Including the invisible: Deep depth-integrated chlorophyll estimates from remote sensing may assist in identifying biologically important areas in oligotrophic coastal margins

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Abstract. Surface chlorophyll from satellite remote sensing is a common predictor variable in marine animal habitat studies but fails to capture d~~D~~eep chlorophyll maxima (DCM)~~ are common in~~ that are unambiguous in persistently stratified water columns. DCMs are also present within the meso-oligotrophic marine environment of Western Australia and have been hypothesised to be an important feature for the growth and maintenance of regional krill populations on which locally endangered pygmy blue whales feed. This study used ~8500 vertical ocean glider profiles collected between 2008 and 2021 to better understand the broad-scale temporal presence of DCMs and their characteristics in West Australian waters. Our results show that DCMs are predominantly present from September to April, with a high proportion of biomass maxima within the euphotic zone in September and March. In summer, DCMs deepen and settle below the euphotic zone. The latter results in a balanced presence of biomass and photo-acclimation maxima, placing Western Australian waters in a unique biogeographical biome. In addition, since DCMs in summer contribute to over 50 % of water column-integrated chlorophyll below the euphotic zone, our results are in support of hypotheses regarding the importance of the DCM for local krill and highlight the need to develop methods to include water column-integrated chlorophyll estimates in habitat models. Linear regression analyses show that this could be achieved through the extension of previously known relationships between surface and water column-integrated chlorophyll over the euphotic zone to twice the euphotic zone depth (i.e., deep depth-integrated chlorophyll). While using water column-integrated chlorophyll estimates from satellite remote sensing has its challenges, it is currently the only means to include DCMs in habitat models fitted to large temporal- or spatial-scale animal presence data. ~~and may support higher trophic levels. Yet, it is challenging to include DCM contributions in studies aiming to identify marine animal foraging habitats and hotspots, because these studies often rely on satellite remote sensing data restricted to the surface. Previously established quantitative relationships between surface and depth-integrated chlorophyll within the euphotic zone of the open ocean and a eutrophic coastal margin encouraged us to assess whether such relationships are also present within the Western Australian intermittent-oligotrophic coastal margin. We also assessed whether the relationships could be extended to greater depths to capture DCMs below the euphotic zone. Based on ~9600 ocean glider profiles, our analyses demonstrate that such a relationship similarly exists off Western Australia and can be extended to twice the euphotic zone depth. Regression parameters were fine-tuned for three different conditions: 1) stratified waters in summer-transition months (September-April),~~

~~characterised by relatively deep biomass maxima; 2) stratified waters in mid-winter (May–August) in which DCMs were less common and more likely a photo-acclimation maximum; and 3) mixed waters. While mean absolute errors increased in relationships over twice the euphotic zone depth (i.e., for estimates of deep depth-integrated chlorophyll), they remained low (i.e., max 16.5 %). These results and an observed chlorophyll increase in summer, unique to deep depth-integrated values, highlight the necessity to include deep depth-integrated chlorophyll estimates from satellite remote sensing in studies that aim to identify biologically important areas and productivity anomalies in (intermittent) oligotrophic environments.~~

1 Introduction

Phytoplankton are instrumental in providing energy to higher trophic levels of aquatic ecosystems. Their biomass is mostly quantified in terms of chlorophyll-a (hereafter called chlorophyll), from which primary productivity is derived, and areas with potentially high prey availability for higher trophic levels are identified (Huot et al., 2007; Hobday and Hartog, 2014). Indeed, several studies identified chlorophyll as a significant predictor variable of foraging habitat and hot spots for primary consumers (e.g., Schmidt et al., 2012; Hellessey et al., 2020) and higher trophic levels (e.g., Suryan et al., 2012; Palacios et al., 2019; Salgado Kent et al., 2020; Speakman et al., 2020).

While chlorophyll levels can be quantified using several techniques (i.e., visual assessment of ocean colour, spectrophotometry, fluorometry, and chromatography; Parsons and Strickland, 1963; Yentsch and Menzel, 1963; Jeffrey, 1974; Gieskes and Kraay, 1977; Jeffrey et al., 1999), phytoplankton biomass and productivity studies flourished with the launch of the first satellite remote sensing ocean colour mission in 1978 (Hovis et al., 1980; McClain, 2009). Not only has satellite remote sensing generated a near-continuous chlorophyll dataset with high spatial resolution (Groom et al., 2019),~~ but~~ the data are also widely accessible, resulting in the inclusion of satellite-derived chlorophyll—almost as a default—in studies aiming to identify crucial marine animal foraging areas. Yet, satellite remote sensing is restricted to the upper water column (2–39 m; Organelli et al., 2017) and likely~~ to~~ excludes Deep Chlorophyll Maxima (DCMs; Gordon and McCluney, 1975; Smith, 1981), which may—at least in some areas—be an essential feature to support higher-order foraging efforts (Rennie et al., 2009a; Scott et al., 2010).

~~DCMs predominantly form in equatorial to subtropical regions between 35° N and 35° S, with increased seasonality when moving away from the equator (Cornec et al., 2021). The seasonality generally follows the seasonal occurrence of~~ DCMs are observed throughout the global oceans, with a year-round and consistent presence in tropical and most sub-tropical regions (Mignot et al., 2014; Bock et al., 2022; Quartly et al., 2023). Seasonal patterns of occurrence become more evident from temperate to high-latitude regions (Cornec et al., 2021), during which DCMs are present in summer but tend to break down or occur less frequently in winter (e.g., Mignot et al., 2014; Baldry et al., 2020; Bock et al., 2022). In well-studied tropical and temperate regions, DCM formation has been linked to permanent or seasonally stable stratified water conditions (Cornec et al., 2021), ~~in which~~with light and nutrient availability driving~~e~~ the formation of true phytoplankton biomass maxima (i.e., deep biomass maxima, DBM) and deep photo-acclimation maxima (DAM; Mignot et al., 2014; Cullen, 2015). ~~The latter~~While

DAMs result~~s~~ from an increased chlorophyll-to-carbon ratio because of low-light adaption rather than an increase in transferrable carbon (Steele, 1962, 1964)~~ and is inherent to extreme oligotrophic systems (Cullen, 2015). However~~, both ~~DCM types~~DBMs and DAMs may contribute to water column productivity adequately enough to be of relevance to higher trophic levels (e.g., Weston et al., 2005; Fernand et al., 2013; Mignot et al., 2014; Marañón et al., 2021).

The marine habitat of Western Australia is characterised by a cross-shelf gradient in surface chlorophyll values decreasing from winter maxima ~1 mg m^{-3} along the coast to ~0.4 mg m^{-3} in offshore waters (i.e., >300 m deep; Lourey et al., 2006; Fearns et al., 2007; Hanson et al., 2007a; Koslow et al., 2008). However, surface chlorophyll values vary seasonally and, offshore, generally do not exceed 0.1 mg m^{-3} in summer (Hanson et al., 2005a, 2005b; Lourey et al., 2006; Koslow et al., 2008). These intermittent oligotrophic conditions result from the poleward flowing Leeuwin Current, which transports warm, low salinity, and low nutrient water along the continental shelf break (Cresswell and Golding, 1980). Despite seasonal variation in current strength with minimum geostrophic flow in January–February (Feng et al., 2003), the Leeuwin Current generally suppresses nutrient upwelling by strong south-westerly winds that blow in spring and summer (i.e., September–February; Rennie et al., 2006, 2009b).~~which suppresses the upwelling of cold nutrient-rich water most of the~~ Stratification weakens or may break down in late autumn and winter, which has been linked to an initial deepening of the mixed layer by an intensification of the Leeuwin Current strength (i.e., peak strength in June–July; Feng et al., 2003) and subsequent maintenance of turbulent conditions by north-westerly winter storms and enhanced eddy kinetic energy (Koslow et al., 2008; Rennie et al., 2006).

DCMs form in the vertically stratified water column of Western Australia in summer at a depth between 50 m and 120 m offshore, shoaling to the surface or seabed on the continental shelf (Hanson et al., 2005b~~a~~, 2007a; Twomey et al., 2007; Koslow et al., 2008; Rennie et al., 2009a; Chen et al., 2019). While DCMs tend to break down around the shelf edge in late autumn and winter (Chen et al., 2019), they may persist offshore at shallower depths (15–70 m; Hanson et al., 2005b~~a~~; Koslow et al., 2008). Previous studies have confirmed that the DCM is often a biomass maximum (Hanson et al., 2005b, 2007a; Rennie et al., 2009a), responsible for 30–70 % of total water column productivity (Hanson et al., 2007a). More importantly, the DCM may be a vital feature for *Euphausia recurva*, the most abundant krill species along the southwest Australian coast, including the Perth Canyon (Sutton and Beckley, 2016). *E. recurva*, in turn, is the common prey for locally endangered pygmy blue whales (*Balaenoptera musculus brevicauda*) known to feed around the Perth Canyon's head, northern rim, and plateau in waters 300–600 m deep (McCauley et al., 2004; Rennie et al., 2009a) and along the continental shelf break (200 m contour line; Owen et al., 2016) from February–June (peak presence February–March; McCauley et al., 2004; Erbe et al., 2015). Acoustic backscatter data from the Perth Canyon in late summer (February) suggests that krill gather at 300–500 m depth during the day, rising to the DCM at night to feast on phytoplankton prey (Rennie et al., 2009a; McCauley and Cato, 2016). Rennie et al. (2009a) highlighted that pygmy blue whales can only be expected to forage in areas where the metabolic gain from foraging supersedes the energy expenditure related to lunge feeding. Based on CTD analyses and numerical and phytoplankton studies, the authors hypothesised that the krill population of Western Australia is maintained throughout the year by increased productivity in both winter (related to surface blooms) and summer (related to subsurface blooms near the

DCM). Sutton (2015) supported this observation with fatty acid and stable isotope analysis on krill caught in the Perth Canyon in April (i.e., prior to the annual increase in surface phytoplankton in May), which did not reflect a diet of surface phytoplankton. ~~*E. recurva*, in turn, is a known prey for both lantern fish (*Myctophum asperum*) and locally endangered pygmy blue whales (*Balaenoptera musculus brevicauda*) foraging in the Perth Canyon (Rennie et al., 2009a; Cohen and Beckley, 2021).~~ Its apparent significance highlights the need to gain a better understanding of the broad-scale seasonal patterns in DCM formation and potential underlying processes and to consider the inclusion of DCMs in phytoplankton biomass estimates and marine animal habitat models~~analyses~~.

While it is known that DCMs form in Western Australian waters, our knowledge of their seasonal presence and characteristics (e.g., DCM depth, type and width, maximum chlorophyll concentration at depth, etc.) is limited to cross-continental shelf time series (e.g., Fearns et al., 2007; Koslow et al., 2008; Chen et al., 2019) and broad-scale temporally restricted analyses (e.g., Hanson et al., 2005b, 2007; Twomey et al., 2007; Thompson et al., 2011). ~~(e.g., Hanson et al., 2005a, b, 2007; Fearns et al., 2007; Twomey et al., 2007; Koslow et al., 2008; Chen et al., 2019)~~ This study used 14 years of ocean glider data to assess broad-scale temporal patterns in water column characteristics, DCM formation, and DCM characteristics in the meso-oligotrophic marine environment of Western Australia, focusing on the area between 27.5º S and 33.8º S where the Perth Canyon lies. In addition, ~~S~~while several studies have shown that surface chlorophyll values measurable by satellite remote sensing can estimate ~~depth-integrated~~ water column-integrated chlorophyll over the euphotic zone (depth over which Photosynthetically Active Radiation, PAR, decreases to 1 % of its surface value $Z_{1\%}^{PAR}$, hereafter referred to as “depth-integrated chlorophyll”; Morel and Berthon, 1989; Uitz et al., 2006; Frolov et al., 2012), ~~However,~~ these studies ~~did not include data collected near Western Australia but rather~~ were based on samples from ~~deep~~ open oceanic regions or a ~~local~~ regional eutrophic continental margin. We, therefore, assessed whether relationships between surface and water column-integrated chlorophyll values were similarly present in waters of Western Australia for potential use in habitat models. ~~In addition, the euphotic zone in these studies was defined as the depth over which Photosynthetically Active Radiation (PAR) decreases to 1% of its surface value ($Z_{1\%}^{PAR}$), which may underestimate the biological compensation depth at which the rate of photosynthesis equals that of autotrophic respiration and, thus, the depth of the productive layer (Wu et al., 2021). Consequently, regression analyses restricted to $Z_{1\%}^{PAR}$ may exclude biologically important DCMs.~~

~~This study aimed to assess whether depth-integrated chlorophyll can be estimated from surface chlorophyll levels measured over the intermittent oligotrophic continental margin of Western Australia, focusing on the area between 27.5° S and 33.8° S where the Perth Canyon lies. For such an assessment to be of value to future inferences of phytoplankton productivity (e.g., hotspots or anomalous productivity events) from satellite-derived surface chlorophyll data, it is imperative to ensure that depth-integrated values capture DCMs and that satellite remote sensing accurately reflects in situ conditions. While previous studies have touched on these topics, they were either spatiotemporally restricted or based on discontinued satellite data (i.e., SeaWIFS, concluded in 2010; Koslow et al., 2008). Hence, this study assessed temporal patterns in water column stratification, DCM formation, and DCM characteristics (i.e., type, depth, width); analysed the relationship between surface and depth-integrated chlorophyll values; and validated satellite-derived against in situ chlorophyll measurements.~~

2 Methods

2.1 In situ ~~chlorophyll~~ ocean glider data retrieval

We ~~obtained~~ downloaded ~~two in situ chlorophyll data sets~~in situ ocean glider data from~~through~~ the Australian Ocean Data Network (AODN) portal. Data were collected between 21 June 2008 and 12 July 2022 by the Integrated Marine Observing System's Australian National Facility for Ocean Gliders (IMOS-ANFOG; IMOS, 2023)~~ for~~ within an area extending from 27.5° S to 33.8° S and 109.7° E to 115.4° E (Fig. 1). Within this area, the Perth Canyon is located at ~32° S. Ocean glider missions were conducted each year but with varying intensity between years and concentrated around the continental shelf, shelf break, and deeper waters surrounding the Perth Canyon (see Supplementary Fig. S1 and S2 for illustrations of temporal and spatial coverage). Consequently, after the filtering process described below and in Sections 2.2 and 2.3, the data were spatially clustered between 31.6° S to 32.1° S and 114.9° E to 115.3° E, collected between 25 July 2008 and 13 December 2021, and obtained from waters with a mean water depth of 422 m (Fig. 1). All ocean gliders were equipped with a Sea-Bird Conductivity-Temperate-Depth sensor (CTD: models CTD41CP, GPCTD, or SBE_CT) and a WET Labs ECO Puck optical sensor pack (models BBFL2S, BBFL2VMT, FLBBCDSLK, or FLBBCDSLC), including a fluorometer and backscattering sensor (650-700 nm, 117° centroid angle). All downloaded data were pre-processed and quality-controlled by IMOS, which included the conversion of raw sensor counts into chlorophyll and particle backscatter coefficient (bbp) parameters with instrument-specific calibration coefficients and dark count values (Mantovanelli and Thomson, 2016; Woo and Gourcuff, 2023). Chlorophyll dark count values were corrected for any mission with >1% of negative values (Woo and Gourcuff, 2023). Quality control processes included automatic sensor drift corrections; automatic flagging of impossible location, date, and range values; manual flagging of measurements affected by biofouling or sensor malfunction; and manual flagging of near-surface measurements (<0.5 m). ~~One set comprised chlorophyll fluorescence data obtained with ocean gliders between 21 June 2008 and 12 July 2022 by the Integrated Marine Observing System's Australian National Facility for Ocean Gliders (IMOS-ANFOG; IMOS, 2023). The second set comprised chlorophyll concentration data obtained via High Performance Liquid Chromatography (HPLC) between 17 August 2002 and 24 May 2019, and which are collated in the chlorophyll-a database of Australian waters (Davies et al., 2017, 2018). We restricted both datasets to samples collected between 04 July 2002 and 21 June 2022. Bathymetry data were extracted from the Australian bathymetry and topography grid (Whiteway, 2009), and all samples from waters <100 m deep were discarded to ensure only data from case 1 waters were included (i.e., water in which optical properties are driven by phytoplankton presence; Morel and Prieur, 1977). All data were processed~~Further data processing was done in MATLAB (Version 2022b; The MathWorks Inc., 2022), while statistical analyses were performed in R and RStudio Statistical Software (V4.2.0 and V2023.03.0, respectively; R Core Team, 2022).

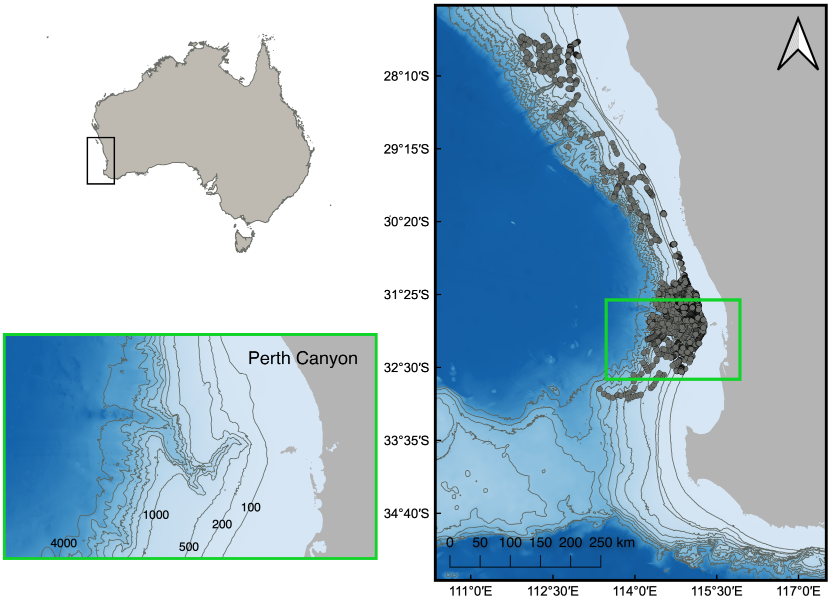

Figure 1: Ocean glider night-time vertical profile samples (grey circles) collected between the 100 m and 3000 m bathymetry contour lines off southwestern Australia, with the Perth Canyon situated at 32° S (within green square). Bathymetry contour lines delineate isobaths at 100 m, 200 m, and 500–4000 m in 500 m increments.

2.2 Ocean glider depth profile extraction

Information extracted from ocean glider data samples included UTC date and time, latitude (DD), longitude (DD), sampling depth (m), chlorophyll concentration (mg m^{-3}), temperature (°C), practical salinity (‰), pressure (dbar)~~, and~~ profile phase (i.e., descent, inflexion, or ascent), and~~. W~~ where available, particle backscattering coefficient data (m^{-1}).~~ were also extracted.~~ We filtered ocean glider data based on IMOS quality control flags to retain data points of which each variable was flagged as good data, probably good data, value adjusted by the quality control centre, or interpolated value (i.e., flags 1, 2, 5, and 8, respectively; Woo and Gourcuff, 2023). ~~We then interpolated d~~Data were interpolated between each decent and subsequent ascent phase to extract one vertical profile to the deepest recorded depth. Only profiles with at least one observation within the first 10 m of the water column ~~and at least four samples at different depths~~ were retained (Uitz et al., 2006). We~~Finally, we~~ then calculated the sun's angle relative to the horizon for each profile with the *suncalc* R-package (Thieurmel and Elmarhraoui, 2022) and removed all~~. Only~~ profiles obtained with the sun ~~below~~ above the horizon (i.e., day-time profiles) ~~were included in~~ from further analyses to avoid underestimating surface chlorophyll concentrations because of non-photochemical quenching (Roesler and Barnard, 2013). Finally, bathymetry data extracted from the Australian bathymetry and topography grid (Whiteway, 2009) were used to omit all samples from waters <100 m and >3000 m deep. This was done to ensure that data analyses were focussed on a section of the continental margin over which pygmy blue whales have been observed (McCauley et al., 2004; Double et al., 2014; Thums et al., 2022). After this initial filtering process, 21303 profiles were kept for further processing.

2.3 Temporal patterns in water column conditions

The prevalence of DCMs and~~ the~~ relationship between surface and depth-integrated chlorophyll concentrations differ between~~in~~ mixed and stratified water columns (Morel and Berthon, 1989; Uitz et al., 2006; Cullen, 2015). ~~Thus, we~~ We therefore split profiles between mixed and stratified water conditions based on the euphotic zone depth (i.e., $Z_{eu} = Z_{1\%}^{PAR}$; see Table 1 for a list of symbols) and~~ the~~ mixed layer depth (MLD~~Z_{mld}~~) as positive values below the surface. Following Uitz et al. (2006), we classified waters as mixed when Z_{eu}<MLD~~Z_{mld}~~ and stratified when Z_{eu}>MLD~~Z_{mld}~~. The euphotic zone depth for each profile was derived from the vertical chlorophyll distribution by progressive trapezoidal integration of chlorophyll over depth (Z; Morel and Berthon, 1989). For each sampling depth (Z_i), we converted depth-integrated chlorophyll concentrations to euphotic zone depth with formulae in Morel and Maritorena (2001) until $Z_{eu}<Z_i$ (Morel and Berthon, 1989). The exact euphotic zone depth was then calculated by interpolating Z_{eu} between Z_i and Z_{i-1} to find where Z equalled Z_{eu} (Morel and Berthon, 1989). Profiles that did not ~~cover~~ reach the euphotic zone depth were discarded, leaving 8486 profiles for statistical analyses.

Table 1: List of symbols used in this study and their denotation.

Symbol	Denotation	Unit
Bbp_{max}	Maximum particle backscattering coefficient within 20 m of the deep chlorophyll maximum.	m^{-1}
Bbp_{min}	Minimum particle backscattering coefficient within the top 15 m of the water column.	m^{-1}
Chl_{HPLC}	Average chlorophyll concentration within the top 10 m of the water column obtained from High-Performance Liquid Chromatography analyses of in situ water samples.	mg m^{-3}
Chl_{max}	Maximum chlorophyll concentration within the top 300 m of the water column.	mg m^{-3}
Chl_{MODIS}	Surface chlorophyll concentration retrieved with the OCI algorithm from ocean colour measurements by MODIS-aqua.	mg m^{-3}
Chl_{zeu}	Total chlorophyll concentration integrated over the euphotic layer.	mg m^{-2}
Chl_{zeu2}	Total chlorophyll concentration integrated over twice the euphotic layer depth.	mg m^{-2}
Chl_{zpd}	Average chlorophyll concentration within the first optical depth.	mg m^{-3}

DCM_{width}	Width of the deep chlorophyll maximum; calculated as the difference in depth between the shallow- and deep half-peak depths.	m
Z	Depth below the water surface (positive).	m
$Z_{1\%}^{PAR}$	Depth at which the Photosynthetically Active Radiation (PAR) is 1 % of its surface value.	m
Z_{DCM}	Depth of Chl_{max}.	m
Z_{DCM50d}	Closest depth to Z_{DCM} at which chlorophyll concentration decreased to 50 % of Chl_{max}; deep half-peak width.	m
Z_{DCM50u}	Closest depth to Z_{DCM} at which chlorophyll concentration increased to 50 % of Chl_{max}; shallow half-peak width.	m
Z_{eu}	Bottom depth of the euphotic layer (in this study equal to $Z_{1\%}^{PAR}$).	m
MLD~~Z_{mld}~~	Bottom depth of the water column mixed layer.	m

Raw temperature, salinity, and pressure data were converted to potential temperature and density values with the Gibbs-SeaWater (GSW) Oceanographic Toolbox (IOC et al., 2010; McDougall and Barker, 2020) to calculate the mixed layer depth. Here, we define the mixed layer depth as the first depth at which either the potential temperature differed by 0.2 °C from the reference potential temperature or the potential density exceeded the reference potential density by 0.03 kg m^{-3}, with samples taken at 10 m depth as reference values (de Boyer Montégut et al., 2004; Boettger et al., 2018).~~ Samples taken at 10 m depth were used as reference values (Boettger et al., 2018).~~

2.4 Temporal patterns in DCM presence, classification, and characteristics

Cornec et al. (2021) identified values and depths of maximum chlorophyll and particle backscatter coefficient data from smoothed vertical profiles before locating the nearest equivalent maximum chlorophyll (Chl_{max}) and particle backscatter coefficient (Bbp_{max}) on the unsmoothed profiles. Maxima values from the unsmoothed profiles were then compared to values over the top 15 m to identify whether a DCM was present (i.e., Chl_{max} exceeded twice the median chlorophyll concentration in the top 15 m) and whether a DCM was a DBM (i.e., Bbp_{max} exceeded 1.3 times the minimum particle backscattering coefficient in the top 15 m) or a DAM. Our methods followed those of Cornec et al. (2021) with a minor modification to the smoothening process. Chlorophyll profiles were smoothened with a 5, 7, or 11-point moving median corresponding to median profile depth resolutions of ≥3 m, <3 m but >1m, and ≤1 m, respectively (Schmechtig et al., 2023). Particle backscatter coefficient profiles were smoothed with an 11-point moving median, followed by an 11-point moving mean. The depth of Chl_{max} (Z_{dcm}; DCM peak depth), shallow half-peak depth (Z_{dcm50u}), and deep half-peak depth (Z_{dcm50d}) were also extracted. The DCM width (DCM_{width}) was calculated as the depth range between the shallow and deep half-peak depths (i.e., $Z_{dcm50d} – Z_{dcm50u}$). Trends in the position of the DCM peak and width relative to the euphotic zone were assessed by calculating their relative positions as Chl_{max}/Z_{eu} and Z_{dcm50d}/Z_{eu}, respectively, where values <1 were indicative of a peak chlorophyll value or full half-peak width within the euphotic zone.~~Identification and classification of DCMs for individual profiles followed methods in Cornec et al. (2021), so we only briefly describe the methods here. We assumed a DCM was present if the maximum chlorophyll concentration (Chl_{max}) within the top 300 m exceeded twice the median chlorophyll concentration over the first 15 m (Cornec et al., 2021). For each DCM, we extracted the depth of Chl_{max} (Z_{dcm}; DCM peak depth), the shallow half-peak depth (Z_{dcm50u}), and the deep half-peak depth (Z_{dcm50d}). The half-peak width (DCM_{width}) was subsequently calculated as the depth range between the shallow and deep half-peak depths (i.e., $Chl_{max} \pm 0.5 \times Chl_{max}$; Li et al., 2022). Trends in the position of the DCM relative to the euphotic zone were assessed by calculating the relative DCM depth as Z_{dcm50d}/Z_{eu}; values <1 indicate that the full half-peak width fell within the euphotic zone. Where backscattering coefficient data were available, the maximum backscattering coefficient (Bbp_{max}) within 20 m of the DCM was compared to the minimum backscattering coefficient (Bbp_{min}) in the top 15 m (Cornec et al., 2021). When Bbp_{max} exceeded 1.3 times Bbp_{min}, we assumed the DCM was a DBM. Otherwise, the DCM was considered a DAM.~~

2.5 Relationships between surface and water column~~(deep) depth~~-integrated chlorophyll

Relationships between surface and water column~~depth~~-integrated chlorophyll concentrations were assessed based on methods described in earlier publications (Morel and Berthon, 1989; Uitz et al., 2006; Frolov et al., 2012). We calculated surface chlorophyll values—assumed measurable by satellite—as the average chlorophyll concentration over the first optical depth (i.e., Chl_{zpd}; Uitz et al., 2006), where the first optical depth refers to $Z_{eu}/4.6$ (Gordon and McCluney, 1975). Since $Z_{1\%}^{PAR}$ may underestimate the biological compensation depth at which the rate of photosynthesis equals that of autotrophic respiration and thus, the depth of the productive layer, we integrated chlorophyll concentrations via trapezoidal integration over the euphotic zone (i.e., depth-integrated chlorophyll; Chl_{zeu})~~Depth-integrated chlorophyll concentrations were calculated over the euphotic zone (Chl_{zeu}; hereafter referred to as “depth-integrated chlorophyll”)~~ and where possible, twice the euphotic zone depth (~~Chl_{zeu2};~~ hereafter referred to as “deep depth-integrated chlorophyll”; Chl_{zeu2})~~ with trapezoidal integration~~. The latter differs from Uitz et al. (2006), who~~ only~~ integrated chlorophyll over a maximum of one-and-a-half times the euphotic zone depth because preliminary analysis indicated that ~~only 60~~34.8 % of DCM half-peak widths ~~fell within that limit~~extended beyond that limit (see Supplementary Fig. S3 for a DCM full-width inclusion curve).

Relationships were quantified using~~with~~ linear regression analyses on $\log_{10}$ transformed data, conducted separately for mixed and stratified water conditions. Previous publications used two regression lines to quantify the relationship in stratified waters because of a change in slope at surface chlorophyll values ~1 mg m^{-3} (Morel and Berthon, 1989; Uitz et al., 2006; Frolov et al., 2012). While preliminary data analysis revealed a similar change in slope ~~for stratified waters ~~in this study, the~~is~~ change

~~in slope~~ appeared seasonal and related to a change in the shape of vertical chlorophyll profiles from ones with low surface chlorophyll values and a pronounced DCM to ones with higher surface chlorophyll values without a DCM (Fig. 2).~~;~~ T~~t~~hus, we carried out one regression analysis for stratified water conditions from September until April and one for stratified water conditions from May until August. For brevity, the two seasons will be referred to as summer-transition and mid-winter, respectively. We evaluated all models with the Mean Absolute Error (MAE) and bias metrics because of tailed distributions in model residual plots (Chai and Draxler, 2014; Seegers et al., 2018; Hodson, 2022). Both metrics were transformed from linear to multiplicative values for ease of interpretation (Seegers et al., 2018). The slope and intercept of the linear regression were ~~used to describe~~converted into a power-law regression to describe the non-linear relationship between non-transformed surface and ~~(deep) depth~~water column-integrated chlorophyll values~~ with a power law regression~~.

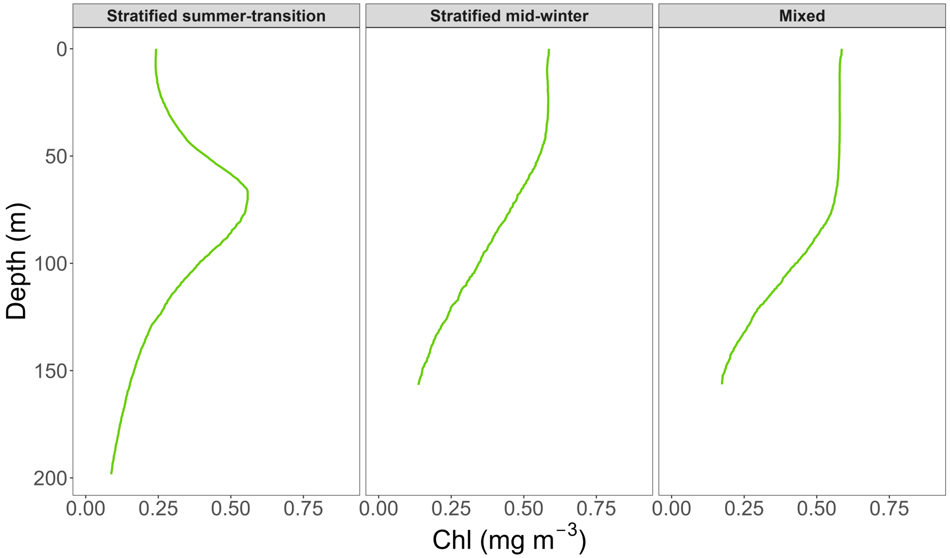

Figure 2: Median vertical chlorophyll profiles for (a) stratified summer-transition (September–April), (b) stratified mid-winter (May–August), and (c) mixed water conditions.

~~2.46 Satellite data match-up and validation~~

~~In situ measurements obtained with HPLC analysis were filtered to retain samples collected from the top 10 m of the water column (Sathyendranath et al., 2019). Replicated and depth profile samples were averaged to one measurement per station in time (i.e., Chl$_{HPLC}$). Further filtering included removing spurious values >1.8 mg m^{-3} that fell outside the typical range reported for this area (i.e., ≤1 mg m^{-3}; Lourey et al., 2006; Koslow et al., 2008; Thompson et al., 2011). Satellite-derived chlorophyll concentrations (i.e., Chl$_{MODIS}$) were extracted from data collected with the NASA Moderate Resolution Imaging~~

~~Spectroradiometer onboard Aqua (i.e., MODIS-aqua[1]). Satellite values were derived using the OCI algorithm that applies the OC3M band-ratio algorithm for retrieval of $\mathrm{Chl_{MODIS}}>0.35$ mg m^{-3}, the band difference Color Index (CI) for retrieval of $\mathrm{Chl_{MODIS}}<0.25$ mg m^{-3}, and a weighted approach to retrieve $0.25\leq\mathrm{Chl_{MODIS}}\leq0.35$ mg m^{-3} (Hu et al., 2012, 2019; O'Reilly and Werdell, 2019).~~

~~Satellite data were validated against in situ data via a match-up process. The match-up process started by searching for level 2 (i.e., L2) satellite granules within the Earth Data Common Metadata Repository, based on in situ sampling locations and a 24 h threshold time difference. All candidate L2 files were extracted from the Ocean Biology Distributed Active Archive Center (OB.DAAC) with Ocean Color Science Software Processors (OCSSW) V2022.3 running in SeaDAS 8.3.0. The following step extracted a box of 3×3 pixels centred on the in situ sampling location and validated each pixel based on the viewing angle (i.e., ≤60°), solar zenith angle (i.e., ≤70°), and standard processing flags (i.e., no cloud cover, cloud shadow, sun glint, stray light, extreme top-of-atmosphere radiance, or atmospheric correction failure; Bailey and Werdell, 2006; Zibordi et al., 2009). Successful match-ups were identified as those with at least six valid pixels and a maximum spatial variability of 15 % around the mean (i.e., coefficient of variation ≤0.15; Bailey and Werdell, 2006).~~

~~We assessed the linear relationship between $\log_{10}$ transformed satellite and in situ chlorophyll values with a Reduced Major Axis (RMA) regression analysis with 9999 permutations from the *lmodel2* R-package (Legendre, 2018). Model errors were normally distributed but increased at the extremes, identifying the MAE and bias as suitable validation metrics (Chai and Draxler, 2014; Seegers et al., 2018; Hodson, 2022).~~

3 Results

3.1 Temporal patterns in water column conditions

We extracted 5543~~6438~~ and 2943~~3234~~ profiles from stratified and mixed water conditions, respectively. Stratified water conditions dominated over the warm late spring,~~ and~~ summer, and early autumn months (October–March; ~~>~~≥85 % of profiles), declining to <39~~5~~ % over May–July when mixed water conditions prevailed (Fig. 3b). Transition conditions were present in April, August, and September, with an approximate 50:50 occurrence of stratified and mixed water conditions. The change in prevailing water condition was predominantly caused by a deepening of the median mixed layer depth from 30.5 m (IQR 21.0 m) in February to 65.5 m (IQR 51.0 m) in July (Fig. 3c). In contrast, ~~shallowing of~~ the euphotic zone depth moved closer to the surface from a median of 73.3~~68.6~~ m (IQR 12.5 m~~SD 12.4; range 22.7–103.5~~) in ~~October–March~~December to 46.3~~53.0~~ m

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~~[1] NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group. Moderate-resolution Imaging Spectroradiometer (MODIS) Aqua Color Data; 2022 Processing. NASA OB.DAAC, Greenbelt, MD, USA; doi: https://doi.org/10.5067/AQUA/MODIS/L2/OC/2022~~

(~~SD 9.3; range 32.7–100.7~~IQR 10.9 m) in May~~–August~~ (Fig. 3c). ~~In contrast, the mean mixed layer depth deepened from 36.3 m (SD 19.2; range 10.5–161.5) to 62.5 m (SD 36.8; range 10.5–202.5), respectively.~~

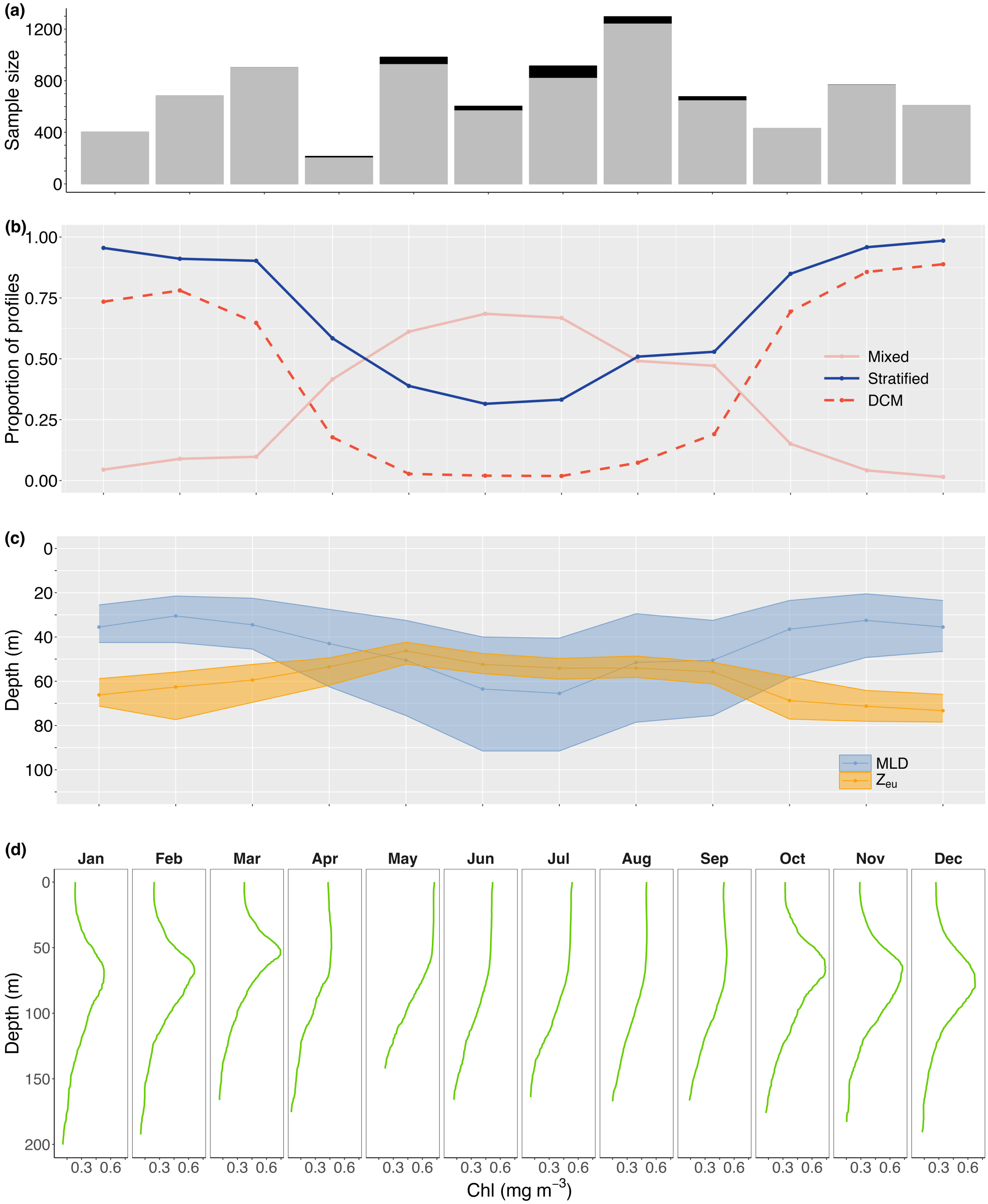


Figure 3~~1~~: Number of profiles extracted for each month (black bars) overlain with the number of profiles for which the mixed layer depth (MLD) was reached (grey bars; panel a). For each month, t~~T~~he proportion of ~~chlorophyll~~ vertical profiles ~~identified as~~

~~coming~~extracted from mixed (solid ~~grey~~pink line) and stratified (~~dashed~~solid blue~~ack~~ line) water conditions~~ for each month of the year~~ is provided in panel (b), along with the proportion of profiles characterised by a DCM (red dashed line; panel b) and the seasonal change in median (with 25th and 75th quartiles as shaded areas) euphotic zone (Z_{eu}) and mixed layer depth (c). Panel (d) shows the monthly median vertical chlorophyll profiles.~~. The density plot reflects the monthly profiles available, ranging from N = 214 to N = 1416 in April and August, respectively.~~

3.2 Temporal patterns in DCM presence, classification, and characteristics

DCMs were predominantly found in stratified water conditions (56.5 % of stratified profiles vs 3.3 % of mixed profiles; 3133/5543 vs 97/2943); thus, the seasonal presence of DCMs followed the seasonal pattern in water column stratification with peak presence from October until March (>64 %; Fig. 3b). However, despite stratification in at least 30 % of profiles in winter, DCMs practically disappeared in May–July (<3 % of profiles; Fig. 3b) changing the vertical chlorophyll distribution into a sigmoid shape (Fig. 3d). Overall, DCMs formed between the surface and 167.1~~78.4~~ m deep, at a median depth of 75.3~~6.5~~ m (IQR 29.3 m). ~~(SD 24.7).~~ However, median DCM depths varied seasonally with shallowing events in January (68.6 m; IQR 19.8 m), April (38.6 m; IQR 19.7 m), and September (65.4 m; IQR 38.4 m). Seasonal maxima depths were reached in February (75.2 m; IQR 32.3 m), July (95.9 m; IQR 130.8 m), and December (83.0 m; IQR 31.1 m), though DCMs in July appeared to either form close to the surface or at great depths (Fig. 4a). From June until December, there was an overall deepening trend during which the chlorophyll maximum moved further away from the mixed layer while remaining at an approximate constant relative distance from the euphotic zone (~1.1 times the euphotic zone depth; Fig. 4b). Median DCM half-peak widths concurrently narrowed (Fig. 4c), while the maximum chlorophyll concentration showed a modest increase (Fig. 4d). The exception to this trend was a brief shallowing to just above the bottom of the euphotic zone in September (0.99; IQR 0.45), characterised by a rapid increase in peak chlorophyll levels at the DCM. A contrasting shallowing trend can be discerned from December until April, positioning the chlorophyll maximum at a nearly constant relative distance from the bottom of the mixed layer (~2.0 times the mixed layer depth), but elevating the chlorophyll maximum to well within the euphotic zone in April (0.75; IQR 0.19). Despite this shallowing trend, DCMs remained of a similar width as in December and modest intensification of the chlorophyll maximum continued until a sudden deepening, widening, and weakening of the DCM in May.

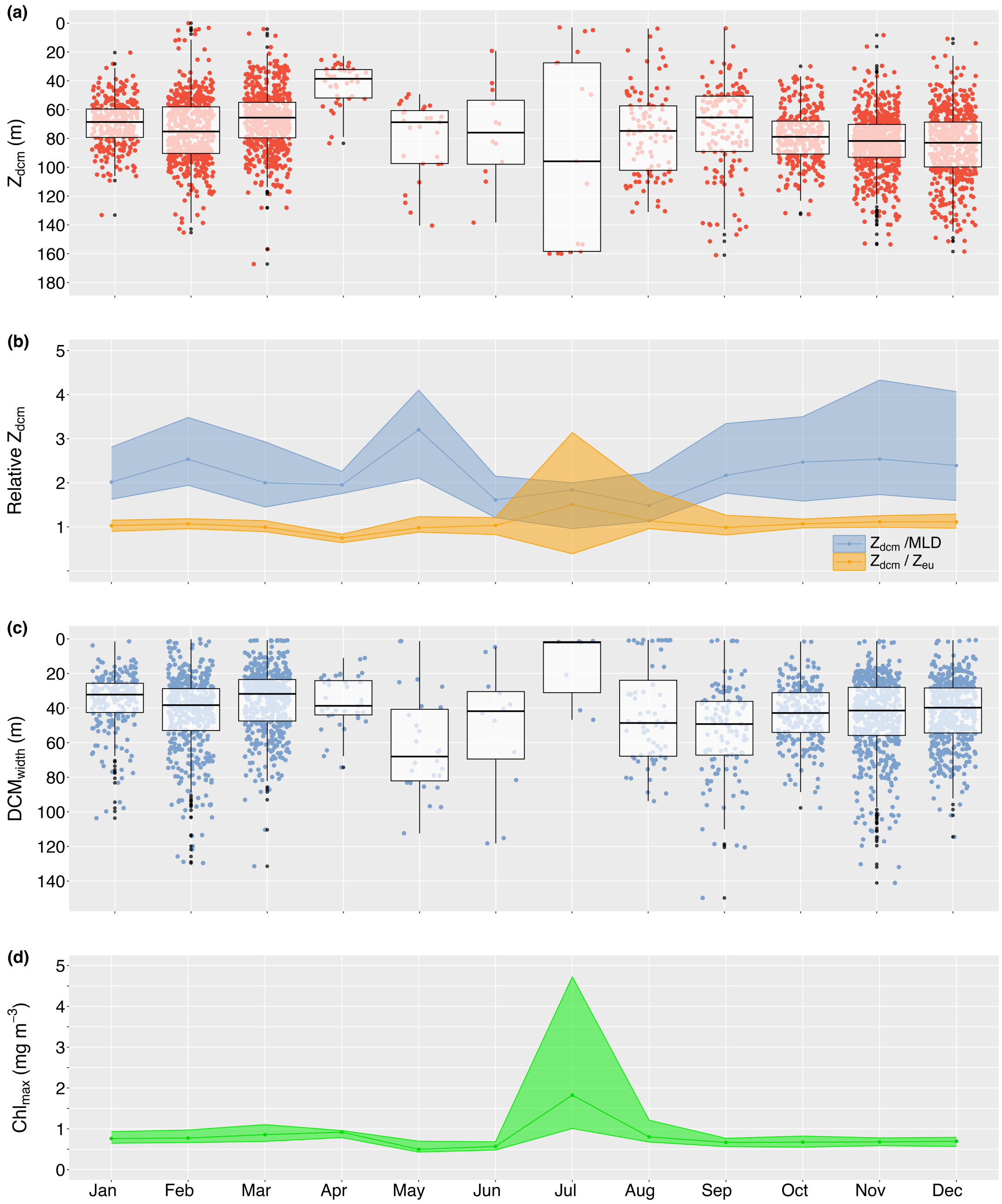


Figure 4~~2~~: Median monthly true DCM depth ~~of the Deep Chlorophyll Maximum~~ (Z_{dcm}; panel a~~black line~~) and relative depth in relation to the bottom of the mixed layer (Z_{dcm}/MLD) and euphotic zone (Z_{dcm}/Z_{eu}; panel b). Panel (c) and (d) reflect the seasonal change in DCM width and maximum chlorophyll concentration at the DCM. Shaded ribbons in panel (b) and (c) indicate the 25th and 75th quartiles. ~~in stratified water columns per month of the year with 95 % confidence intervals (grey boxes). All data points are plotted as open grey circles, with white violins indicating the data density distribution.~~

Particle backscatter data were available for 1551 profiles, of which 95.8 % were collected in September–March (1487/1551). Over this time, the proportion of DBMs gradually declined from 69.7 % in September to 46.2 % in January, which is also shown by a disproportional change in maximum particle backscatter and chlorophyll amplitudes (see Supplementary Fig. S4 for temporal patterns in DBM and DAM characteristics). As the DCM shallowed in late summer, DBMs became more prevalent again with a peak presence in March (81 %). However, the sudden deepening, widening, and weakening of the DCM in May pivoted DCM-type classifications to a prevalence of DAMs (70 %), which generally dominated in winter (i.e., 66.1 %). Overall, DAMs were moderately weaker, wider, and positioned deeper in the water column than DBMs; yet the position of the maximum chlorophyll relative to the euphotic zone depth remained within 1.2 times the euphotic zone depth.

~~DCMs were common in stratified water conditions (~60 % of profiles; 3892/6438), where the formation followed a seasonal trend. From October until March, >75 % of profiles were characterised by a DCM, reducing to <20 % from May until August. April and September were transition months in which 33 % and 47 % of stratified profiles had a DCM, respectively. Backscattering data were available for 1985 stratified profiles with a DCM, revealing that DBMs were more common over September–March (58–75 % of DCMs) than over May–August (23–38 % of DCMs). There was a weak seasonal trend in mean DCM depth, with a deepening from 40.5 m (SD 23.2; range 7.0–80.0) in July to 83.0 m (SD 24.4; range 4.5–158.6) in December (Fig. 2). The DCM moved closer to the surface in January–March (68.4–75.1 m), before occupying a more variable depth from April to July (i.e., mean depth changed between 40.5 m and 80.2 m: Fig. 2). This seasonal trend in DCM depth was observed for both DCM types, but DAMs lay deeper than DBMs year-round. Consequently, the mean overall depth of DAMs (83.0 m; SD 21.9; range 18.3–169.1) exceeded that of DBMs (75.4 m; SD 24.1; range 3.3–73.4). Similarly, DAMs were generally more expansive than DBMs (especially in May–July), as reflected by the mean half-peak widths of 55.3 m (SD 24.0; range 12.8–152.2) and 44.8 m (SD 24.9; range 0.5–143.1), respectively. Yet, regardless of DCM type, only 6 % of half-peak widths in stratified waters fell within the euphotic zone, increasing to 96 % when looking over twice the euphotic zone depth.~~

~~DCM formation in mixed water conditions was rare (~6 % of profiles; 195/3234), and profiles for which backscatter data were available revealed that these chlorophyll maxima were nearly always a DBM (91 %, 60/66). While DCMs in mixed water conditions were found at a variable depth (mean 83.0 m; SD 45.0; range 2.9–178.4), they were commonly thin (mean 19.4 m, SD 30.8, range 0.3–128.2). In fact, 66 % of all DCMs and 85 % of DBMs in mixed water conditions had a half-peak less than 5 m wide (i.e., DCM_{width}<5). DBMs were also more commonly found within the euphotic zone (55 %), while the limited observation of DAMs occurred mostly beyond the euphotic zone depth (80 %).~~

3.3 Relationships between surface and ~~(deep) depth~~water column-integrated chlorophyll

Surface chlorophyll concentrations (Chl_{zpd}) ranged between 0.04~~0~~ and 1.58~~6~~ mg m^{-3} (median 0.44~~8~~ mg m^{-3}, ~~SD 0.272~~IQR 0.38 mg m^{-3}), with marked seasonal changes (Fig. 5a). Monthly median surface chlorophyll values peaked in May (~~mean~~ 0.77~~58~~ mg m^{-3}, ~~SD 0.271~~IQR 0.37 mg m^{-3}; Fig. 5a), remained >0.5 mg m^{-3} in winter, but rapidly decreased over September to minimum median levels ~0.20 mg m^{-3} in November and December. A subsequent increase can be discerned for January (0.27

mg m^{-3}, IQR 0.13 mg m^{-3}), though values remained <0.33 mg m^{-3} throughout early autumn before rapidly transitioning to peak levels over April. ~~, with relatively higher levels maintained in winter (i.e., monthly means >0.5 mg m^{-3}; Fig. 3a). A modest secondary increase occurs in August after which surface chlorophyll levels decrease to means <0.4 mg m^{-3} in summer. April and September can be considered as transition months.~~ A similar seasonal pattern ~~can be discerned for~~was present in depth-integrated chlorophyll values, albeit less pronounced (Chl$_{zeu}$; Fig. 5b). Interestingly, monthly median deep depth-integrated chlorophyll similarly peaked in May (Chl$_{zeu2}$; 62.2 mg m^{-2}, IQR 17.3 mg m^{-2}) but a secondary increase can be discerned in August (53.9 mg m^{-2}, IQR 14.1 mg m^{-2}), after which levels declined less rapidly to the seasonal minimum in December (48.7 mg m^{-2}, IQR 9.2 mg m^{-2}; Fig. 5b). In January, deep-depth integrated chlorophyll increased more evidently than depth-integrated values and subsequently remained relatively constant from February until April (i.e., ~52.0 mg m^{-2}). Overall, chlorophyll below the euphotic zone depth accounted for 50–60% of deep depth-integrated values from October until March, declining to a minimum of 44 % in April, May, and July. ~~which ranged between 13.3 and 74.5 mg m^{-2} (Fig. 3b). Interestingly, while monthly mean deep depth-integrated chlorophyll similarly peaked in May (mean 61.5 mg m^{-2}, SD 13.6), the increase in August (mean 54.3 mg m^{-2}, SD 11.1) appears more pronounced and a third increase was present in January (mean 54.8 mg m^{-2}, SD 9.4; Fig. 3b).~~

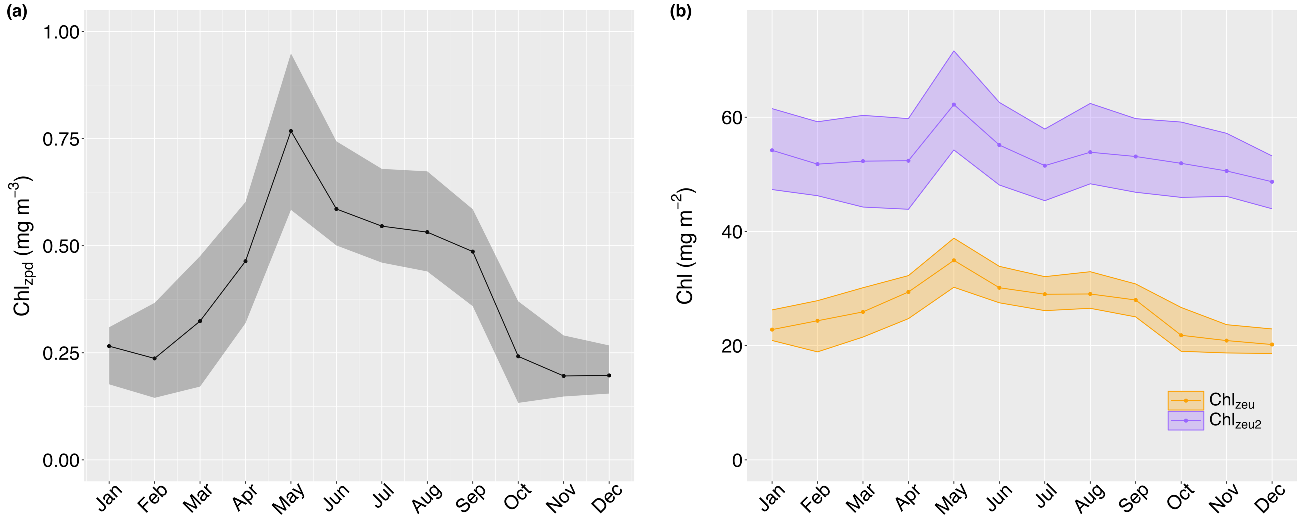


Figure 5~~3~~: Monthly median surface (Chl$_{zpd}$; panel a), depth-integrated (Chl$_{zeu}$; orange~~black~~ solid line in panel b) and deep depth-integrated (Chl$_{zeu2}$; ~~grey dashed~~purple solid line in panel b) chlorophyll values with their 25th and 75th quartiles as shaded areas. ~~Error bars represent the standard deviations to illustrate the data variation around the mean.~~

Profiles collected from stratified water conditions in summer-transition months showed a significant linear relationship between surface and depth-integrated chlorophyll concentrations (R^2 = 0.72~~3~~, F$_{(1,4002}$~~$_{574}$~~$_{)}$ = 10420~~2370~~, p<0.001; Fig. 6a). A stronger relationship with a steeper slope and less scatter was seen for the stratified mid-winter~~cooler~~ months (~~mid-winter;~~ R^2 = 0.87~~8~~, F$_{(1,1533}$~~$_{857}$~~$_{)}$ = 10080~~3400~~, p<0.001; Fig. 6b) and mixed water columns (R^2 = 0.97, F$_{(1,2940)}$ = 90400, p<0.001; Fig. 6c).

Scatter around the regression line resulted from the presence of DCMs with no apparent difference between the contribution of DBMs and DAMs. Thus, the mean relative error was highest (8.9 %; MAE = 1.089) for estimates of observed depth-integrated chlorophyll from surface chlorophyll values under stratified water conditions in summer-transition months, when DCMs were more common. Under stratified water conditions in winter and mixed water conditions, the mean relative error reduced to 5.6 % and 1.7 %, respectively (i.e., MAE: 1.056 and 1.017, respectively).~~Models estimated observed depth-integrated chlorophyll values with mean relative errors of 9.0 % and 6.0 %, respectively (i.e., MAE: 1.090 and 1.060, respectively).~~ Scatter in the data increased for deep depth-integrated values, resulting in a weak linear relationship in stratified summer-transition months (R^2 = 0.15~~22~~, $F_{(1,2729}$~~$_{3302}$~~$_{)}$ = ~~920~~498.5, $p<0.001$; Fig. 6d) and a moderate relationship in both stratified mid-winter months (R^2 = 0.48~~52~~, $F_{(1,1351}$~~$_{674}$~~$_{)}$ = 12321~~808~~, $p<0.001$; Fig. 6e) and mixed water columns ($R^2 = 0.63$, $F_{(1,2512)} = 4239$, $p<0.001$; Fig. 6f). As a result,~~. The~~ mean relative errors increased to 15.7~~6.3~~ %,~~, and~~ 15.2~~7~~ %, and 8.6 %, respectively. All~~The~~ derived non-linear relationships are summarised in Table 2.~~.~~

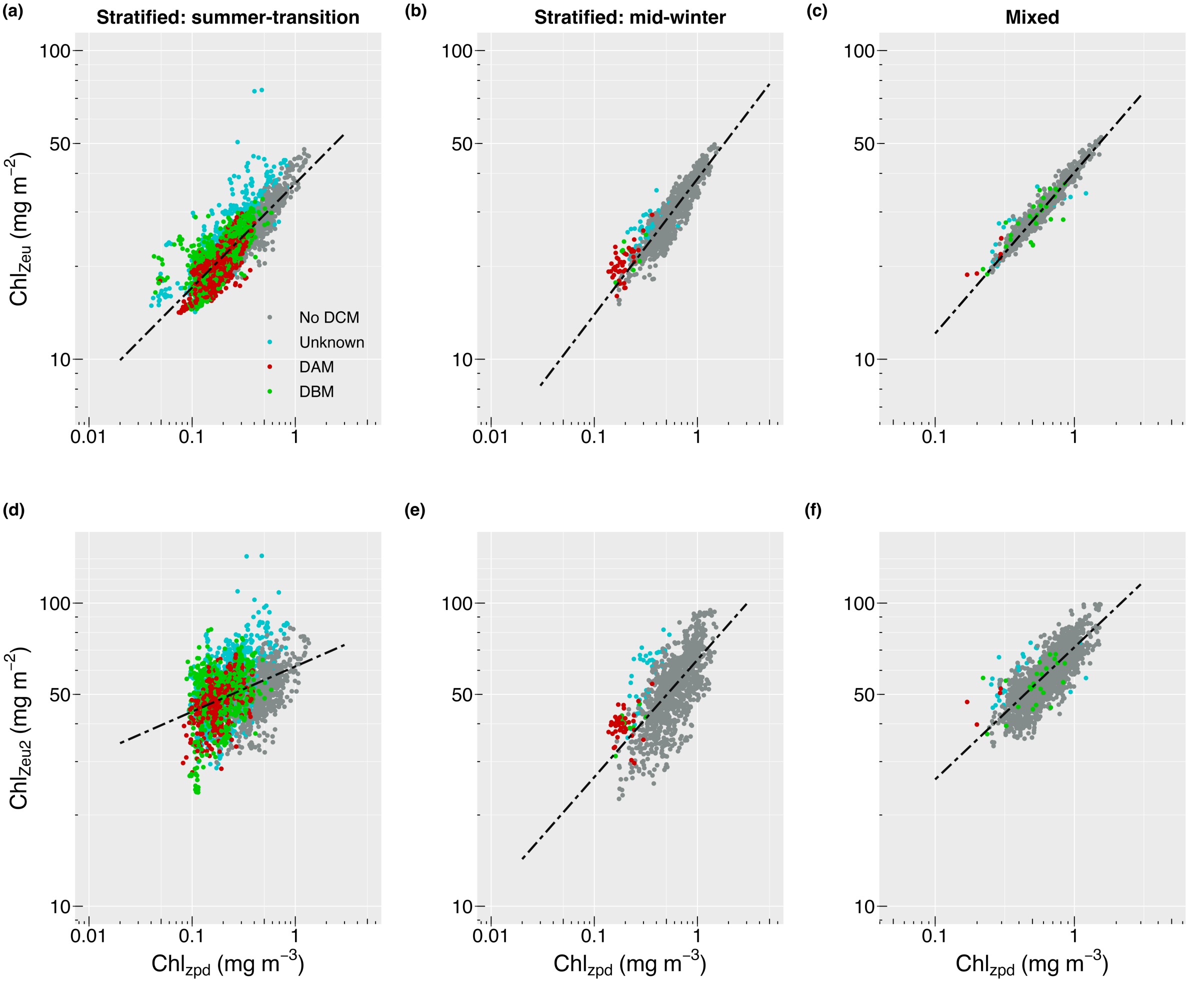


Figure 6~~4~~: Relationship between surface (Chl_{zpd}) and depth-integrated (Chl_{zeu}) vs. deep depth-integrated (Chl_{zeu2}) chlorophyll values for stratified water conditions in summer-transition months (i.e., September–April; a, d~~e~~), stratified water conditions in ~~and~~ mid-winter months (i.e., May–August; b, e~~d~~), and mixed water conditions (c, f) ~~in stratified waters~~. Dots are coloured according to whether a DCM was absent (grey), present but of unknown type (turquoise), a DBM (green), or a DAM (dark red).~~Red~~ Black dashed lines indicate the derived regression lines. Note the change in ~~the~~ y-axis range between panels a–c~~b~~ and d~~e~~–f~~d~~ and the change in x-axis range between stratified (Z_{eu}>MLD) and mixed water (Z_{eu}<MLD) conditions.

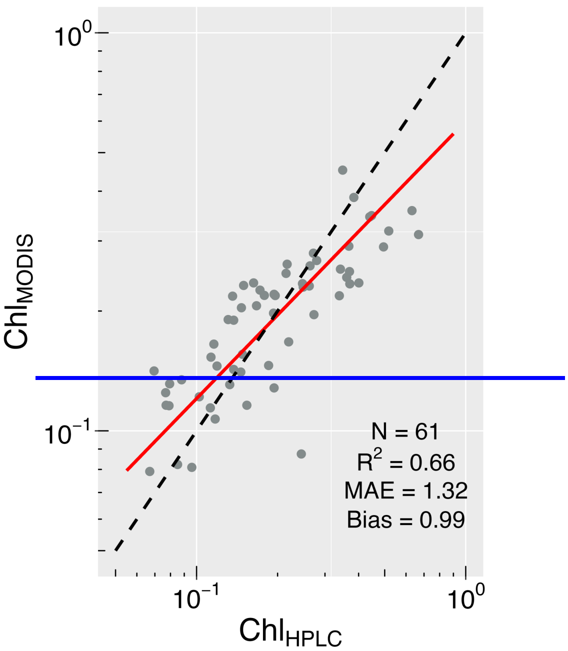
~~Profiles from mixed water conditions revealed a strong linear relationship between surface and depth-integrated values over the euphotic zone ($R^2 = 0.97$, $F_{(1,3230)} = 105700$, $p<0.001$; Fig. 5a). The slope was steeper than that observed in stratified water (i.e., 0.521 against 0.343 and 0.433; Table 2) and data were concentrated around the regression line, resulting in a low MAE of 1.018 (i.e., 1.8 % relative error) without bias. As for stratified water, scatter in the data increased for deep depth-integrated values, but a moderate relationship was still found ($R^2 = 0.65$, $F_{(1,2797)} = 5220$, $p<0.001$; Fig. 5b) with an increase in mean relative error to 8.6 %.~~

Table 2: Summary of non-linear relationships between surface (Chl_{zpd}) and depth-integrated (Chl_{zeu}) vs. deep depth-integrated (Chl_{zeu2}) chlorophyll under stratified and mixed water conditions. Relationships in stratified waters are given for both summer-transition (~~i.e.,~~ September–April) and mid-winter months (May–August).

Water condition	Integration depth	Regression	R^2	MAE	Bias
Stratified					
Summer-Transition	Z_{eu}	$\mathrm{Chl}_{zeu} = 37.1 \times \mathrm{Chl}_{zpd}^{0.3374\cancel{41}}$	0.72~~3~~	1.089~~90~~	1.00
Mid-Winter	Z_{eu}	$\mathrm{Chl}_{zeu} = 38.4\cancel{2} \times \mathrm{Chl}_{zpd}^{0.440\cancel{33}}$	0.87~~8~~	1.056~~0~~	1.00
Summer-Transition	Z_{eu2}	$\mathrm{Chl}_{zeu2} = 61\cancel{3}.84 \times \mathrm{Chl}_{zpd}^{0.149\cancel{82}}$	0.15~~22~~	1.157~~63~~	1.00
Mid-Winter	Z_{eu2}	$\mathrm{Chl}_{zeu2} = 65\cancel{3}.0 \times \mathrm{Chl}_{zpd}^{0.387\cancel{5}}$	0.48~~52~~	1.152~~7~~	1.00
Mixed					
Year-round	Z_{eu}	$\mathrm{Chl}_{zeu} = 40.3 \times \mathrm{Chl}_{zpd}^{0.522\cancel{1}}$	0.97	1.017~~8~~	1.00
Year-round	Z_{eu2}	$\mathrm{Chl}_{zeu2} = 71.54 \times \mathrm{Chl}_{zpd}^{0.436\cancel{3}}$	0.63~~5~~	1.086	1.00

~~3.4 Satellite data match-up and validation~~

~~We identified 61 valid match-ups under the 24 h time-difference threshold, with in situ chlorophyll measurements ranging between 0.07 and 0.67 mg m^{-3}. The RMA regression confirmed a positive relationship between satellite and in situ data with scatter around the regression line ($R^2 = 0.66$; Fig. 6). The OCI algorithm predicted satellite values on average within 32 % accuracy of observed measurements (MAE = 1.32). While an overestimation in satellite values can be discerned at $\mathrm{Chl}_{HPLC}<0.17$ mg m^{-3}, the OCI algorithm underestimated measured chlorophyll on average by 1 % (bias = 0.99).~~



~~**Figure 6: Chlorophyll data derived from MODIS-aqua with the OCI algorithm (Chl$_{MODIS}$) plotted against in situ chlorophyll measurements obtained with HPLC analyses (Chl$_{HPLC}$). Reduced Major Axis (RMA; red line) and 1:1 ratio (black dashed line) visualise the error trend.**~~

4 Discussion

4.1. Seasonality in water column characteristics and DCM formation

The marine environment of Western Australia is governed by the warm poleward-flowing Leeuwin Current of tropical origin, with signatures from the higher salinity subtropical Indian central waters (Waite et al., 2007; Woo and Pattiaratchi, 2008). Because of generally low surface chlorophyll values beyond the continental shelf and a broad winter increase in surface chlorophyll from May until September, Western Australian waters are often labelled as oligotrophic (e.g., Twomey et al., 2007; Feng et al., 2009; Rennie et al., 2009a; Chen et al., 2019) with a surface productivity regime comparable to subtropical gyres (Koslow et al., 2008). These subtropical areas are characterised by either permanently stratified water columns or brief (~1 month) mixing periods, resulting in a (near) permanent DCM presence (Mignot et al., 2014; Quartly et al., 2023). Our results show that stratification in winter (May–August) is intermittent and that DCM formation is the exception rather than the norm (i.e., <3% of profiles). The disappearance of DCMs from vertical profiles corresponds to a period of intense Leeuwin Current strength, which is known to weaken stratification (i.e., May–July; Koslow et al., 2008; Feng et al., 2003, 2009). In addition, north-westerly down-welling favourable storms (wind speeds >15 m s^{-1}; most frequent June–August) and concomitant surface cooling mix the water column down to 200 m depth, breaking down the stratified layer and DCM (Rennie et al., 2006; Chen et al., 2020). While re-stratification has been shown to occur during subsequently calm post-storm south-westerly winds (wind speeds <7 m s^{-1}; Rennie et al., 2006), our data reveal that these re-stratification periods often do not persist long enough for DCMs to reform. This is likely because of the additive effect of increased eddy kinetic energy, which peaks in July (Feng et al., 2005). Warm-core eddies, in particular, are frequent in late autumn and winter between 28° and 31° S, generating well-mixed layers extending beyond the euphotic zone depth (Thompson et al., 2007; Waite et al., 2007). Consequently, our area experiences a mixing period of approximately three months, which is more comparable to the duration of mixing periods in the Mediterranean (Mignot et al., 2014; Barbieux et al., 2019) and oligotrophic sub-tropical open oceans (Chiswell et al., 2022).

4.2. DCM characteristics

Leeuwin Current strength significantly drops (Feng et al., 2003) and winter storms settle in September (Pearce et al., 2015), which is when stratified water columns return. However, eddy kinetic energy remains persistent (Feng et al., 2009). Warm-core eddies have been hypothesised to allow late winter/early autumn phytoplankton blooms through the injection of nitrogen into surface waters (Lourey et al., 2013) and the formation of a shallow nutricline (~60 m depth) under a relaxed Leeuwin Current after eddies detach from the shelf (Koslow et al., 2008). Our data supports this hypothesis with a reappearance of DCMs in September at a median depth of 65.4 m, which were predominantly biomass maxima. The subsequently observed deepening of the DCM through spring and summer is common for oligotrophic regions (Mignot et al., 2014; Chiswell et al., 2022). In our study area, as the DCM deepened and intensified, backscatter vertical profiles changed disproportional to chlorophyll vertical profiles, reflecting the decreased occurrence of DBMs until biomass and photo-acclimation maxima occurred in approximately equal proportions from December until February. DCM formation is always at least in part caused by photo-acclimation of phytoplankton to low light conditions (Cullen, 2015) but deep DCMs in summer may approach the nutricline, allowing for phytoplankton growth and thus, DBM formation (Mignot et al., 2014). DCM settlement within a nearly constant distance from the euphotic zone depth (i.e., ~1.1 times the euphotic zone depth), regardless of DCM type, suggests photo-acclimation processes in response to light limitation as the main driver of DCM formation from September until late summer. However, the balanced presence of photo-acclimation and biomass maxima in our study indicates that access to nutrients is indeed available throughout summer. These findings fit the equal occurrence of upwelling and downwelling days detected in temperature time series by Rennie et al. (2006) and positioning of the summer DCM just above the nutricline in earlier studies (e.g., Hanson et al., 2007a, 2007b; Koslow et al., 2008). In addition, Rennie et al., (2006) detected a concentration of upwelling events in late February–early March, which temporally matches with an initial weakening of stratification as the Leeuwin Current starts to intensify (Feng et al., 2003; Koslow et al., 2008) and in our study, with the timing of DCM shallowing, intensification, and a rapid increase in biomass maxima. Thus, while the DCM formation is first-order light-driven, nutrient limitation in the upper water column in autumn and at depth in summer likely drives the balance between biomass and photo-acclimation maxima until upwelling and increased water turbidity potentially synergistically increase nutrient levels within the bottom layer of the euphotic zone. Our results suggest that DCMs in Western Australian waters form via bio-optical mechanisms that match neither pattern observed in subtropical oceanic (Mignot et al., 2014; Chiswell et al., 2022; Quartly et al., 2023) and more productive temperate regions (Mignot et al., 2014; Barbieux et al., 2019), but instead are similar to the mid-Mediterranean Sea, which forms a transition between the meso-oligotrophic western and oligotropic eastern basins (Barbieux et al., 2019). However, a broad-scale long-term study, including nutrient and irradiance parameters, is required to elucidate our hypothesis.

4.3. Water column-integrated productivity

Seasonal surface chlorophyll fluctuations followed the commonly observed pattern of a winter surface chlorophyll increase, albeit our observed peak in May proceeding the June–July winter bloom previously described by Lourey et al. (2006) and Koslow et al. (2008). This shift could be related to changing trends in environmental and oceanographic drivers. Long-term data series from IMOS national reference stations around Australia have shown, for example, that mixed layer and euphotic zone depth follow an overall deepening trend from 2008 to 2018 by 1.02 m yr^{-1} and 1.7 m yr^{-1}, respectively (van Ruth et al., 2020). The seasonal pattern in depth-integrated chlorophyll levels showed a flatter annual cycle but remained largely similar in shape. This flattening originates from the inclusion of DCMs in depth-integrated values in summer. Since DCMs predominantly formed below our defined euphotic zone depth, contributing >50 % to water column integrated values in summer, the seasonal cycle diminished even further when integrating over twice the euphotic zone depth (i.e., deep depth-integrated chlorophyll). Interestingly, deep-depth integrated values showed chlorophyll increases in May, August, and January, which correspond to previously identified temporal peaks in water-column integrated net primary productivity (Koslow et al., 2008), albeit again with an apparent one-month advance. These findings support our hypothesis that deep-depth integrated values may be a better predictor variable to include in marine animal habitat models for ocean regions where DCMs are present. However, there are currently no means to include water column-integrated chlorophyll levels in habitat models that aim to relate large spatiotemporal animal presence data sets with environmental variables such as chlorophyll. While ocean glider and biogeochemical-Argo float datasets have greatly advanced our ability to study subsurface biogeochemical processes, the spatiotemporal extent of these data often does not align with animal presence data from land-based, boat-based, and underwater acoustic platforms. It is, therefore, pivotal to develop our knowledge of potential methods that facilitate depth-integrated chlorophyll estimates from openly available data sources, such as satellite remote sensing.

The lack of existing methods and presence of a DCM with potential importance to migrating locally endangered pygmy blue whales was the main driving factor for us to assess whether known relationships between surface and depth-integrated chlorophyll in open ocean and mesotrophic regions (Morel and Berthon, 1989; Uitz et al., 2006; Frolov et al., 2012), were also present in the unique marine environment of Western Australia. Our results confirm that similar relationships are present within the nutrient-deprived western boundary current system of Western Australia, albeit with a replacement of the traditional two-part regression line for stratified water columns with a seasonally dependent regression line. T~~he~~his seasonal change~~s in the functional relationships between surface and depth-integrated chlorophyll~~ reflects the seasonal patterns in water stratification and DCM formation. Low surface chlorophyll levels and deeper DCMs characterised the stratified water column in summer-transition months, while alternating periods of increased winter mixing and weak re-stratifications from May until August predominantly break down the DCM.~~. These deeper DCMs are likely less intense (Cornec et al., 2021), explaining the relatively gentle regression slope (0.341). Conditions changed with the onset of a phytoplankton surface bloom in May, which is distinct for our study area (e.g., Koslow et al., 2008; Chen et al., 2020) and marks the start of the mid-winter season during which mixed and stratified water conditions alternate.~~ Graff and Behrenfeld (2018) found that deep water entrainment followed by re-stratification in the North Atlantic rapidly increased surface chlorophyll (and phytoplankton biomass) over three days post-entrainment event, while chlorophyll decreased at a much slower rate at depth. Hence, changes in surface chlorophyll contributed more strongly to changing depth-integrated values. The sigmoid vertical chlorophyll profiles in winter suggest that s~~S~~imilar processes may be at play during ~~post-storm~~calm winter periods in our study area, accounting for the steeper slope derived from stratified water profiles in mid-winter (i.e., 0.440~~33~~). The strong relationship with an even steeper slope (0.522~~1~~; $R^2 = 0.97$) and little error in mixed water conditions reflect~~s~~ the even more extensive homogenous vertical distribution of chlorophyll present under these conditions (Morel and Berthon, 1989; Uitz et al., 2006). Extending chlorophyll integrations to twice the euphotic zone depth showed similar functional relationships, albeit with a higher MAE, especially in summer-transition months. Scatter in the data at low surface chlorophyll values was predominantly attributable to the inclusion of full DCM widths in deep depth-integrated values, confirming earlier statements by Morel and Berthon (1989) and Uitz et al., (2006). However, despite the increased scatter, ~~,~~the MAEs for relationships over twice the euphotic zone depth remained low for all three conditions (i.e., 16.3 %, 15.7 %, and 8.6 %).

4.4. From water column-integrated chlorophyll estimates to whales

Potential links between the physical oceanography, biogeochemical processes, and pygmy blue whale presence in the Perth Canyon have been studied previously (Rennie, 2005). Based on numerical models (Rennie et al., 2009b), moored temperature time series analyses (Rennie et al., 2006), and in situ data collection during oceanic cruises (Rennie et al., 2009a), Rennie and co-authors hypothesised that winter productivity supports the local krill population through spring with sporadic summer upwelling events allowing krill to grow to an appropriate size for whale consumption from February onward (Rennie et al., 2009a). Indeed, food availability is a crucial driver of Euphausiid health (i.e., lipid content; Fisher et al., 2020; Hellessey et al., 2020; Steinke et al., 2021), timing of reproduction (Quentin and Ross, 2001; Schmidt et al., 2012), hatching success (Yoshida et al., 2011; Steinke et al., 2021), and growth rate (Bahlburg et al., 2023). Thus, a regular supply of phytoplankton prey seems crucial for population maintenance. In addition, b~~B~~aleen whales show a preference for krill >16 mm (Croll et al., 2005; Cade et al., 2022)~~. and~~ C~~c~~onsequently, peak abundances of foraging baleen whales reportedly lag the onset or peak intensity of phytoplankton blooms by ~~one to four~~1–4 months (Croll et al., 2005; Visser et al., 2010). In the absence of a defined sub-surface chlorophyll bloom and instead a consistent balanced presence of photo-acclimation and biomass maxima, we believe that our results are in support of continuous krill population maintenance through DCM formation in summer. However, rather than the winter surface bloom, we suggest that an increase in productivity at the DCM around September (i.e., early spring) sets the scene for krill maintenance through summer and a sufficient prey abundance for arriving foraging pygmy blue whales ~4 months later. In addition, the sudden increased presence of biomass maxima in March may be a crucial feature in support of pygmy blue whale foraging efforts throughout autumn and early winter or alternatively, support a new spawning event (e.g., Paul et al., 1990; Feinberg and Peterson, 2003; Plourde et al., 2011).

4.5. Future habitat models and potential pitfalls

Based on our results and in the absence of other means to include high spatiotemporal resolution subsurface chlorophyll data, we encourage the use of water column-integrated chlorophyll (over twice the euphotic zone depth) estimates from satellite remote sensing in future marine animal habitat models. Of course, we acknowledge challenges related to potential regression biases and the translation from fluorescence-derived relationships to satellite-derived estimates. Besides scatter in the regression line being caused by DCM presence, there are other sources of potential bias that deserve further investigation. For instance, we may have introduced additional scatter in our regression lines with our definition of the euphotic zone depth as $Z_{1\%}^{PAR}$ and simple extension to "twice the euphotic zone depth". At low- and mid-latitudes specifically, $Z_{1\%}^{PAR}$ likely underestimates the compensation depth and so, $Z_{0.5\%}^{PAR}$, $Z_{0.9\%}^{USR}$ (i.e., depth at which 0.9 % of surface solar radiation is available; 400–560 nm), or $Z_{1.5\%}^{490}$ (i.e., depth at which 1.5 % of surface downwelling irradiance is available; 490 nm) have been suggested as more robust alternatives (Wu et al., 2021). Euphotic zone depth estimates based on these alternative definitions do not vary in lockstep with those based on $Z_{1\%}^{PAR}$ (Wu et al., 2021), so using a more appropriate definition of the euphotic zone may decrease the scatter observed. In addition, and more of a general concern, Roesler et al. (2017) recently found that factory-calibrated chlorophyll concentrations, as estimated by WET Labs ECO optical sensors used in our study, overestimate measured chlorophyll on average by a factor of 2. While a study on the northwest Western Australian shelf, which has a similar phytoplankton community as found in the Perth Canyon, showed good agreement between chlorophyll concentrations from optical sensors and HPLC-derived chlorophyll from simultaneously collected water samples ($R^2 = 0.75$, slope factor = 1.2; Thomson et al., 2015), we highlight the need for a similar comparative study in any area of interest. These sources of uncertainty come on top of the well-known inconsistency in chlorophyll to carbon ratio related to changing phytoplankton communities and environmental effects other than photo-acclimation (Cullen, 1982).

It is also worth noting that the data set used in this study provided insufficient consistent spatial and temporal coverage, with some years (e.g., 2008, 2019, and 2020) and some months (e.g., January, April, and October) sampled considerably less than others (see Supplementary Fig. S1). This was especially true for particle backscatter coefficient data. Inconsistencies in spatial and temporal replication make seasonal analyses less robust and prohibit the elucidation of potential environmental effects on seasonal patterns. I~~i~~nter-annual variation in productivity within the Western Australian marine environment~~, which in our study area~~ is primarily related to fluctuations in the Leeuwin Current strength following the El Niño Southern Oscillation (ENSO; Feng et al., 2009; Chen et al., 2019). Three strong ENSO events occurred during the study period (i.e., one El Niño and two La Niña's; Australian Bureau of Meteorology, 2023), and we recommend that their effects on the robustness of seasonal patterns in DCM formation and characteristics as well as linear relationships found are further assessed. Such assessments will require dedicated data collection, preferably within areas of biological interest to marine animals.

~~Several studies have highlighted that in oceanic regions (Morel and Berthon, 1989; Uitz et al., 2006) and over eutrophic continental margins (Frolov et al., 2012), the relationship between surface and depth-integrated chlorophyll in stratified and mixed waters can be approximated with a power law regression. Here, we used in situ ocean glider data to demonstrate that such a relationship similarly exists over the intermittent oligotrophic continental margin of Western Australia and can be extended to twice the euphotic zone depth, albeit with higher uncertainty when integrating over greater depths. Regression parameters were extracted for 1) stratified waters in summer-transition months (September–April), characterised by relatively deep DBMs, 2) stratified waters in mid-winter (May–August) in which DCMs were less common and more likely a DAM, and 3) mixed waters.~~

~~Ocean glider data revealed that stratified water with a DCM dominated in summer, while a more balanced occurrence of mixed and stratified waters with a reduced probability of DCMs was observed during transition months and in mid-winter. DCM depth similarly varied seasonally from relatively stable deep DCMs in summer to more variable depths in mid-winter. These seasonal changes are typical at the 30–50° latitudinal bands (Cornec et al., 2021) because winter surface cooling and wind-induced mixing deepen the mixed layer (Kara et al., 2003; de Boyer Montégut et al., 2004), while an increase in surface chlorophyll and reduced solar irradiance cause a shallowing of isolumes (i.e., level where the daily integrated photon flux is constant) and the associated DCM (Mignot et al., 2014). In the area surrounding the Perth Canyon, north-westerly down-welling favourable storms (wind speeds >15 m s^{-1}; most frequent June–August) mix the water column down to 200 m depth, breaking down the stratified layer and DCM (Rennie et al., 2006; Chen et al., 2020). Re-stratification occurs during subsequent calm post-storm south-westerly winds (wind speeds <7 m s^{-1}; Rennie et al., 2006), allowing for the reformation and progressive deepening of DCMs as the stratification intensifies. Warm-core eddies are also known to generate well-mixed layers extending beyond the euphotic zone depth (Pearce and Griffiths, 1991; Thompson et al., 2007). Both short- and long-lived warm-core eddies are formed year-round along the Western Australian coast (Pearce and Griffiths, 1991; Fang and Morrow, 2003), but are more frequent between 28° and 31° S in late autumn and winter (Fang and Morrow, 2003). Thus, wind-induced mixing and more frequent eddy formation likely contributed to the more pronounced occurrence of mixed water conditions without DCMs in mid-winter.~~

~~While DCM formation is always at least in part caused by photo-acclimation of phytoplankton to low light conditions (Cullen, 2015), deep DCMs in summer may approach the nitracline, allowing for phytoplankton growth and thus, DBM formation (Mignot et al., 2014). Summer DBMs in the Leeuwin Current and offshore waters of Western Australia have indeed been found to approach the nitracline (Hanson et al., 2005b; Rennie et al., 2009a). In addition, south-westerly wind-driven upwelling events and enhanced vertical transport caused by eddy features within the Perth Canyon walls may bring nutrients close enough to the DCM for biomass maxima to form (Rennie et al., 2009b). In winter, the stronger Leeuwin Current pushes down the nitracline (Feng et al., 2009), potentially decoupling the DCM from its nutrient source and thus, increasing the formation of photo-acclimation maxima. Interestingly, the existence of thin shallow DBMs in winter fits the discovery of a thin nitrate layer~~

~~off Western Australia, which forms under the Leeuwin Current independently of the deep nitracline (through nitrification) and sometimes reaches the euphotic zone within our study area (Thompson et al., 2011b).~~

~~The seasonal changes in the functional relationships between surface and depth-integrated chlorophyll reflect the seasonal patterns in water stratification and DCM formation. Low surface chlorophyll levels and deeper DCMs characterised the stratified water column in summer-transition months. These deeper DCMs are likely less intense (Cornec et al., 2021), explaining the relatively gentle regression slope (0.341). Conditions changed with the onset of a phytoplankton surface bloom in May, which is distinct for our study area (e.g., Koslow et al., 2008; Chen et al., 2020) and marks the start of the mid-winter season during which mixed and stratified water conditions alternate. Graff and Behrenfeld (2018) found that deep water entrainment followed by re-stratification in the North Atlantic rapidly increased surface chlorophyll (and phytoplankton biomass) over three days post-entrainment event, while chlorophyll decreased at a much slower rate at depth. Hence, changes in surface chlorophyll contributed more strongly to changing depth-integrated values. Similar processes may be at play during post-storm periods in our study area, accounting for the steeper slope derived from stratified water profiles in mid-winter (i.e., 0.433). The strong relationship with an even steeper slope (0.521) and little error in mixed water conditions reflects the homogenous vertical distribution of chlorophyll present under these conditions (Morel and Berthon, 1989; Uitz et al., 2006).~~

~~Extending chlorophyll integrations to twice the euphotic zone depth showed similar functional relationships, albeit with a higher MAE, especially in summer-transition months. Scatter in the data at low surface chlorophyll values has previously been attributed to the presence of DCMs (Morel and Berthon, 1989; Uitz et al., 2006), which similarly could explain the increase in scatter for deep depth-integrated values observed here. However, we may have introduced additional errors with our definition of the euphotic zone depth as $Z_{1\%}^{PAR}$ and simple extension to "twice the euphotic zone depth". At low- and mid-latitudes specifically, $Z_{1\%}^{PAR}$ likely underestimates the compensation depth and so, $Z_{0.5\%}^{PAR}$, $Z_{0.9\%}^{USR}$ (i.e., depth at which 0.9 % of surface solar radiation is available; 400–560 nm), or $Z_{1.5\%}^{490}$ (i.e., depth at which 1.5 % of surface downwelling irradiance is available; 490 nm) have been suggested as more robust alternatives (Wu et al., 2021). Euphotic zone depth estimates based on these alternative definitions do not vary in lockstep with those based on $Z_{1\%}^{PAR}$ (Wu et al., 2021), so using a more appropriate definition of the euphotic zone may decrease the scatter observed. A lesser-known source of variation may have come from inter-annual variation in productivity, which in our study area is primarily related to fluctuations in the Leeuwin Current strength following the El Niño Southern Oscillation (ENSO; Feng et al., 2009; Chen et al., 2019). Three strong ENSO events occurred during the study period (i.e., one El Niño and two La Niña's; Australian Bureau of Meteorology, 2023), and we recommend that their effects on the relationships found are further assessed.~~ Finally, ~~Roessler et al. (2017) recently found that factory-calibrated chlorophyll concentrations, as estimated by optical sensors, overestimate measured chlorophyll on average by a factor of 2. While a study on the northwest Western Australian shelf, which has a similar phytoplankton community as found in the Perth Canyon, showed good agreement between chlorophyll concentrations from optical sensors and HPLC-derived chlorophyll from simultaneously collected water samples ($R^2 = 0.75$, slope factor = 1.2; Thomson et al., 2015), we highlight the need for a similar comparative study in the area of interest.~~ Despite these potential sources of variation~~, the MAEs for relationships over twice the euphotic zone depth remained low for all three conditions (i.e., 16.3 %, 15.7 %, and 8.6 %).~~

~~Arguably, the small coefficient of determination (R^2) obtained for the summer-transition regression disputes surface chlorophyll as a valuable predictor of deep depth-integrated values. However, the coefficient of determination can be misinterpreted for small data ranges, such as ours (Seegers et al., 2018).~~

~~Interestingly, we observed a third increase in mean deep depth-integrated chlorophyll in January, which was not registered at the surface or within the euphotic zone. DCMs at this time of year were predominantly DBMs and so, Alternatively, as Rennie et al. (2009b) suggested, the winter surface and summer sub-surface phytoplankton bloom may additively contribute to a peak krill abundance at the end of summer and early autumn.~~

~~If the aim is to look at productivity patterns from satellite remote sensing, the question remains whether satellite-derived surface chlorophyll measurements were estimated with an acceptable error. Our validation shows that satellite-derived surface chlorophyll values estimated measured values with a mean error of 32 %, which falls within the generally accepted 35 % for satellite remote-sensing chlorophyll products (Hooker and McClain, 2000). Satellite and in situ measurements commonly differ because of the spatial (i.e., 3×3 block vs. point measurement) and temporal (here max. 24 h) mismatch of samples (Werdell et al., 2018), which likely plays an influential role in our study area where oceanic processes change the water column structure and associated surface chlorophyll at small spatial- and temporal scales (Rennie et al., 2009a; Chen et al., 2020). While strict exclusion criteria for satellite data may reduce discrepancies, we followed a standardised exclusion protocol with flexible criteria to maximise the number of matches (Concha et al., 2021). It should be noted that our sample size is small, and MAEs are not robust when based on small sample sizes (Chai and Draxler, 2014). Recalculation of the MAE as increased matches become available is therefore encouraged to ensure error measurement stability.~~

5 Conclusion

To our best available knowledge, this is the first study to classify the productivity biome of Western Australian marine waters as an intermediate version of subtropical and temperate (meso) oligotrophic areas, highlighting the concealing nature of traditional biogeographical classifications (Bock et al., 2022). Our results provide evidence of phytoplankton biomass increases in early spring and autumn, which, together with a consistently balanced presence of photo-acclimation and biomass maxima in summer, likely support the local krill population sufficiently enough to be of relevance to foraging pygmy blue whales. Our results highlight the potential and need to monitor deep depth-integrated primary productivity patterns via~~with~~ satellite remote sensing~~ data~~ in regions where DCMs occur, which can be achieved through water-column integrated chlorophyll estimates from surface chlorophyll values. We suggest including satellite-derived deep depth-integrated chlorophyll estimates (i.e., integrations over twice the euphotic zone depth) in future efforts to identify productivity hotspots and anomalies off Western Australia ~~to help~~in an attempt to better understand the ~~relationships between productivity patterns and marine animal presence~~occurrence and behaviour of marine animal species, such as~~ foraging~~ pygmy blue whales. Similar methods can be applied to other (intermittent) oligotrophic areas where DCMs may be an important feature for higher trophic levels. However, while our regression line slopes for the euphotic zone closely resemble those previously obtainSupped from stratified (range

0.310–0.425 for Chl$_{zpd}$<1 mg m^{-3}; Morel and Berthon, 1989; Uitz et al., 2006; Frolov et al., 2012) and mixed water samples (0.551 and 0.538; Morel and Berthon, 1989; Uitz et al., 2006), it is clear that regression parameters need to be locally tuned and that ~~a redefinition of the euphotic zone depth to a more biologically important definition may be required.~~sources of potential estimate biases need to be further explored.

Data availability

All raw ocean glider data (i.e., IMOS – Australian National Facility for Ocean Gliders (ANFOG) – delayed mode glider deployments), subsetted to the spatial extent in this manuscript, are openly available from the Australian Ocean Data Network portal at https://portal.aodn.org.au/. The extracted vertical profiles used for data analysis in this study are available from the corresponding author upon request.

Author contributions

Author Contributions: RPS: Conceptualisation, methodology, coding, data acquisition & analysis, visualisation, original draft preparation, reviewing & editing; CE: Conceptualisation (supporting), supervision, reviewing & editing; RDM: Conceptualisation (supporting), supervision, reviewing & editing.

Competing interests

The authors declare that they have no conflict of interest.

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