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An optimised method for correcting quenched fluorescence yield

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Abstract

Under high light intensity, phytoplankton protect their photosystems from bleaching through non-photochemical quenching processes. The consequence of this is suppression of fluorescence emission, which must be corrected when measuring in situ yield with fluorometers. Previously, this has been done using the limit of the mixed layer, assuming that phytoplankton are uniformly mixed from the surface to this depth. However, the assumption of homogeneity is not robust in oceanic regimes that support deep chlorophyll maxima. To account for these features, we correct from the limit of the euphotic zone, defined as the depth at which light is at ~ 1 % of the surface value. This method was applied to fluorescence data collected by eleven animal-borne fluorometers deployed in the Southern Ocean over four austral summers. Six tags returned data showing evidence of deep chlorophyll features. Using the depth of the euphotic layer, quenching was corrected without masking subsurface fluorescence signals.

1 Introduction

Monitoring distribution and abundance of primary producers in the marine environment is useful for understanding larger physical and environmental processes. Phytoplankton are predominantly single-celled, green microscopic organisms; present at variable concentrations in every ocean (Falkowski and Kolber, 1995; Behrenfeld et al., 2009). They are the first stepping-stone in transferring energy into the marine ecosystem. When conditions allow for growth, their collective impact is such that they are able to change the spectral properties of the water (McClain, 2009). This can be exploited to measure abundance and distribution using their photosynthetic pigment, chlorophyll *a* (Chl *a*) as a marker (Morel and Prieur, 1977; Gordon and Morel, 1983; Falkowski et al., 1998; Henson et al., 2010).

Satellite-derived ocean colour is the most comprehensive dataset available for monitoring surface Chl *a* concentration. However, the limitations of remote sensing are

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significant (Dierssen and Smith, 2000; McClain, 2009). Perhaps most significantly, satellite sensors can only "see" ocean colour from the surface to one optical depth; providing little information on the vertical structure of the water column (Morel and Berthon, 1989). Despite innovative algorithms to improve data collected by satellites, limitations are not likely to be resolved with the next generation of ocean colour sensors. Continued collection of in situ data on phytoplankton distribution and abundance is thus essential (Johnson et al., 2009).

Fluorescence has been widely used as a relatively inexpensive, non-invasive method for studying phytoplankton and quantifying Chl *a* since the 1960's (Lorenzen, 1966; Lorenzen and Jeffrey, 1980; Cullen and Eppley, 1981; Falkowski and Kolber, 1995; Xing et al., 2011; Lavigne et al., 2012). Chlorophyll pigments packaged inside phytoplankton cells re-radiate ~ 2 % of light energy as fluorescence. Active fluorescence can thus be measured by a fluorometer delivering voltage output equivalent to 460 nm (excitation in the blue) and measuring resultant fluorescence in the 620–715 nm range (detection in the red). Assuming that the measured yield is proportional to the abundance of photosynthesising phytoplankton, relative values of fluorescence can be used to quantify primary biomass. However, yield (and thus proportionality) is affected by several factors, including the intensity of sunlight each cell is exposed to (Behrenfeld and Boss, 2006).

To regulate high sunlight intensity, phytoplankton employ the mechanism of non-photochemical quenching. This process helps cells protect themselves in environments where light energy absorption exceeds the capacity for light utilisation (Müller et al., 2001; Behrenfeld et al., 2009). During periods of high light stress, shallow-mixed phytoplankton in the upper euphotic layer protect their photosystems from bleaching by emitting excess energy as heat (Milligan et al., 2012). In this state of photo-protection, photosynthesis is inhibited and fluorescence yield drops (Müller et al., 2001). However, phytoplankton distributed deeper in the water column are shaded by surface biomass and protected by light-attenuating properties of the water itself. Thus, inside a homogeneously mixed layer, deeply-mixed phytoplankton will fluoresce while

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shallow-mixed biomass will be “invisible” to a fluorometer. If uncorrected, quenched fluorescence yields will generate surface values under-representative of phytoplankton abundance. Avoiding such under-representation is particularly important for studies comparing satellite-derived surface Chl *a* with in situ fluorescence derived Chl *a*.

On the vertical scale, quenched fluorescence profiles are also problematic in that they have the same shape as deep fluorescence maxima (DFM). Sub-surface fluorescence maxima can be indicative of deep chlorophyll maxima (DCM), which form when the bulk of phytoplankton biomass settles to depths where both nutrients and light are sufficient (Cullen and Eppley, 1981; Holm-Hansen and Hewes, 2004). Because DCM are usually found below one optical depth, abundance and distribution of such features cannot be measured by satellite (McClain, 2009; Charrassin et al., 2010). However, DCM play important roles in the organisation of pelagic trophic food webs, as well as underreported roles in contributing to net primary production and carbon fixation (Fairbanks et al., 1982; Estrada et al., 1993; Claustre et al., 2008). It is therefore necessary to accurately identify and map these features.

In previous work on glider data, correcting for quenching involved using backscatter (Sackmann, 2008) or surface light intensity (Todd et al., 2009); each measured simultaneously to fluorescence. For autonomous platforms collecting “only” fluorescence, salinity and temperature data, this is not possible. Using the depth of the density-derived mixed layer, Xing et al. (2011) corrected quenched fluorescence data collected by Argo floats in Pacific, Atlantic, and Mediterranean offshore zones. This mixed layer depth (MLD) method was then extended to fluorescence data collected by tagged southern elephant seals (*Mirounga leonina*) off Kerguelen Island in the Southern Ocean (Xing et al., 2012; Guinet et al., 2013). Following the method of Xing et al. (2011), the maximum fluorescence yield within the density-derived mixed layer would be representative of the whole; assuming homogeneity. However, while the vertical distribution of phytoplankton is strongly controlled by density, it is also driven by nutrient and light gradients (Navarro et al., 2006). When these change with depth over time, so too will the vertical distribution of phytoplankton in the water column. This

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is especially true for motile (flagellated) and seasonally successive (heavily silicified) species (Mengesha et al., 1998; Quéguiner, 2013).

In this paper, we present a method to correct for quenching using the limit of the euphotic zone (Z_{eu}), defined as the depth at which light is at ~ 1 % of the surface value. At this level, light should be sufficient for photosynthesis but too weak to cause quenching. This method is applied to fluorescence data collected by 11 animal-borne fluorometer, conductivity, temperature and depth satellite-relayed data loggers (FCTD-SRDLs) deployed in the Southern Ocean over several austral summers. Surface waters of this oceanic regime are well-mixed and DCM are thought to be rare. However, a southern elephant seal tagged on Marion Island travelled to a region correctly hypothesised to support sub-surface features (Holm-Hansen et al., 2005). Animals tagged on Kerguelen Island also returned fluorescence profiles exhibiting deep features.

2 Methods

2.1 In-situ data

Between 2009 and 2013 ten adult female southern elephant seals from Kerguelen and one from Marion Island were equipped with FCTD-SRDLs (Sea Mammal Research Unit, St Andrews University, Scotland) before they undertook their post-breeding foraging migration over the austral summer (Fig. 1). Following established tagging protocols (Bester, 1988; McIntyre et al., 2010), the seal on Marion Island was immobilized with ketamine using a remote injection method and the tag was glued to the fur on the head with quick-setting epoxy resin. Seals on Kerguelen were anesthetised with an intravenous injection of tiletamine and zolazepam 1 : 1 and tags were glued to the fur on the head using a two component industrial epoxy (Araldite AW 2101) (Jaud et al., 2012).

The FCTD-SRDL instrument records behavioural data as well as in situ pressure, temperature, salinity and fluorescence (Charrassin et al., 2010; Xing et al., 2012).

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At-sea data were relayed via the Argos satellite system (http://www.argos-system.org). Location estimates were calculated by Service Argos from Doppler Shift measurements between uplinks and raw data were downloaded from the Sea Mammal Research Unit (SMRU) website (http://www.smru.st-andrews.ac.uk/). Detailed information on the hardware and software of the CTD-SRDL is described by Boehme et al. (2009), and on-board data processing is described comprehensively by Fedak et al. (2002).

Fluorescence is recorded by a Cyclops 7 fluorometer (Turner Designs, CA, USA), which delivers a voltage output proportional to the fluorescence detected in a wavelength between 620 and 715 nm. The Cyclops instrument is programmed to measure fluorescence every 2 s during the ascent (upcast), from 180 m to the surface. Due to the tight limits on data transfer through the Argos satellite system, fluorescence data have to be compressed (Boehme et al., 2009) into 10 m vertical bins. The reading for "175 m" is thus a weighted mean of all fluorescence readings taken between 180 m and 170 m. This is the deepest bin available – deep and dark enough to anticipate an absence of live, photosynthesising phytoplankton (Guinet et al., 2013). However, instruments do not return readings of zero at these depths. This "dark count" is an offset value added by the manufacturers; useful because at very low signal, readings are indistinguishable from noise. The offset value increases the signal to noise ratio, which must be removed during data processing (Lavigne et al., 2012). We therefore calculated the mean of readings at 175 m and subtracted this from all measurements collected by the same tag (Xing et al., 2011). This is not only useful for making the fluorescence values more representative, it also serves to reduce variability between tags (Xing et al., 2012). The resulting values are considered proportional to fluorescence, and are termed Relative Fluorescence Units (RFU).

2.2 Satellite data

The depth of the euphotic zone (Z_{eu}) reflects the limit where photosynthetic available radiation (PAR) is 1 % of its surface value. In this study, we use an estimate of Z_{eu} based on an algorithm by Lee et al. (2007). These estimates are derived from measurements

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of the water-leaving radiance by the Moderate Imaging Spectrometer (MODIS) as 4 × 4 km monthly composites (http://oceancolor.gsfc.nasa.gov).

MODIS provides two products of Z_{eu} from remotely derived ocean colour (Lee et al., 2007; Morel, 1988; Morel et al., 2007). Morel's Chl-approach is an empirical method centred on the assumption that the optical properties of the water are "only" affected by Chl *a* (Case-1 waters). The calculation of Z_{eu} is thus solely based on remotely-sensed Chl *a* concentration. Lee's IOP-approach, on the other hand, is derived with the addition of inherent optical properties (IOPs). Knowledge of Z_{eu} thus requires information on backscattering and absorption coefficients at 490 nm (Shang et al., 2011). While open waters of the Southern Ocean likely conform to case-1 assumptions (Soppa et al., 2013), Lee's approach was selected because the addition of IOPs are potentially beneficial for improved accuracy and reliability (Dierssen and Smith, 2000).

For adequate temporal and spatial coverage in a region as cloudy as the Southern Ocean, monthly composites of Z_{eu} were favoured over 8 day. Basic correlations were applied to test reliability of the monthly product against the 8 day product. Good agreement between the two supported the decision to use monthly composites ($n = 480$, $R^2 = 0.82$, $p < 0.0001$). However, despite the broad coverage in time, gaps were still present in space. For each fluorometer profile the closest Z_{eu} value in space was extracted from the gridded dataset. If no value was available, Z_{eu} was interpolated linearly from the nearest seal position with an associated Z_{eu} value.

2.3 Correcting for quenching

In this study, we compare the results of fluorescence quenching correction from two depths. The first is the depth of Z_{eu} using Lee's algorithm (2007). The second is a density-derived MLD calculated from the concurrent CTD measurements of the FCTD-SRDL. Here, MLD is defined as the depth where the vertical density gradient equals or exceeds a threshold value (Kara et al., 2000). To date, a range of thresholds have been used in the literature; from the most sensitive of 0.005 kg m^{-3} (e.g. Brainerd and Gregg, 1995; de Boyer Montégut et al., 2004; Xing et al., 2012) to the least at

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$0.15\,kg\,m^{-3}$ (e.g. Lewis et al., 1990; Weller and Plueddemann, 1996). Visual inspection of the density along seal tracks supported a threshold of $\Delta\rho = 0.03\,kg\,m^{-3}$, which is small enough to not increase a mixed-layer heat budget (Dong et al., 2008), while also accounting for all possible uncertainties within the derived density profiles.

Quenching occurs in surface waters during periods of high light stress. Despite daily variability attributed to cloud (changing light intensity), and differences in phytoplankton concentrations between years and regions, suppression of fluorescence is a ubiquitous feature. Fitting a non-linear model (sin-function) to surface fluorescence as a function of time of day showed that quenching around midday was significant ($n = 1267$, $R^2 = 0.26$, $P < 0.001$) (Fig. S1). Data were thus categorised as "day: possibly quenched" (from sunrise to sunset, with the sun 6° above the horizon) or "night: unquenched". To illustrate the quenching effect without interannual and regional variability, "day" yields were divided by the preceding "night" yields to generate ratios. Data were then binned by hour and plotted using boxplots (Fig. 2).

To find deep fluorescence features, the "night: unquenched" data were normalised and each profile was interrogated for maximum values below the near-surface yield. For this step, the small proportion of profiles with maximum fluorescence yields below 0.15 RFU were removed from the dataset. These low signals tend to fall within the noise, and the resulting vertical profiles cannot be meaningfully interpreted. Remaining profiles exhibiting a deep fluorescence yield of 15 % or higher than the near-surface fluorescence were then visually inspected. Vertical profiles conforming to the shape of DFM in this dataset were considered "true" DFM, independent of quenching (Fig. S2). The "day: quenched" data were corrected using both Z_{eu} and MLD; creating two separate subsets for comparison. In both cases, the maximum fluorescence yield between Z_{eu} and the surface, or MLD and the surface, was then extended to fill in supressed yield (Fig. 3).

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3 Results

The at-sea phases of the eleven tagged southern elephant seals (Fig. 1) tended to start in November and end in January of the following year, meaning data were collected over the height of the austral summer. In the top 10–15 m of the upper mixed layer across all years of sampling, suppression of daytime fluorescence yield was significant. To correct for this, surface values collected between dawn and dusk were "filled in" with maximum values from the depth of Z_{eu}. For comparative analysis, the same data were then corrected from the depth of the mixed layer. The difference between the two methods is illustrated in Fig. 3, where normalised fluorescence profiles were treated with both correction schemes. Using Z_{eu} prevents the distinct deep features from being masked in all cases.

Applying the two different correction schemes does not always result in significant differences in yield at the surface; however correcting from Z_{eu} serves to conserve "unusual" (not homogenously mixed) phytoplankton dynamics on the vertical scale. This is illustrated in Fig. 3d and e where the shallow- and deep-mixed phyotoplankton appear to have settled into two distinct layers. Corrected surface fluorescence yields are only negligibly overestimated using the depth of the mixed layer; but perhaps more importantly, vertical complexity is lost.

Of the eleven seals tagged with FCTD-SRDLs between 2009 and 2013, only one instrument returned data completely absent of subsurface fluorescence maxima. For the remaining ten "night: unquenched" datasets, approximately 24 % (Std. Dev. = 16) of the 231 profiles showed "true" DFM (Fig. S2).

One seal was tagged on Marion Island in 2012 as part of an initiative to search for DFM in a region hypothesised to support DCM (approximately 20° E to 20° W, 57 to 60° S) (Holm-Hansen et al., 2005). We extended this region to the limit of the Polar Front at around 50° S (Orsi and Ryan, 2001) after reviewing the physics of the region. The tagged seal entered this extended region (20° E to 20° W, 50 to 60° S) and measured fluorescence in near-real time. The weak DFM evident inside the extended

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region has a surface signature, but the signal maximum is at ~ 60 m (Fig. 3c). This is just below euphotic depth but inside the mixed layer. The feature is thus conserved when correcting from Z_{eu} (blue line) but masked when using MLD (red line).

The same is true for DFM measured off Kerguelen (Fig. 4). The distinct deep fluorescence feature in Fig. 4a has a maximal yield below euphotic depth but within the mixed layer. This deep signal is masked when correcting from MLD (Fig. 4c) but remains distinct when using Z_{eu} (Fig. 4b). Vertical complexity of fluorescence in Fig. 4d is also lost when correcting from the depth of the mixed layer (Fig. 4f) but conserved when correcting from Z_{eu} (Fig. 4e). Uncorrected profiles (Fig. 4a and d) illustrate how evident suppression of daytime fluorescence yield is in the surface layers. Corresponding daylight hours are shown in white on the greyscale bar, scaling to black for night.

4 Discussion

The phenomenon of non-photochemical quenching is well described and appears to ubiquitous across oceans and seasons (Sackmann et al., 2008; Milligan et al., 2012). The depth where light levels are sufficient for photosynthesis but too weak to generate quenching is key for correcting in situ fluorescence data; ensuring fluorescence yield is representative of phytoplankton abundance. However, when fluorescence data is collected autonomously, this depth cannot always be measured in space and time.

For this study, removing quenched fluorescence would mean discarding 831 of the 1381 profiles collected by 11 animal-borne tags over several austral summers in the Southern Ocean. Losing approximately 60 % of the data collected from such an undersampled region is simply not viable. Thus, two proxy depths for where light levels are too weak to cause suppression of fluorescence yield are compared for quenching correction. The first is a density-derived MLD, calculated from CTD data measured concurrently by the tag (Xing et al., 2012; Guinet et al., 2013). The second is the depth of the euphotic zone, Z_{eu} (Lee et al., 2007).

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Composites of MODIS Z_{eu} are provided as evaluative products and these were used to determine euphotic depth. Lee's method benefits from the addition of inherent optical properties (IOPs), and this approach provided comparatively accurate and reliable estimates of Z_{eu} in open waters of the China Sea (Lee et al., 2007; Shang et al., 2011). We thus assume that this method can reliably estimate the limit of the euphotic zone in the open waters of the Southern Ocean. However, Z_{eu} is an evaluative product and validation at the high latitudes would be beneficial for quantifying errors associated with this method. For example, possible underestimation of the depth light penetrates to around midday, and overestimation around sunrise (this study).

Monthly Z_{eu} products were selected over 8 day to account for the gaps in coverage. Satellites cannot "see" through cloud, and the high latitudes are persistently cloudy. Despite the large temporal compromise, 8 day and monthly products showed excellent agreement. This is unlikely be true for coastal or near-coastal regimes, where dynamics change on finer scales. For this reason, we would recommend using daily data, 3 day or 8 day composites in these areas, or any region where cloud cover is less of a problem. As a compromise, generating 16 day composites using SeaDAS 7.0 (Fu et al., 1998) would address the temporal compromise as well as fill in some of the gaps. However, this step requires custom processing, rather than use of existing products. This may limit wider application of the method. Our aim is to create an algorithm that is easily applied and universally useful for autonomously collected fluorescence data in regions where DCM may be features.

Surface waters of the Antarctic are well mixed and distinct deep features are thought to be rare. However, six of the eleven seals tagged with FCTD-SRDLs between 2009 and 2013 returned DFM potentially indicative of DCM. These in situ fluorescence datasets add to growing evidence that DCM may be regionally and seasonally persistent in the Southern Ocean (Holm-Hansen and Hewes, 2004; Charrassin et al., 2010; Quéguiner, 2013). Previous studies have shown that a proportion of instrumented southern elephant seals travel into the extended region first proposed by Holm-Hansen et al. (2005) during their post-breeding migration, possibly orientating along the

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South-West Indian Ridge (Biermann, 2011). One seal tagged on Marion followed this southwest route; relaying near-real time fluorescence data from within the area of interest. Presence of the DFM inside this region was not surprising, but the number of potential DCM found off Kerguelen was unexpected. Most deep features were corroborated by night data and it is thus unlikely that they are errors arising from the correction method.

Not all DFM are DCM, due to the variability of chlorophyll packaging within phytoplankton. The amount chlorophyll per cell can vary depending on nutrient history, light regime, depth and temperature (Steele, 1964; Cullen, 1982; Behrenfeld and Boss, 2006). It can also vary between species of the same community. Under laboratory conditions, dinoflagellates have been shown to package more chlorophyll per cell than diatoms, for example (Chan, 1980). The consequence is that chlorophyll concentration and resulting fluorescence yield can change with depth, even inside homogeneously mixed layers. Shallow-mixed phytoplankton (near the surface) experiencing high light energy and low nutrient concentration will have minimal Chl *a*. Deep-mixed phytoplankton of the same species, on the other hand, will have comparatively high Chl *a* per cell (Milligan et al., 2012; Cullen, 1982). This difference will create a DFM that is independent of biomass.

We cannot confirm that the distinct deep fluorescence maxima measured by these animal-borne fluorometers are DCM without concurrent laboratory analysis. However, Holm-Hansen and Hewes (2004) found annually recurring deep phytoplankton biomass maxima on the nutricline at 60–90 m in Drake Passage waters. Closer to Marion Island, results from the Antarktis XIII/2 “Frontendynamik und Biologie” expedition (December 1995–January 1996) confirmed that heavily silicated species of diatoms accumulated in deep layers as the summer season progressed (Quéguiner, 2013). Furthermore, a significant proportion of the open water community should also be composed of non-diatom species by the mid- to late-summer months. Mengesha et al. (1998) measured dinoflagellates and other motile species in greater abundances than diatoms in the open waters of the high latitudes. Dinoflagellates are mixotrophic and are able to

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switch between photosynthesis and predation upon other microorganisms. Studies on DCM composed of dinoflagellates in the Baltic Sea showed abundant biomass below euphotic depth (Carpenter et al., 1995). If DFM were merely artefacts of chlorophyll packaging or species composition, we could reasonably expect maximum yields at depth to be more common, if not ubiquitous. However, these features are rare and appear to be distinct. While we cannot confirm with certainty that these deep fluorescence maxima are also deep chlorophyll maxima, with an insight into the physics and the phytoplankton dynamics in the region, it is likely that they are.

In order to prevent surface yield from being overestimated and ensure distinct DFM are not masked during quenching correction procedures, using the depth of the euphotic layer is more effective than MLD. Furthermore, correcting from Z_{eu} serves to conserve "unusual" (not homogenously mixed) phytoplankton dynamics on the vertical scale. This vertical information may provide useful insights into mixing and settling patterns of different phytoplankton species within the same assemblages in time and space (floristic shifts), or differences in chlorophyll packaging in the same species (photoacclimation).

Had the assumption of homogeneity within the mixed layer remained true for all waters profiled by the tagged seals, correcting quenching from the MLD would have been sufficient. The problem of phytoplankton not being uniformly mixed in the mixed layer was commented on by Xing et al. (2012), but not addressed until now. The limitations of our own correction scheme would be improved with testing of Z_{eu} in Southern Ocean waters. Furthermore, until we are able to apply our quenching method to more fluorescence data in and outside of the high latitudes, we are only able to suggest that using Z_{eu} improves the current method in regions where DCM may be features.

Supplementary material related to this article is available online at http://www.ocean-sci-discuss.net/11/1243/2014/osd-11-1243-2014-supplement.pdf.

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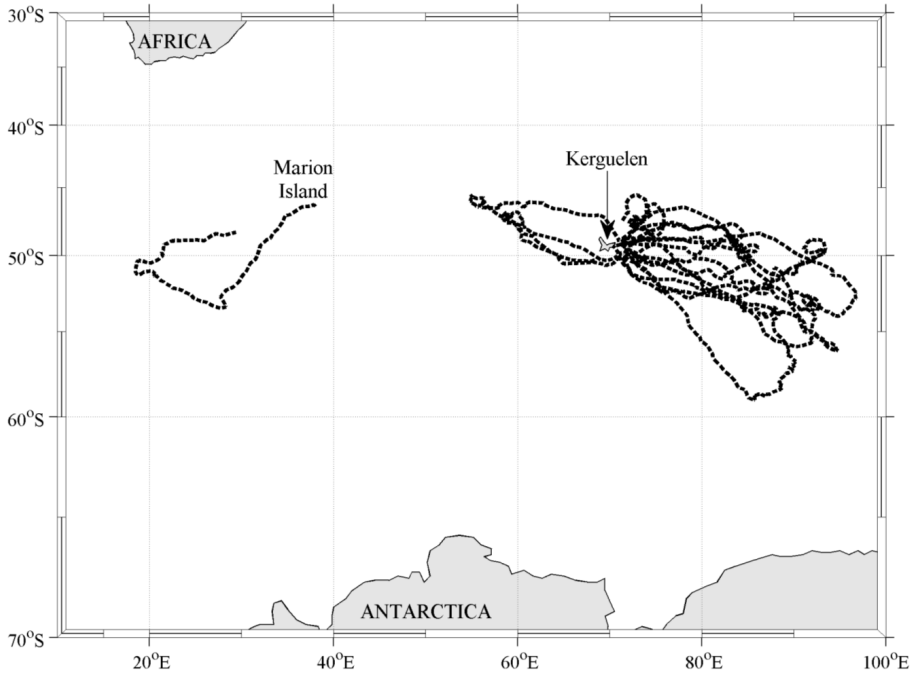

Fig. 1. Tracks of southern elephant seals tagged with FCTD-SRDLs over the austral summers of 2009, 2010, 2012 and 2013. Tags fall off with the fur during the annual moulting process (upon return from the post-breeding trip). However, the incomplete track off Marion Island is either due to the FCTD-SRDL battery failing or tag falling off at sea off after 55 days.

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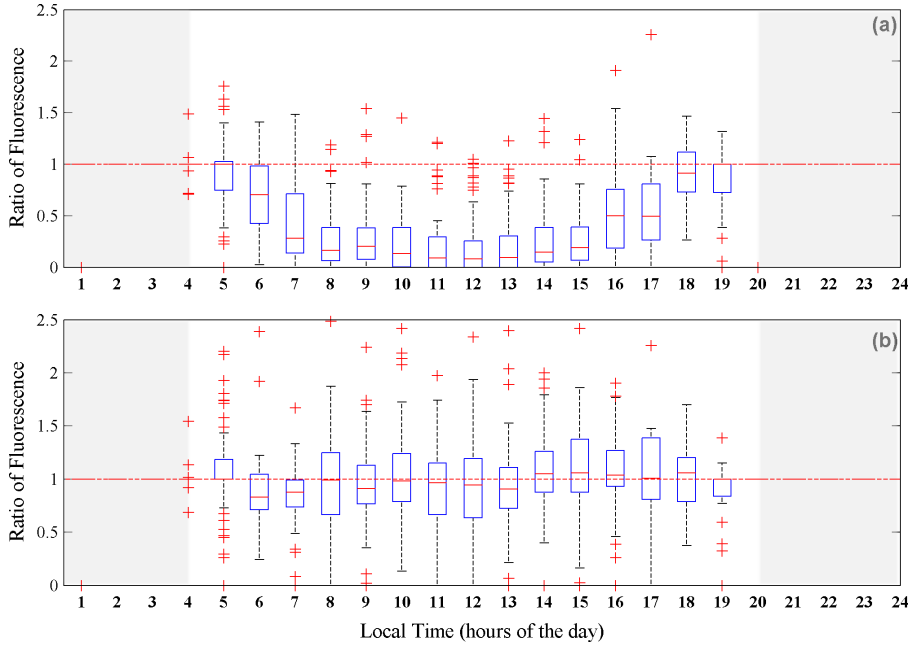

Fig. 2. Ratios of day to night surface fluorescence yields (first 15 m) collected by 11 animal-borne fluorometers over austral summers. Boxplots show the distribution of "day" to "night" ratios in **(a)**, representing quenched to unquenched yield. The horizontal red line at 1 indicates the 1 : 1 ratio. Ratios of fluorescence yield decrease from around 06:00 LT until around 13:00 LT, where yields begin recovering to the 1 : 1 ratio. Corrected ratios of fluorescence in **(b)** do not follow the same trend of deviation from the 1 : 1 ratio line at 1. Flanking grey sections represent times of the day where the sun is less than 6° below the horizon.

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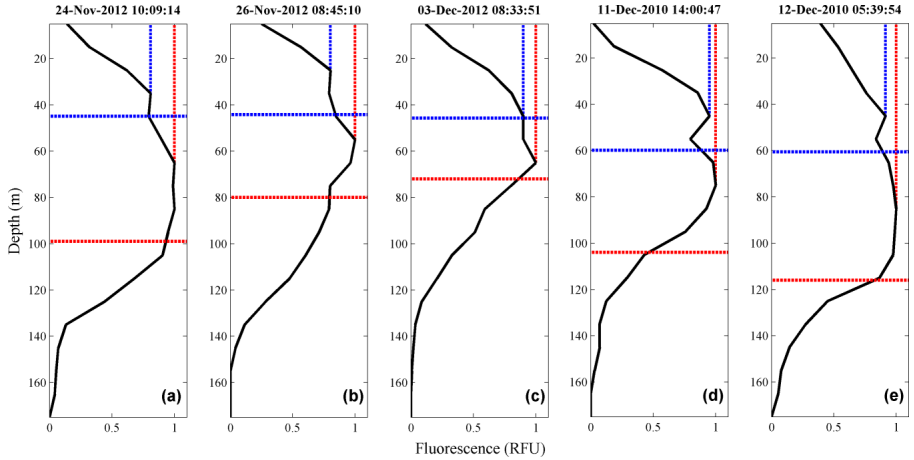

Fig. 3. Discreet vertical profiles of quenched fluorescence (solid black line) corrected using either the depth of the mixed layer (dashed red line) or the depth of the euphotic zone (dashed blue line). Profiles **(a–c)** were collected off Marion Island in the austral summer of 2012. Profiles **(d)** and **(e)** were collected off Kerguelen in December 2010. Quenched fluorescence with the offset subtracted (black line) is corrected using MLD (depth and corresponding fluorescence yield shown with dashed red line) and Z_{eu} (depth and corresponding fluorescence yield shown with dashed blue line).

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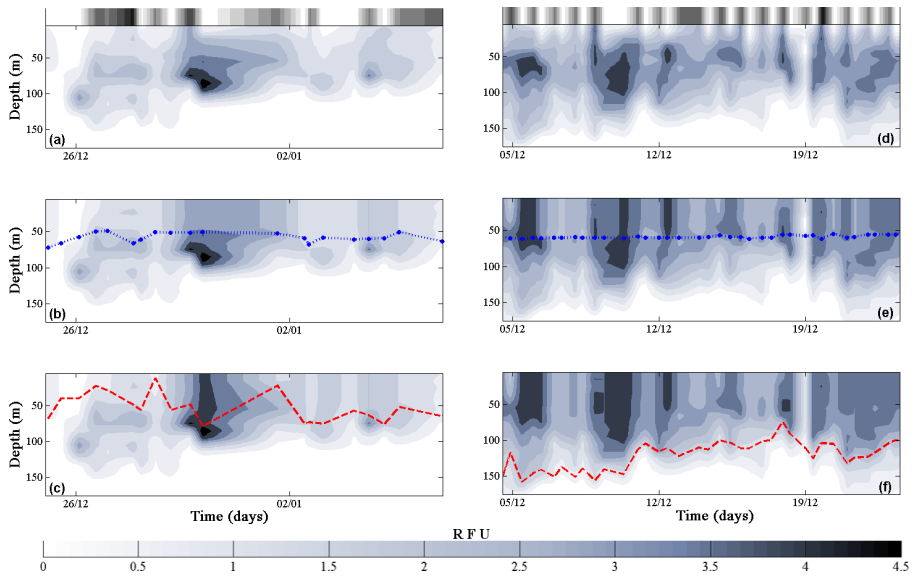

Fig. 4. Sections of quenched fluorescence collected by animal-borne fluorometers, corrected using either the depth of the euphotic zone or the depth of the mixed layer. The top row of vertical profiles **(a)** and **(d)** show sections of uncorrected fluorescence data collected by instrumented seals from Kerguelen over the austral summer of 2010. The greyscale bar attached to the top row illustrates when fluorescence data was collected relative to the time of day, with black for night and white for day. The second row of vertical profiles **(b)** and **(e)** have been corrected using euphotic depth (Z_{eu} shown with dashed blue line). The last row of profiles **(c)** and **(f)** have been corrected using mixed layer depth (MLD shown using dashed red line).

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