that our analysis does not include the effect of submesoscale processes outside eddies as well as any unstructured turbulence in general.

## 5 Summary and Conclusions

The prevalent and strong correlations between anomalies in surface Chl and mesoscale variability have triggered substantial research, but many unresolved issues remain, particularly regarding their causes (Lévy, 2008; Gaube et al., 2014; McGillicuddy Jr., 2016). With this study, we aim to provide an observational reference for the seasonal climatological  $\delta\text{Chl}$  associated with mesoscale eddies across the Southern Ocean, a region where the detailed regional and seasonal relationship of eddies and Chl previously had not been discussed. To this end, we combined satellite estimates of Chl with ocean mesoscale eddies (diameters larger than  $\sim 50$  km) identified based on satellite estimates of SLA. The very large number of collocations of eddies and Chl allowed us to retrieve statistically robust results despite the frequent data gaps and the high spatio-temporal variability of Chl.

We found a relatively complex pattern of Chl anomalies associated with mesoscale eddies, i.e.,  $\delta\text{Chl}$ , with many anomalies exceeding  $\pm 10\%$  of their mean value over wide areas in the Southern Ocean. The  $\delta\text{Chl}$  for cyclones is positive in subtropical waters, but negative along the ACC; anticyclones show a similar pattern, but of opposite sign. A pronounced seasonality of the imprint is apparent especially along the ACC and in Antarctic waters, featuring a sign switch of the anomaly over the course of the year.

While multiple mechanisms may be at play at the same time to cause the observed  $\delta\text{Chl}$  (Gaube et al., 2014; McGillicuddy Jr., 2016), our analyses suggest that lateral advection due to *stirring* by eddies and associated lateral entrainment and permeable *trapping* explain a large fraction of the observed  $\delta\text{Chl}$ . This conclusion is based on our analysis of the climatological Chl gradients, eddy rotation and propagation pathways, and the local shape of the  $\delta\text{Chl}$  of eddies.

A prominent region and season where eddy-induced advection is insufficient to explain  $\delta\text{Chl}$  are the northern ACC characterized by deep mixed layers in winter to spring and the seasonal sign switch of  $\delta\text{Chl}$  in the same region: Here, winter to spring negative and positive  $\delta\text{Chl}$  of anticyclones and cyclones, respectively, are consistent with an enhancement and reduction of deep mixed layer light limitation. The opposite signs of  $\delta\text{Chl}$  in summer to autumn are consistent with an abatement of iron limitation by anticyclones via a relatively weak stratification facilitating vertical mixing, and, more speculatively, with an abatement of grazing pressure caused by anticyclones via deepened mixed layers; and vice versa for cyclones. In other regions and seasons our analysis does not exclude a modulation of  $\delta\text{Chl}$  by effects of eddies on biogeochemical rates, even though our results suggest that lateral advection is likely the dominant mechanism.

Future work may include the investigation of where and when Southern Ocean eddies substantially affect biogeochemical rates, such as through modulation of alternating roles of iron and light limitation as well as grazing pressure along the ACC (Song et al., 2018). The growing number of sub-surface biogeochemical measurements across eddies may be of help here, such as those collected by the growing number of biogeochemical floats (<http://biogeochemical-argo.org>). In addition, targeted experiments with numerical ocean-biogeochemical models with the option to alternately switch on and off Chl sources and sinks could be employed to shed light on the questions of what the role of eddy-effects is on Chl sources and sinks relative to advection, for higher trophic levels (Nel et al., 2001; Godø et al., 2012), or for the magnitude and structure of export (Waite et al., 2016). Furthermore, such models could be used to assess if these effects of eddies on Chl substantially affect Southern Ocean biogeochemistry. Of particular interest are their modifications of the mode waters that originate from the Southern

Ocean region with deep winter mixed layers. This is crucial, as these mode waters supply the low latitude ocean with nutrients and sequester a substantial amount of anthropogenic carbon (Sarmiento et al., 2004; Sallée et al., 2012). The final thread is the expansion of this work to smaller scales, and perhaps also more ephemeral turbulent structures, such as fronts.

*Data availability.* The identified eddies we used in this study including their Chl characteristics are publicly available (<http://dx.doi.org/10.3929/ethz-b-000238826>). Other presented data are available from the corresponding author upon request.

*Author contributions.* I.F., N.G., and M.M. conceived the project, I.F. carried out the analyses, all authors contributed to the writing of the manuscript.

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