Biological production in two contrasted regions of the Mediterranean Sea during the oligotrophic period: An estimate based on the diel cycle of optical properties measured by BGC-Argo profiling floats

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Abstract

This study assesses marine community production based on the diel variability of bio-optical properties monitored by two BioGeoChemical-Argo (BGC-Argo) floats. Experiments were conducted in two distinct Mediterranean systems, the Northwestern Ligurian Sea and the Central Ionian Sea, during summer months. We derived particulate organic carbon (POC) stock and gross community production integrated within the surface, euphotic and subsurface chlorophyll maximum (SCM) layers, using an existing approach applied to diel cycle measurements of the particulate beam attenuation (c_p) and backscattering (b_{bp}) coefficients. The diel cycle of c_p provided a robust proxy for quantifying biological production in both systems; that of b_{bp} was comparatively less robust. Derived primary production estimates vary by a factor of 2 depending upon the choice of the bio-optical relationship that converts the measured optical coefficient to POC, which is thus a critical step to constrain. Our results indicate a substantial contribution to the water column production of the SCM layer (16–42%), that varies largely with the considered system. In the Ligurian Sea, the SCM is a seasonal feature that behaves as a subsurface biomass maximum (SBM) with the ability to respond to episodic abiotic forcing by increasing production. In contrast, in the Ionian Sea, the SCM is permanent, primarily induced by phytoplankton photoacclimation and contributes moderately to water column production. These results clearly demonstrate the strong potential for transmissometers deployed on BGC-Argo profiling floats to quantify non-intrusively *in situ* biological production of organic carbon in the water column of stratified oligotrophic systems with recurring or permanent SCMs, which are widespread features in the global ocean.

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1 Introduction

Primary production is an essential process in the global ocean carbon cycle (Field et al. 1998). As a major driver of the biological carbon pump, this biogeochemical process plays a critical role in the regulation of the Earth's climate (e.g. Sarmiento & Siegenthaler 1992; Falkowski 2012). Hence, quantifying primary production as a function of time and space in the ocean stands as a major challenge in the context of climate change. The balance between gross primary production and community respiration in the ocean determines the trophic status of marine systems, i.e. whether the system acts as a source or a sink of carbon (Williams 1993). This balance depends on the considered region and varies substantially according to spatial and temporal scales (Geider et al. 1997; Duarte & Agusti 1998; del Giorgio & Duarte 2002). It is therefore necessary to develop capabilities not only for assessing primary production on a global scale, but also for characterizing and quantifying the biogeochemical functioning of marine ecosystems at smaller spatial and temporal scales (Serret et al. 1999; González et al. 2001 & 2002).

Traditionally, primary production measurements are based on *in situ* or *in vitro* incubation experiments (i.e. on board the ship, under controlled conditions) coupled with isotopic carbon analysis (Nielsen 1952; Fitzwater et al. 1982; Dandonneau 1993; Barber & Hitling 2002) or measurements of oxygen concentration (Williams & Jenkinson 1982; Williams & Purdie 1991). These methods involve seawater sampling during field campaigns, sample manipulation and subsequent laboratory analyses, which are both time consuming and require strong technical expertise. As a result, the availability of field primary production measurements is relatively limited in terms of spatial and temporal coverage, which hinders the possibility of extrapolation to other systems or to larger space and time scales for modeling purposes. Active chlorophyll fluorescence techniques, such as Fast Repetition Rate Fluorometry (FRRF), yield in situ phytoplankton physiological parameters, which when combined with appropriate modeling,

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provide estimates of derive primary production (e.g. Kolber & Falkowski 1993; Smyth et al. 2004). This technique has the major advantage of providing an instantaneous, fine-scale estimation of primary production in a non-invasive manner. Nevertheless, it is subject to assumptions and uncertainties, in particular related to the interpretation of fluorescence-light curve information in terms of carbon fixation, that still limit its use (see., e.g., Suggett et al. 2004; Corno et al. 2005; Regaudie-de-Gioux et al. 2014 and references herein).

Bio-optical primary production models coupled with ocean color satellite imagery represent another approach for obtaining primary production estimates (Morel 1991; Longhurst et al. 1995; Antoine et al. 1996; Behrenfeld et al. 2002). Such models are extremely valuable for assessing primary production with a large spatial coverage and over a broad range of temporal scales (Sathyendranath et al. 1995; Uitz et al. 2010; Chavez et al. 2011). Yet, most of these models suffer from several sources of uncertainty, that can generate potential errors in the production estimates (e.g. Sarmiento et al. 2004; Saba et al. 2010; Saba et al. 2011). Sources of uncertainty, include, in particular, the extrapolation of the satellite chlorophyll product, which is weighted to the upper portion of the euphotic zone, to the entirety of the productive region of the water column not sensed remotely. In addition, the *in situ*-based parameterization of phytoplankton photophysiology tends to lack robustness when applied to large (regional or global) scales and over seasonal to interannual time scales.

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Diel cycles observed in bio-optical properties provide a less-empirical and more mechanistic approach to assess biological production. In a seminal paper published in 1989, Siegel et al. observed the *in situ* diurnal variability of the particulate beam attenuation coefficient (c_p) and used it as a surrogate for the diurnal variations in the abundance of biogenic particles and associated production in the oligotrophic North Pacific Ocean. Several studies subsequently pursued the investigation of the diurnal variability of marine bio-optical properties as a means for determining non-intrusively *in situ* biological production (e.g. Stramska &

Dickey 1992; Durand and Olson 1996; Claustre et al. 1999; Claustre 2008; Gernez et al. 2011; White et al. 2017; Briggs et al. 2018).

Among this large body of literature, Claustre et al. (2008) carried further the principle of the Siegel et al. (1989) approach for application to the South Pacific Subtropical Ocean. Based upon the generally observed relationship between the c_p coefficient and the stock of particulate organic carbon, POC (e.g. Stramski et al. 1999; Garner et al. 2006), Claustre et al. (2008) assumed that diel variations in c_p reflect diel variations in POC. Thus, the observed daytime increase and nighttime decrease in c_p-derived POC are used to estimate gross community production, community losses and, assuming equivalent day and night losses, net community production. Because the c_p coefficient is not specific to phytoplankton but includes the POC contribution of both autotrophic and heterotrophic particles, the c_p-based method yields estimate of community production.

Two studies (Kheireddine & Antoine 2014; Barnes & Antoine 2014) extended the approach to the particulate backscattering coefficient (b_{bp}). The application opens up opportunities for assessing community production from geostationary ocean color satellite observations, from which a nearly continuous daytime b_{bp} coefficient can be retrieved. Both studies focused on surface data obtained from moored observations from the Ligurian Sea (Northwestern Mediterranean) and found that the diel cycle of b_{bp} may not necessarily be interchanged with that of c_p, which calls for further investigations.

The optics-based approach has proven to be particularly relevant for appraising particulate biological production in stratified oligotrophic systems such as subtropical gyres (e.g. Siegel et al. 1998; Claustre et al. 2008; White et al. 2017). Interestingly, in such systems, the biological production of organic carbon is difficult to quantify and potentially underestimated by ^{14}C incubation methods (Juranek & Quay 2005; Quay et al. 2010). This might be attributed to an inadequacy of traditional measurement methods for adequately

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capturing the spatial and temporal heterogeneity of biological production that may exhibit local or episodic events (Karl et al. 2003; Williams et al. 2004; McGillicuddy 2016). Moreover, in stratified oligotrophic systems, the vertical distribution of phytoplankton is frequently characterized by the presence of a deep chlorophyll maximum (DCM), also referred as subsurface chlorophyll maximum (SCM; e.g. Cullen 1982; Hense & Beckmann 2008; Cullen 2015; Mignot et al., 2014). SCMs are not necessarily resolved by *in situ* discrete sampling and cannot be observed from ocean color satellites that are limited to the surface ocean. They are typically attributed to phytoplankton photoacclimation, the physiological process by which phytoplankton cells adjust to light limitation by increasing their intracellular chlorophyll content without concomitant increase in carbon (Kiefer et al. 1976; Cullen 1982; Fennel & Boss 2003; Letelier et al., 2004; Dubinsky & Stambler 2009). Yet, SCMs resulting from an actual increase in phytoplankton (carbon) biomass, and so referred to as subsurface biomass maximum (SBM), have also been observed episodically and/or seasonally in oligotrophic regions of the global ocean (Beckmann & Hense 2007; Mignot et al. 2014; Barbieux et al. 2019; Cornec et al. 2021). Considering the large (45%) surface areas covered by stratified oligotrophic regions in the global ocean (McClain et al. 2004), improving the quantification of biological production of organic carbon and characterizing the contribution of SCMs to the water-column production in such regions are critical. For this purpose, *in situ* diel-resolved measurements with high spatio-temporal resolution in the entire water column represent an intriguing opportunity of vital importance.

In this study, we exploit summertime observations acquired by two BioGeoChemical-Argo (BGC-Argo) profiling floats deployed in contrasted systems of the Mediterranean Sea. This offers a unique opportunity for pursuing the exploration of the bio-optical diel cycle-based approach to biological production in oligotrophic environments. One of the two BGC-Argo floats was deployed in the Ligurian Sea in the vicinity of the BOUSSOLE fixed mooring

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(BOUée pour l'acquiSition d'une Série Optique à Long termE; Antoine et al. 2008). This area is representative of a seasonally stratified oligotrophic system, with a potentially productive SCM (e.g. Mignot et al. 2014; Barbieux et al. 2019) that follows a recurrent spring bloom. The second float was deployed in the Ionian Sea (Central Mediterranean) as part of the PEACETIME (ProcEss studies at the Air-sEa Interface after dust deposition in the MEditerranean sea) project (Guieu et al. 2020). The Ionian Sea is a nearly permanent oligotrophic system (e.g. Lavigne et al. 2015) with an SCM induced mostly by photoacclimation of phytoplankton cells without concomitant increase of carbon biomass (e.g. Mignot et al. 2014; Barbieux et al. 2019).

The BGC-Argo profiling floats used in this study measured, among a suite of physical and biogeochemical properties, the c_p and b_{bp} coefficients and were both programmed to sample the entire water column at a high temporal resolution (4 vertical profiles per 24h), in order to monitor the diel variations of the bio-optical properties. We applied, for the first time, a modified version of the method of Claustre et al. (2008) to the diel c_p and b_{bp} measurements acquired by the BGC-Argo floats to derive community production. Using this dataset, we (1) assess the relevance of the diel cycle-based method for estimating biological production of organic carbon in the considered regions and discuss the applicability of the method to b_{bp}, in addition to c_p; (2) investigate the regional and vertical variability of the production estimates with a focus on the SCM layer in relation to the biological and abiotic context; (3) discuss the relative contribution of the SCM layer to the water-column community production.

2 Data and methods

2.1 Study region

The Mediterranean Sea provides a unique environment for investigating the biogeochemical functioning of oligotrophic systems that exhibit either a seasonal or permanent

SCM. The Mediterranean is a deep ocean basin characterized by a West-to-East gradient in nutrients and chlorophyll *a* concentration (e.g. Dugdale & Wilkerson 1988; Bethoux et al. 1992; Antoine et al. 1995; Bosc et al. 2004; D'Ortenzio & D'Alcalà 2009) associated with a deepening of the SCM (Lavigne et al. 2012; Barbieux et al. 2019). The Ionian Sea in the eastern Mediterranean is defined as permanently oligotrophic, with the SCM settled at depth over the whole year. This system represents the oligotrophic end-member type of SCM (Barbieux et al. 2019), much like the subtropical South Pacific Ocean Gyre. By contrast, the Ligurian Sea in the western Mediterranean is seasonally productive akin to a temperate system (e.g. Casotti et al. 2003; Marty & Chiavérini 2010; Siokou-Frangou et al. 2010; Lavigne et al. 2015). The mixed layer deepens significantly during the winter period, inducing seasonal renewal of nutrients in the surface layer that supports the spring bloom (Marty et al. 2002; Lavigne et al. 2013; Pasqueron de Fommervault et al. 2015; Mayot et al. 2016). After the seasonal bloom, the SBM intensifies throughout the summer and into early fall. This system represents the temperate end-member type of SCM.

2.2 BGC-Argo multi-profiling floats and data processing

We deployed BGC-Argo floats programmed for "multi-profile" sampling in each of these two regions (Fig. 1). The Ligurian Sea float (hereafter noted fLig, WMO: 6901776), was deployed in the vicinity of the BOUSSOLE fixed mooring (7°54'E, 43°22'N) during one of the monthly cruises of the BOUSSOLE program (Antoine et al. 2008) and profiled from April 9, 2014 to March 15, 2015. For the purpose of this study focusing on oligotrophic systems, we selected the fLig float measurements acquired during the time period May 24 to September 13, 2014 to coincide in months with the Ionian Sea float time series. The Ionian Sea float (hereafter noted fIon, WMO: 6902828) was deployed as part of the PEACETIME project (Guieu et al. 2020). We used the fIon float measurements acquired during the time period May 28 to

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The BGC-Argo floats used in this study are "PROVOR CTS-4" (nke Instrumentation, Inc.). They were both equipped with the following sensors and derived data products: (1) a CTD sensor for depth, temperature and salinity; (2) a "remA" combo sensor that couples a Satlantic OCR-504 (for downwelling irradiance at three wavelengths in addition to photosynthetic available radiation, PAR) and a WET Labs ECO Puck Triplet (for both chlorophyll *a* (excitation/emission wavelengths of 470 nm/695 nm) and colored dissolved organic matter (CDOM; 370 nm/460 nm) fluorescence, and particulate backscattering coefficient at 700 nm); and (3) a WET Labs C-Rover (for particulate beam attenuation coefficient at 660 nm, 25-cm pathlength). Data were collected along water column profiles from 1000 m up to the surface with a vertical resolution of 10 m between 1000 and 250 m, 1 m between 250 and 10 m, and 0.2 m between 10 m and the surface. First, the BGC-Argo raw counts were converted into geophysical units by applying factory calibration. Second, we applied corrections following the BGC-Argo QC procedures (Schmechtig et al. 2015, 2016; Organelli et al. 2017).

Factory-calibrated chlorophyll fluorescence requires additional corrections for determining the chlorophyll *a* concentration (*Chl*). Values collected during daylight hours were corrected for non-photochemical quenching following Xing et al. (2012). A global analysis of factory-calibrated chlorophyll fluorescence measured with WET Labs ECO sensors relative to concurrent chlorophyll *a* concentrations, determined by High Performance Liquid Chromatography (HPLC), yielded a global overestimate bias of 2 (Roesler et al. 2017), with statistically significant regional biases varying between 0.5 and 6. The Mediterranean Sea is known to show very small regional variations of the fluorescence-to-*Chl* ratio (Taillandier et al. 2018), with a mean value close to 2 (1.66±0.28 and 1.72±0.23 for the Western and Eastern

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Mediterranean, respectively; Roesler et al. 2017). Hence the bias correction factor of 2 was applied to BGC-Argo fluorescence data from both the Ligurian and Ionian regions, consistently with the processing performed at the Coriolis Data Center.

For the particulate backscattering coefficient (b_{bp}), we followed the BGC-Argo calibration and quality control procedure of Schmechtig et al. (2016). The backscattering coefficient at 700 nm (m^{-1}) is retrieved following Eq. (1):

$$b_{bp}(700) = 2\,\pi\,\chi\,[(\beta b_{bp} - Dark b_{bp}) \times Scale b_{bp} - \beta sw] \quad (1)$$

where $\chi = 1.076$ is the empirical weighting function that converts particulate volume scattering function at 124° to total backscattering coefficient (Sullivan et al. 2013); βb_{bp} is the raw observations from the backscattering meter (digital counts); $Dark b_{bp}$ (digital counts) and $Scale b_{bp}$ (m^{-1} sr^{-1} $count^{-1}$) are the calibration coefficients provided by the manufacturer; and βsw is the contribution to the Volume Scattering Function (VSF) by the pure seawater at the 700 nm measurement wavelength that is a function of temperature and salinity (Zhang et al. 2009).

The calibration procedure applied to the particulate beam attenuation coefficient (c_p) is similar to that described in Mignot et al. (2014). The beam transmission, T (%), is transformed into the beam attenuation coefficient, c (m^{-1}), using the relationship:

$$c = -\frac{1}{x} \ln \frac{T}{100} \quad (2)$$

where x is the transmissometer pathlength (25 cm). The beam attenuation coefficient c is the sum of the absorption and scattering by seawater and its particulate and dissolved constituents. At 660 nm, the contribution of CDOM (c_{CDOM}) can be considered negligible in oligotrophic waters because, although its absorption in the blue is comparable to that of particulate material (Organelli et al. 2014), the c_{CDOM} spectrum decays exponentially towards near zero in the red

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(Bricaud et al. 1981), and because it is comprised of dissolved molecules and colloids, its scattering is negligible (Boss and Zaneveld 2003). Meanwhile c_w(660) for pure water is constant and removed in the application of the factory calibration; effects due to dissolved salt are accounted for according to Zhang et al. (2009). Hence, at a wavelength of 660 nm, the particle beam attenuation coefficient, c_p (m^{-1}), is retrieved by subtracting the seawater contribution to c. The biofouling-induced signal increase that is observed in clear deep waters and results in a drift in c_p values with time, is corrected as follows. For each profile, a median c_p value, used as an "offset", is computed from the c_p values acquired between 300 m and the maximum sampled depth, and subtracted from the entire profile.

Using the solar noon Photosynthetically Available Radiation (PAR) measurements, we computed the euphotic layer depth (Z_{eu}) as the depth at which the PAR is reduced to 1% of its value just below the surface (Gordon & McCluney 1975) and the penetration depth (Z_{pd}; also known as the e-folding depth or first attenuation depth) as Z_{eu} / 4.6. We define the surface layer from 0 m to Z_{pd}. We also define the SCM layer as in Barbieux et al. (2019), whereby a Gaussian model is fit to each *Chl* vertical profile measured by the floats in order to determine the depth interval of the full width half maximum of the SCM. Finally, the Mixed Layer Depth (MLD) is derived from the float CTD data as the depth at which the potential density difference relative to the surface reference value is 0.03 kg m^{-3} (de Boyer Montégut et al. 2004).

Unlike the majority of BGC-Argo floats that collect profile measurements every 10 days, the two platforms used in this study sampled the water column with 4 profiles per day, albeit with slightly different regimes (Fig. 2). The fLig float cycle commences with the first profile at sunrise (t_{sr}), a second at solar noon (t_n), a third profile at sunset the same day (t_{ss}), and a fourth profile at sunrise the next day (t_{sr+1}). The fLig float then acquires a profile at solar noon 4 days later (t_{n+4}), and then restarts 3 days later the acquisition of 4 profiles in 24 hours from sunrise (t_{sr+7}). The fIon cycle is performed over a single 24-hour period; it begins at sunrise (t_{sr}),

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followed by a second profile at solar noon (t_n), a third at sunset (t_{ss}) and a last night profile at approximately midnight (t_m). For this float, the sampling cycle is repeated each day.

2.3 Characterization of the diel cycle of the bio-optical properties

In order to characterize the amplitude and variability of the diel cycle of the c_p and b_{bp} coefficients, we use the metrics defined by Gernez et al. (2011) and Kheireddine & Antoine (2014). First, we compute the amplitude of the diurnal variation of the c_p and b_{bp} coefficients as:

$$\Delta c_p = c_p(t_{ss}) - c_p(t_{sr}) \quad (3a)$$

$$\Delta b_{bp} = b_{bp}(t_{ss}) - b_{bp}(t_{sr}) \quad (3b)$$

with $c_p(t_{sr})$ and $b_{bp}(t_{sr})$ the values of c_p and b_{bp} at sunrise and $c_p(t_{ss})$ and $b_{bp}(t_{ss})$ the values at sunset the same day.

We also consider the relative daily variation Δc_p and Δb_{bp} (expressed as % change) for each float and each day of observation, from sunrise to sunrise as follows:

$$\Delta c_p = 100 \left(\frac{c_p(t_{sr})}{c_p(t_{sr+1})} - 1\right) \quad (4a)$$

$$\Delta b_{bp} = 100 \left(\frac{b_{bp}(t_{sr})}{b_{bp}(t_{sr+1})} - 1\right) \quad (4b)$$

with $c_p(t_{sr})$ and $b_{bp}(t_{sr})$ being the values of c_p and b_{bp} at sunrise and $c_p(t_{sr+1})$ and $b_{bp}(t_{sr+1})$ the values at sunrise the next day. Then the mean and range in relative daily variations ($\widehat{m}\Delta$ and $\widehat{r}\Delta$, respectively) are computed for each float over the entire time series.

2.4 Principle of the bio-optical diel cycle-based approach to biological production

The two bio-optical properties that we considered in this study, c_p and b_{bp}, are both linearly correlated to, and thus may be used as a proxy for, the stock of POC (e.g. Oubelkheir et al. 2005; Gardner et al. 2006; Cetinić et al. 2012). Both of these bio-optical proxies have been

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shown to exhibit a diurnal cycle (e.g. Oubelkheir & Sciandra 2008; Loisel et al. 2011; Kheireddine & Antoine 2014). The daily solar cycle is a major driver of biological activity in all oceanic euphotic zones, which influences the abundance of microorganisms, including phytoplankton (Jacquet et al. 1998; Vaulot & Marie 1999; Brunet et al. 2007) and heterotrophic bacteria (Oubelkheir & Sciandra 2008; Claustre et al. 2008) and, therefore, the magnitude of the c_p and b_{bp} coefficients. Diel changes in the c_p or b_{bp} coefficient reflect processes that affect the cellular abundance (number) and the attenuation, or backscattering, cross-section, which varies with cell size and refractive index. The diurnal increase in c_p or b_{bp} has primarily been attributed to photosynthetic cellular organic carbon production (Siegel et al. 1998), that will first result in an increase in cell size, or an increase in cell abundance and a decrease in cell size following cell division often occurring at night. In addition, the diurnal increase in c_p or b_{bp} may be caused by variations in cellular shape and refractive index that accompany intracellular carbon accumulation (Stramski & Reynolds 1993; Durand & Olson 1996; Claustre et al. 2002; Durand et al. 2002). The nighttime decrease in c_p or b_{bp} may be explained by a decrease in cellular abundance due to aggregation, sinking or grazing (Cullen et al. 1992), a reduction in cell size and/or refractive index associated with cell division and respiration, the latter involving changes in intracellular carbon concentration with effect on the refractive index (Stramski & Reynolds 1993). Community composition and cell physiology (in response to diel fluctuations of the light field) might also influence the optical diel variability through their effects on cell size and refractive index. Diel variation in photoacclimation can be important in coastal communities dominated by microplankton (Litaker et al. 2002; Brunet et al. 2008). Nevertheless, previous studies conducted in oligotrophic environments suggest that photosynthetic growth is the major driver of the diurnal changes in c_p or b_{bp} (Gernez et al. 2002; Claustre et al. 2008). In addition, Claustre et al. (2002), in an experimental work based on *Prochlorococcus*, a frequent taxon in oligotrophic regions, show that although non-negligible,

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the diel variability in photoacclimation is much less pronounced than that in phytoplankton growth.

Following a modified version of Claustre et al. (2008), the observed daytime increase and nighttime decrease in c_p-derived (or b_{bp}-derived) POC are used to estimate gross community production. For this purpose, the c_p and b_{bp} coefficients, measured *in situ* by the BGC-Argo profiling floats, are converted into POC equivalent using a constant c_p-to-POC (or b_{bp}-to-POC) relationship from the literature (see below). By definition, the c_p and b_{bp} coefficients target particles so that the dissolved biological matter is not accounted for by the present method.

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2.5 Bio-optical properties-to-POC relationships

The conversion of c_p and b_{bp} into POC relies on the use of empirical proxy relationships and assumptions concerning the variations in those relationships. First, as in Claustre et al. (2008), we assume that the c_p- or b_{bp}-to-POC relationship remains constant on a daily timescale, consistently with previous works (Stramski & Reynolds 1993; Cullen & Lewis 1995), so that observed variations in the optical coefficients can be interpreted as variations in POC. Second, the specific proxy value is not constant, as many empirical relationships between POC and c_p (e.g. Claustre et al. 1999; Oubelkheir et al. 2005; Gardner et al. 2006; Loisel et al. 2011) or b_{bp} (e.g. Stramski et al. 2008; Loisel et al. 2011; Cetinić et al. 2012) have been proposed for specific regions (Tables 1 and 2). In the present study, we used the relationships from Oubelkheir et al. (2005) and Loisel et al. (2011) for c_p and b_{bp}, respectively. Both relationships were established from *in situ* measurements collected in the Mediterranean Sea and produce c_p- or b_{bp}-derived POC values falling in the middle of the range of all the POC values resulting from the different bio-optical relationships taken from the literature (Tables 1 and 2).

2.6 Estimating biological production from the diel cycle of POC

2.6.1 Hypotheses

The time-rate-of-change in depth-resolved POC biomass, $b(z,t)$, can be described by a partial differential equation:

$$\frac{\partial b(z,t)}{\partial t} = \mu(z,t)\, b(z,t) - l(z,t)\, b(z,t), \quad (5)$$

where $\mu(z,t)$ is the particle photosynthetic growth rate and $l(z,t)$ the particle loss rate at depth z and time t (both in units of d^{-1}). As in previous studies (Claustre et al. 2008, Gernez et al. 2011; Barnes and Antoine 2014), we assume a 1D framework. In other words, we ignore the effects of lateral transport of particles by oceanic currents and assume that there is no vertical transport of particles into or out of the layer considered. We also assume that the loss rate is constant throughout the day and uniform with depth, i.e. $l(z,t) = l$. In this context, the time series of profiles are first converted to depth-integrated biomass (from $b(z,t)$ to $B(t)$) for each of the layers in question, and then integrated over time to determine daytime gain, nighttime loss, and net daily production.

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2.6.2 Calculation of the loss rate

During nighttime, there is no photosynthetic growth, so that Eq. (5) becomes:

$$\frac{\partial b(z,t)}{\partial t} = l\, b(z,t). \quad (6)$$

The integration of Eq. (6) over depth yields an expression of the rate of change of the depth-integrated POC biomass, $B(t)$:

$$\frac{\partial B(t)}{\partial t} = -\, l\, B(t), \quad (7)$$

with $B(t) = \int_{z2}^{z1} b(z,t)\mathrm{d}z$, the POC integrated within a given layer of the water column, comprised between the depths z_1 and z_2 (in gC m^{-2}). In this respect, we consider three different

layers: the euphotic layer extending from $z1 = 0$ m to $z2 = Z_{eu}$; the surface layer extending from $z1 = 0$ m to $z2 = Z_{pd}$; and the SCM layer extending from $z1 = Z_{SCM} - Z_{SCM,1/2}$ and $z2 = Z_{SCM} + Z_{SCM,1/2}$, with Z_{SCM} the depth of the SCM and $Z_{SCM,1/2}$ the depth at which *Chl* is half of the SCM value.

Eq. (7) can be integrated over nighttime to obtain an equation for the loss rate l, as a function of the nocturnal variation of B:

$$l = \frac{\ln\left(\frac{B_{ss}}{B_{sr+1}}\right)}{t_{sr+1} - t_{ss}}, \quad (8)$$

with $B(t_{ss})$ and $B(t_{sr+1})$ corresponding to the POC integrated within the layer of interest, at t_{ss} (sunset) and t_{sr+1} (sunrise of the next day).

2.6.3 Calculation of the production rate

The daily (24-hour) depth-integrated gross production of POC, P (in units of gC m^{-2} d^{-1}), is defined as:

$$P = \int_{t_{sr}}^{t_{sr+1}} \int_{z2}^{z1} \mu(z,t)\, b(z,t)\, dz\, dt, \quad (9)$$

with t_{sr} the time of sunrise on day 1 and t_{sr+1} the time of sunrise the following day. Equation (5) can be used to express P as a function of l, $b(z,t)$, and the rate of change of $b(z,t)$:

$$P = \int_{t_{sr}}^{t_{sr+1}} \int_{z2}^{z1} \left(\frac{\partial b(z,t)}{\partial t} + l\, b(z,t)\right) dz\, dt, \quad (10)$$

which yields:

$$P = B_{t_{sr+1}} - B_{t_{sr}} + l \int_{t_{sr}}^{t_{sr+1}} B(t)\, dt. \quad (11)$$

where the gross production P is calculated as the sum of the net daily changes in POC biomass plus POC losses, assuming a constant rate (l) during daytime and nighttime.

Finally, using the trapezoidal rule, Eq. (11) simplifies into

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$$P = B_{t_{sr+1}} - B_{t_{sr}} + l \sum_{i=1}^{j} (t_{i+1} - t_i) \frac{B_{i+1}+B_i}{2}, \quad (12)$$

with l calculated from Eq. (8) and the index i corresponding to the different measurement time steps over the course of the diel cycle (t_{sr}, t_n, t_{ss}, and t_{sr+1}; Fig. 2).

In summary, Eq. (12) is applied to the time series of the BGC-Argo floats by using b_{bp} and c_p converted into POC equivalents, integrated within the euphotic, surface, and SCM layers to compute c_p- and b_{bp}-derived estimates of gross community production, P, in all three layers of the water column.

2.7 Primary production model

The community production estimates obtained from the bio-optical diel cycle-based method are evaluated against primary production values computed with the bio-optical primary production model of Morel (1991). Morel's model estimates the daily depth-resolved organic carbon concentration fixed by photosynthesis, using the noontime measurements of *Chl*, temperature and PAR within the water column by the BGC-Argo profiling floats as model inputs. The standard phytoplankton photophysiological parameterization is used for these calculations (Morel 1991; Morel et al. 1996).

2.8 Phytoplankton pigments and community composition

During the BOUSSOLE cruises conducted in 2014 (cruises #143 to #154) and the PEACETIME cruise, discrete seawater samples were taken at 10–12 depths within the water column from Niskin bottles mounted on a CTD-rosette system and then filtered under low vacuum onto Whatman GF/F filters (0.7-µm nominal pore size, 25-mm diameter). The filters were flash-frozen in liquid nitrogen and stored at -80°C until analysis by HPLC following the protocol of Ras et al. (2008). The concentrations of phytoplankton pigments resulting from these analyses were used to estimate the composition of the phytoplankton assemblage. For this purpose, we used the diagnostic pigment-based approach (Claustre et al. 1994; Vidussi et al.

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2001; Uitz et al. 2006) with the coefficients of Di Cicco et al. (2017) to account for the specificities of Mediterranean phytoplankton communities. This approach yields the relative contribution to chlorophyll *a* biomass of major taxonomic groups merged into three size classes (micro-, nano and picophytoplankton).

The fLig float was spatially distanced from the location of sampling at the BOUSSOLE mooring site. Thus, it was necessary to identify the time shift for matching the cruise-sampled analyses to the float profile measurements. This was achieved by performing a cross-correlation analysis of the bio-optical time series measurements collected on the float with that on the mooring (in this case *Chl*, c_p and b_{bp}). A positive time lag between the BOUSSOLE site and the position of the fLig float during its drift is observed suggesting that the variations observed by the float led that observed at BOUSSOLE by ~2 days. This small-time lag coupled with high correlation coefficient values and long decorrelation time scales, indicate that the monthly interpolated pigment data measured at the BOUSSOLE site may be considered as representative of the pigment composition along the fLig float trajectory.

3 Results and discussion

We first provide an overview of the biogeochemical and bio-optical characteristics measured by the two BGC-Argo profiling floats in the Ligurian and Ionian Seas. We then assess the usefulness of the diel cycle of the b_{bp} coefficient for deriving community production, in comparison to the c_p-derived estimates as a reference, and discuss the c_p-derived estimates. Finally, we examine the community production estimates in both study regions, with an emphasis on the SCM layer and its biogeochemical significance.

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3.1 Biogeochemical and bio-optical context in the study regions

Both study regions are characterized by either seasonal or persistent oligotrophy, with mean surface *Chl* values ranging within 0.08–0.22 mg m^{-3} (Fig. 3), and a stratified water column with a consistently shallow MLD (<30 m). They do exhibit very different euphotic depths, with a mean Z_{eu} of 47±5 m and 89±4 m in the Ligurian and Ionian Seas, respectively. Consistently, the instantaneous midday PAR values are much lower in the upper layer of the Ligurian Sea (93±70 µE m^{-2} s^{-1}) than in the Ionian Sea (500±60 µE m^{-2} s^{-1}) and shows a more rapid decrease within the water column as phytoplankton biomass absorbs light. Both regions also display a SCM, the depth of which co-occurs with Z_{eu} and the isopycnal 28.85 (i.e. the isoline of potential density 28.85 kg m^{-3}) over the considered time series, except for the last month of observation in the Ionian Sea.

In the Ligurian Sea, the SCM is intense (1.06±0.34 mg Chl m^{-3}; Fig. 3a), relatively shallow (41±7 m), and associated with the subsurface c_p and b_{bp} maxima (0.27±0.09 and 0.0015±0.0006 m^{-1}, respectively; Fig. 3b–c). The *Chl* and c_p values are 5 times larger in the SCM layer than at surface, and the b_{bp} values 3.6 times larger. In contrast, in the Ionian Sea, the SCM is associated with lower values of *Chl* (0.27±0.07 mg m^{-3}; Fig. 3d), c_p (0.05±0.01 m^{-1}; Fig. 3e) and b_{bp} (0.0005±0.0001 m^{-1}; Fig. 3f). Compared to the Ligurian Sea SCM, the Ionian Sea SCM is located twice as deep (97±11 m) and is uncoupled from the c_p and b_{bp} maxima that occur at shallower depth.

Hence, the selected regions are representative of two contrasted SCM systems with distinct degree of oligotrophy, consistent with our expectations (e.g. D'Ortenzio & Ribera D'Alcalà 2009; Barbieux et al. 2019). Such a contrast in the SCM characteristics in relation with the trophic gradient of the environment has already been observed in the Mediterranean Sea (e.g. Lavigne et al. 2015; Barbieux et al. 2019) and on a global scale (e.g. Cullen 2015 and references therein; Mignot et al. 2014; Cornec et al. 2021). These studies report that the depth

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of the SCM is inversely correlated with the surface *Chl* (an index of the trophic status) and light attenuation within the water column. Previous studies (Mignot et al. 2014; Barbieux et al. 2019; Cornec et al. 2021) indicate that moderately oligotrophic, temperate conditions are generally associated with a relatively shallow SCM coupled to a maximum in c_p or b_{bp}, reflecting an increase in phytoplankton carbon biomass (SBM). In contrast, in the most oligotrophic environments, the vertical distribution of *Chl* shows a maximum at greater depths and is decoupled from the c_p or b_{bp} vertical distribution. Furthermore, Barbieux et al. (2019) show that, in the northwestern Mediterranean region, the SCM mirrors a biomass maximum located slightly above Z_{eu}, which benefits from an adequate light-nutrient regime thanks to a deep winter convective mixing allowing nutrient replenishment in the upper ocean. In the Ionian Sea where the MLD and nutricline are permanently decoupled, the SCM establishes below Z_{eu} as phytoplankton organisms attempt to reach nutrient resources. Prevailing low-light conditions lead to pronounced photoadaptation of phytoplankton. Thus, consistently with previous work, the present observations indicate that the Ligurian Sea SCM is a phytoplankton carbon biomass (SBM) likely resulting from favorable light and nutrient conditions, whereas the Ionian SCM would be essentially induced by photoacclimation of phytoplankton cells.

Although the summer period is typically considered stable, some temporal variations are observed over the time series that are more pronounced in the SCM layer than at surface. In the Ligurian Sea SCM, the *Chl*, c_p and b_{bp} exhibit similar temporal evolution, with relatively high values in late May 2014, followed by a marked decrease until mid-July (Figs. 4a–c). Then we observe two local minima in *Chl*, c_p and b_{bp} that delineate a second peak between July 14 and August 16, 2014 (as indicated by the dashed lines in Fig. 4a–c). In the Ionian Sea SCM, the *Chl*, c_p and b_{bp} values all decrease from late May until a minimum is reached on August 11, 2017 (dashed line in Figs. 4d–e) and a second increase is recorded later in the season. These

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temporal patterns are further discussed in relation with the variability in the estimated POC and production rates (Section 3.4).

3.2 Assessment of the method

3.2.1 Analysis of the diel cycle of the c_p and b_{bp} coefficients

Diel cycles, characterized by a daytime increase and a nighttime decrease, are observed in both c_p and b_{bp} time series in all layers of the water column, as illustrated for the SCM layer of the Ionian Sea in Fig. 5 (examples of the diel cycles of c_p and b_{bp} for both the Ligurian and Ionian Seas are provided in Appendix A). Considering the time series of the Ligurian and Ionian Seas, as well as the surface and SCM layers, the c_p and b_{bp} coefficients show mean diurnal amplitudes, Δc_p and Δb_{bp}, spanning between 0.001 m^{-1} and 0.02 m^{-1} and 7 x 10^{-6} m^{-1} and 9 x 10^{-5} m^{-1}, respectively. These results are consistent with Gernez et al. (2011), who observed Δc_p values ranging within 0.01 m^{-1} and 0.07 m^{-1} in the surface layer of the Ligurian Sea (BOUSSOLE mooring) during the summer to fall oligotrophic period. Relative to the mean c_p and b_{bp} values, the mean Δc_p and Δb_{bp} correspond to diurnal variations of 9–20% and 5–10%, respectively.

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In the surface layer of the Ligurian Sea, the diel cycles of c_p and b_{bp} exhibit, respectively, mean relative daily variation ($\widehat{m\Delta}$) of 12.7% and 2.3%, and a range in relative daily variations ($\widehat{r\Delta}$) of 256.7% and 28.5% (Table 3). These values are of the same order of magnitude as those reported by Kheireddine & Antoine (2014), acquired from the BOUSSOLE surface mooring in the same area and during the oligotrophic season (from -5% to 25% for c_p and from -2% to 10% for b_{bp}). Interestingly, the diel cycle of the c_p coefficient appears systematically more pronounced than that of b_{bp}, with larger values of $\widehat{m\Delta}$ and $\widehat{r\Delta}$, regardless of the considered region and layer of the water column (Table 3).

To first order, the variability in the b_{bp} and c_p coefficients is determined by the variability in particle concentration, which underpins their robustness as POC proxies in open-ocean conditions and explains their coherent evolution on a monthly timescale (Figs. 3–4). Nevertheless, to second order, these coefficients vary differentially with the size and composition of the particle pool. In particular, phytoplankton make a larger contribution to c_p than b_{bp}, in part due to their strong absorption efficiency. In addition, b_{bp} is more sensitive to smaller (<1 µm) particles (Stramski & Kiefer 1991; Ahn et al. 1992; Stramski et al. 2001; Boss et al. 2004) and to particle shape and internal structure (Bernard et al. 2009; Neukermans et al. 2012; Moutier et al. 2017; Organelli et al. 2018). While the diel cycle of c_p would be essentially driven by photosynthetic processes due to the influence of phytoplankton on c_p, b_{bp} would be more responsive to detritus and/or heterotrophic bacteria that show minor, if not negligible, daily variability. Hence, such specificities in the bio-optical coefficients may explain the observed differences in their diel cycles.

Based on high-frequency surface measurements in the Ligurian Sea in various seasons, the studies of Kheireddine & Antoine (2014) and Barnes & Antoine (2014) demonstrated that the diel cycle of b_{bp} not only exhibits much reduced relative amplitude compared to that of c_p, but the features of the b_{bp} cycle are not synchronous with that of the c_p cycle. Thus, b_{bp} cannot be used interchangeably with c_p for assessing daily changes in POC or community production, but perhaps provides additional information on the particulate matter and its production rates. Our results support these previous findings, not only for the surface layer of the Ligurian Sea, but also for the whole water column of both the Ligurian and Ionian regions.

We now consider the integrated euphotic zone gross community production estimates derived from the bio-optical diel cycle-based method (Fig. 6). We compare the c_p- and b_{bp}-based estimates with primary production estimates computed with the model of Morel (1991). The b_{bp}-derived production rates underestimate those derived from c_p in both regions by about

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615 a factor of ten, with respective mean values of 0.11±0.28 gC m^{-2} d^{-1} and 1.18 ±1.13 gC m^{-2} d^{-1}
616 in the Ligurian Sea, and 0.04±0.04 gC m^{-2} d^{-1} and 0.46 ±0.11 gC m^{-2} d^{-1} in the Ionian Sea. In
617 addition, the b_{bp}-derived production is much lower than the primary production computed with
618 the model of Morel (1991), which has mean values of 0.91±0.14 gC m^{-2} d^{-1} in the Ligurian Sea
619 and 0.31 ±0.04 gC m^{-2} d^{-1} in the Ionian Sea. The significantly lower community production
620 rates are a direct effect of the dampened relative daily amplitude of the b_{bp} diel cycle (Table 3),
621 and the sensitivity of b_{bp} to the smaller heterotrophic and detrital particulate matter. The bio-
622 optical diel cycle-based method, whether applied to c_p or b_{bp}, yields an estimate of the
623 community production, i.e. that associated with the accumulation of phytoplankton *and* bacteria
624 biomass, which is necessarily larger than the primary (photo-autotrophic) production rates from
625 the Morel (1991) model. These questionable low values of community production, along with
626 the observation of a weak daily variability in b_{bp}, support the idea that the diel cycle of b_{bp} may
627 not be a reliable index for total community production rates, consistently with previous studies
628 (Kheireddine & Antoine 2014; Barnes & Antoine 2014). However, the utility of a b_{bp}-derived
629 community production may be revealed in elucidating rates for distinct size-based groups of
630 organisms, such as picoplankton. A better understanding of the specific size range that
631 dominates the diel cycle in b_{bp} will be important to understand. Yet, for our purposes, we
632 disregard the b_{bp}-based estimates and focus our analysis on the c_p-derived gross community
633 production estimates.

634 **3.2.2 Community production derived from the c_p coefficient**

635 The c_p-derived estimates of gross community production, integrated within the euphotic
636 layer, compare favorably with those found in the literature for similar Mediterranean areas (see
637 Table 4 and references therein). The c_p-based estimates show a 2.5-fold difference between the
638 Ligurian Sea and the Ionian Sea (mean of 1.18 gC m^{-2} d^{-1} and 0.46 gC m^{-2} d^{-1}, respectively;
639 Table 6). In comparison, water column-integrated primary production values, either inferred

640 from satellite observations and biogeochemical models or measured *in situ*, vary within the
641 range 0.13–1 gC m^{-2} d^{-1} and 0.14–0.69 gC m^{-2} d^{-1} for the Western (or Ligurian) and Eastern (or
642 Ionian) region, respectively (Table 4). As expected, our c_p-based community production rates
643 are larger than published primary production rates. The present c_p-derived values also compare
644 favorably with gross community production estimates inferred from a similar approach applied
645 to bio-optical measurements from the BOUSSOLE mooring in the Ligurian Sea (0.5–0.8 gC m^{-2}
646 d^{-1} in Gernez et al. 2011; 0.8–1.5 gC m^{-2} d^{-1} in Barnes & Antoine 2014) and along an
647 oligotrophic gradient in the South Pacific Subtropical Ocean (0.85 gC m^{-2} d^{-1}; Claustre et al.
648 2008).

649 The empirical relationships linking the c_p (or b_{bp}) coefficient to POC are known to exhibit
650 regional and seasonal variability in response to changes in the composition of the particle
651 assemblage and associated changes in particle size, shape and type, i.e. biogenic or mineral
652 (e.g. Stramski et al. 2004; Neukermans et al. 2012; Slade & Boss 2015). Hence, the choice of
653 such relationships strongly affects the conversion of the measured daily bio-optical variability
654 into POC fluxes. For the time period and study regions here, the c_p-based community
655 production varies by a factor of 2, depending on the selected bio-optical relationship, so that c_p-
656 based estimates vary between 0.89±0.84 gC m^{-2} d^{-1} and 1.62±1.54 gC m^{-2} d^{-1} in the Ligurian
657 Sea, and between 0.35±0.09 gC m^{-2} d^{-1} and 0.63±0.16 gC m^{-2} d^{-1} in the Ionian Sea. The minimal
658 and maximal values are obtained with the bio-optical relationships from Marra et al. (1995) and
659 Stramski et al. (2008), respectively (Table 5). Compared to the reference value obtained using
660 the Oubelkheir et al. (2005) relationship, the c_p-based estimates are 25% lower and 37% higher
661 using the relationships of Marra et al. (1995) and Stramski et al. (2008), respectively. We also
662 note that using the Mediterranean relationship of Loisel et al. (2011), instead of that of
663 Oubelkheir et al. (2005), would reduce the c_p-based estimates by 17% in both study regions

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(Table 5). That said, although the absolute magnitudes vary depending upon proxy choice, the differences observed between locations is robust.

The use of the single relationship established from Mediterranean waters (Oubelkheir et al. 2005) appears as a reasonable choice for the study region. Yet, if more relevant bio-optical proxy relationships are available, such as one that accounts for spatial and seasonal variations, and even applicable to different layers of the water column, that would certainly reduce the uncertainty in the rate estimation. Although this is beyond the scope of the present study, we recognize that such investigations should be conducted in the future in order to refine optics-based biomass (POC) and community production estimates.

3.3 Regional and vertical variability of production

The temporal evolution of the c_p-derived POC biomass integrated within the three distinct layers of the water column is presented for the two study regions in Fig. 7. The integrated POC concentration values follow similar temporal trends as reported for c_p (Figs. 3–4). In the Ligurian Sea, the euphotic layer-integrated POC varies between 1.5 and 6.0 gC m^{-2} (mean of 3.7±1.1 gC m^{-2}; Fig. 7a and Table 6). There was a decrease from late May to mid-July (6.0 to 1.5 gC m^{-2}) followed by a moderate peak (3.9 gC m^{-2}) between mid-July and mid-August (as bounded by the dashed lines in Fig. 5). The c_p-based community production did exhibit large variability over the time period (Fig. 7b and Table 6), but interestingly, the moderate POC peak observed in the core of the oligotrophic season (between mid-July and mid-August) is associated with the maximum production rate of the time series (4.3 gC m^{-2} d^{-1}).

In the Ionian Sea, the POC biomass integrated within the euphotic zone is much lower than in the Ligurian Sea and remains more stable over the time period (1.9±0.24 gC m^{-2}; Fig. 7c and Table 6). As with POC, the community production is much lower in the Ionian Sea than in the Ligurian Sea, but still exhibits substantial variability with values ranging within 0.06–

689 0.68 gC m^{-2} d^{-1} (Fig. 7d). These results are consistent with multiple studies reporting a large
690 difference in the trophic status and productivity of the Ligurian and Ionian Seas, on seasonal
691 and annual timescales (D'Ortenzio & Ribera d'Alcala, 2009; Siokou-Frangou et al. 2010;
692 Lavigne et al. 2013; Mayot et al. 2016). Our results confirm this difference, yet on a monthly
693 timescale during the oligotrophic summer period.

694 The gross community production estimates integrated over different layers of the water
695 column reveal distinct patterns. In the Ligurian Sea, both the euphotic and SCM layers show
696 large production rates (0.96±1.3 gC m^{-2} d^{-1}), with production in the SCM layer frequently
697 equaling or overtaking on the production in the euphotic layer (Fig. 7b). This is particularly
698 striking in late July, when the production peak is actually associated with a large enhancement
699 of the production in the SCM layer (4.9 gC m^{-2} d^{-1}). In contrast, the surface layer shows reduced
700 production rates (0.29±0.33 gC m^{-2} d^{-1}), a pattern also observed in the Ionian Sea (0.11±0.04
701 gC m^{-2} d^{-1}). In the Ionian Sea, the production is maximal in the euphotic zone, and very variable
702 and occasionally larger in the SCM layer (0.14±0.39 gC m^{-2} d^{-1}; Fig. 7d). The bio-optical diel
703 cycle-based method produces several occurrences of negative values in the SCM layer,
704 indicating that the 1D assumption is occasionally not satisfied in the lower part of the euphotic
705 layer. This could arise when physical processes that transport particles are larger than local
706 growth and loss of POC.

707 Our results support the hypothesis raised in previous studies (e.g. Mignot et al. 2014;
708 Barbieux et al. 2019) that, in the Ligurian temperate-like system, the SCM, which is in fact a
709 SBM, may be highly productive. Conversely, in the Ionian region, which shows similarities
710 with subtropical stratified oligotrophic systems, the SCM primarily reflects photoacclimation
711 and is less productive. Beyond these mean regional trends, both SCM systems exhibit some
712 temporal variability in production, a somewhat unexpected pattern at the core of the presumably
713 stable oligotrophic season.

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3.4 Production in the SCM layer in relation with the biotic and abiotic context

Here we investigate the temporal variability in the SCM layer production and attempt to interpret the observed patterns in the context of biological and abiotic conditions.

3.4.1 Phytoplankton and particulate assemblage

The pigment data collected during the BOUSSOLE and PEACETIME cruises concomitantly with the deployments of the fLig and fIon floats, respectively, are used as proxies for phytoplankton community structure (Fig. 8). In the Ligurian Sea, nanophytoplankton (mainly prymnesiophytes) appear as dominant contributors to the phytoplankton assemblage both in the surface layer (48±8%; Fig. 8b) and SCM layer (54±10%). Picophytoplankton (prokaryotes and small chlorophytes) and microphytoplankton (diatoms and dinoflagellates) are present in moderate proportions, with 30±11% and 22±5% in the upper layer, and 19±7% and 27±9% in the SCM layer, respectively (Figs. 8a and 8c). No marked shift in the community composition is observed during the timeseries, although occasional increase in the contribution of microphytoplankton is observed in the SCM layer, with no clear temporal trend (Fig. 8a and Appendix B). In the Ionian Sea, the surface layer displays large contribution of nanophytoplankton (56±2%; Fig. 8e) and, to a lesser extent, picophytoplankton (29±3%; Fig. 8d). However, the SCM level is characterized by an enhanced contribution of microphytoplankton (diatoms) to the algal assemblage (49±5%; Fig. 8f), as discussed in Marañón et al. (2021). The Ionian PEACETIME data was limited to the period from May 25 to 28, 2017, and thus it was not possible to determine whether the composition of phytoplankton communities evolved with time. Although not characterized by the prokaryotic populations (*Synechococcus* and *Prochlorococcus*) that typically prevail in stratified oligotrophic environments, our observations are consistent with previous studies reporting enhanced contributions of nanophytoplankton (e.g. Gitelson et al. 1996; Vidussi et al. 2001) and the

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743 occurrence of diatoms at depth (Siokou-Frangou et al. 2010; Crombet et al. 2011; Marañón et
744 al. 2021) in the Mediterranean Sea.

745 Bio-optical properties and their ratios provide indication about variations in the constituents
746 (algal or nonalgal) and size of the particulate pool, the composition of the phytoplankton
747 assemblage and the physiological status of phytoplankton cells (e.g. Geider 1987; Ulloa et al.
748 1994; Stramski et al. 2004; Loisel et al. 2007). Here we consider the bio-optical ratios b_{bp} / c_p,
749 c_p / *Chl*, and b_{bp} / *Chl* in the SCM layer (Fig. 9). The b_{bp} / c_p ratio, while at slightly different
750 wavelengths (700 nm and 660 nm, respectively) are at absorption minima and thus this ratio is
751 comparable to the backscattering ratio b_{bp} / b_p. The b_{bp} / b_p ratio is a demonstrated proxy for
752 determining relative constituent composition (Twardowski et al. 2001), with phytoplankton
753 exhibiting lower ratios than nonalgal particles (approximately 0.5% and 1%, respectively; Boss
754 et al. 2004; Whitmire et al. 2007; Westberry et al. 2010). The b_{bp} / *Chl* and c_p / *Chl* ratios are
755 both proxies for the POC / *Chl* ratio (e.g. Claustre et al. 1999; Oubelkheir et al. 2005;
756 Behrenfeld et al. 2015; Álvarez et al. 2016), and thus an indicator of the contribution of
757 phytoplankton to the whole organic carbon pool. The variations are also interpreted as changes
758 in the composition of phytoplankton communities (e.g. Sathyendranath et al. 2009) and their
759 acclimation to the light-nutrient regime (e.g. Geider et al. 1987; Loisel & Morel 1998; Geider
760 et al. 1997; Cloern 1999) if one assumes that nonalgal particles are negligible (e.g., as indicated
761 by the backscattering ratio) or not varying in concentration. The differences between the b_{bp} /
762 *Chl* and c_p / *Chl* ratios lie in the fact that they are sensitive to different particle size ranges
763 (Roesler and Boss 2008) and, thus, when they are not correlated, one can qualitatively discern
764 differing dynamics across the phytoplankton size spectrum.

765 The b_{bp} / c_p ratio is very different between the Ligurian and Ionian Seas, with significantly
766 lower values in the Ligurian Sea (0.0068±0.0009, and 0.0095±0.0009; Fig. 9). These ratios
767 indicate that, in the general sense, the Ligurian Sea SCM is more phytoplankton dominated than

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770 the Ionian Sea SCM, which tends towards nonalgal particles. In the Ligurian Sea, the b_{bp} / c_p
771 ratio remains <0.0087 and reaches a minimum of 0.0055 over the period coinciding with the
772 production event from mid-July to mid-August (Fig. 9a), consistent with phytoplankton
773 dominance. In contrast, in the Ionian Sea SCM, the b_{bp} / c_p ratio increases from 0.0085 in late
774 May, peaking at nearly 0.012 in early August, and then decreasing back to 0.0085 in September
775 (Fig. 9b). The tendency towards a ratio of 0.01 (or 1%) in the core of the oligotrophic season,
776 evidences the increased proportion of nonalgal particles to the bulk pool as previously observed
777 in oligotrophic environments (Yentsch & Phinney 1989; Stramski et al. 2004; Loisel et al.
778 2007).

779 The c_p and b_{bp} to *Chl* ratios exhibit not only different temporal patterns between the Ligurian
780 and Ionian Sea SCMs, they also exhibit different relative values. The c_p / *Chl* ratio in the
781 Ligurian Sea SCM is higher than that of the Ionian Sea, ranging from 0.18 to 0.45 m^2 mg Chl^{-1}
782 (mean value of 0.29±0.06 m^2 mg Chl^{-1}), compared to 0.15 to 0.26 m^2 mg Chl^{-1} (mean value
783 of 0.20±0.03 m^2 mg Chl^{-1}), respectively. These results are consistent with the study of Loisel
784 & Morel (1998), reporting low values ranging within 0.1–0.2 m^2 mg Chl^{-1} at the deep
785 chlorophyll maximum level of oligotrophic sites. In contrast, although the b_{bp} / *Chl* ratio in the
786 Ligurian Sea SCM ranges from 0.0011 to 0.0023 m^2 mg Chl^{-1}, and the Ionian Sea from 0.0015
787 to 0.0021 m^2 mg Chl^{-1}, they have essentially identical mean values over the time series
788 (0.0017±0.0006 and 0.0017±0.0001, respectively). The b_{bp} / *Chl* ratio being more sensitive to
789 small-sized particles than the c_p / *Chl* ratio, these results suggest that, in the SCM layer, the
790 POC in the small size fractions of the Ligurian and Ionian Seas is more similar than that in the
791 large size fractions.

792 Temporally, the Ligurian Sea SCM exhibits significantly more temporal variations in both
793 ratios compared to the Ionian Sea SCM, and the temporal variations are highly correlated. Both
794 the c_p / *Chl* and b_{bp} / *Chl* ratios in the Ligurian Sea SCM exhibit a peak at the start of the time

a supprimé: (0.87%)

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series in late May that decreases to mid-July, followed by a second peak during the period coinciding with the production episode from mid-July to mid-August, and then a third increase until the end of the time series (Figs. 9b–c). In contrast, both ratios in the Ionian Sea SCM exhibit significantly reduced temporal variability (Figs. 9e–f), with a weak increase is observed starting in early August.

Despite differing temporal variability, the b_{bp} / *Chl* ratio in both Seas remains moderate to low (<0.0025 m^2 mg Chl^{-1}; Figs. 9c and 9f), consistent with global SCM values (Barbieux et al., 2018). The enhanced b_{bp} / *Chl* values observed in the Ligurian Sea SCM in early May, late July and late August suggest an increased contribution of small (pico- and nano-sized) phytoplankton (Cetinić et al. 2012; Cetinić et al. 2015). Yet, the BOUSSOLE pigment data do not reveal pronounced changes in the phytoplankton assemblage. Low-light conditions typically prevailing in the SCM layer are usually associated with low values of the c_p / *Chl* and b_{bp} / *Chl* ratios (e.g. Loisel & Morel 1998; Behrenfeld & Boss 2003; Westberry et al., 2008; Barbieux et al. 2019). These low values may reflect photoacclimation, by which phytoplankton organisms increase their intracellular *Chl*, and/or an increase in the fluorescence-to-*Chl* ratio in relation to limited or null non-photochemical chlorophyll fluorescence quenching. Nevertheless, the temporal variability in the c_p / *Chl* and b_{bp} / *Chl* values may be resulting from fluctuations in the light conditions at the SCM in the Ligurian Sea. In the Ionian Sea, the invariant low c_p / *Chl* and b_{bp} / *Chl* values are consistent with both photoacclimation of phytoplankton to low-light conditions and a diatom-dominated phytoplankton assemblage (Cetinić et al. 2015; Barbieux et al. 2018). The relatively stable ratios observed in this region suggest a relative steadiness in the composition of the phytoplankton assemblage over the considered period.

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3.4.2 Relation to abiotic conditions

The Ligurian Sea exhibits enhanced community production during the period from mid-July to mid-August 2014, which is associated with a comparatively moderate increase in the biomass indicators (Figs. 3–4) and c_p-derived POC (Fig. 7a). During this time period, the depth of the SCM shoals by 25 m. This change occurs concurrently with a slight shoaling of the density isopycnals (Figs. 3a–c), and a doubling (from 0.5 to 1 mol quanta m^{-2} d^{-1}) in the daily PAR within the SCM layer (Fig. 10a). Therefore, we suggest that the observed production episode may result from physical forcing that induces an upwelling of the water mass, thereby resulting in an alleviation of the light/nutrient limitation and an adequate balance between light and nutrient availability in the SCM layer. This SCM production episode is associated with a moderate phytoplankton biomass (0.8 Chl mg m^{-3}), dominated by a nanoplankton community. It coincides with an increase in the c_p / *Chl* and b_{bp} / *Chl* ratios, which we attribute to a boost in the carbon-to-*Chl* ratio resulting from production in enhanced light conditions. Because it appears to result from changes in light conditions, we may attribute this production event to photosynthetic (not community) growth.

a supprimé: phytoplankton

In the Ionian Sea, the depth of the SCM follows the depth of the isopycnal 28.85 during the period from late to May to mid-August 2017 (Figs. 3d–f). In mid-August, the SCM reaches its deepest point (~125 m) concurrent with deepening isopycnals, decreased PAR levels within the SCM layer (Fig. 10b) and minimum values of *Chl*, c_p and b_{bp}. Afterwards, the SCM depth decouples from the position of the isopycnals (Fig. 3d–f), the SCM becomes shallower and the mean daily PAR in the SCM layer increases. Nevertheless, the observed temporal fluctuations in the abiotic forcing and biological indicators do not seem to relate with any clear change in the community production (Figs. 7d–f). This suggests that physics-induced changes in the position of the SCM are not sufficient to alleviate the light and/or nutrient limitation occurring at this time in the study location (Guieu et al. 2020). Considering the large contribution of

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diatoms at the SCM, one may conclude that the low, yet non-negligible, production levels estimated in the SCM layer are supported by diatoms. This result supports previous findings that indicate, contrary to the classic view of diatoms thriving essentially in dynamic eutrophic conditions, these organisms have the ability to maintain in stratified oligotrophic environments, including in deep layers under low light-nutrient conditions (Kemp & Villareal 2013; Kemp & Villareal, 2018). This was also highlighted by Marañón et al. (2021) based on observations in the Mediterranean Sea (PEACETIME cruise).

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3.5 Contribution of the SCM to the water column production

In order to assess the relative contribution of the SCM layer to the production occurring in the whole water column, we compare the c_p-based estimates integrated within the productive layer (0–1.5 Z_{eu}) and SCM layers. Our results suggest that, for these oligotrophic systems, the production integrated within the SCM layer represents a substantial fraction (F_{SCM}) of the gross community production integrated within the productive layer. This is particularly the case for the Ligurian Sea where F_{SCM} reaches ~42%, and to a lesser extent for the Ionian Sea with F_{SCM} ~16%.

Subtropical stratified oligotrophic gyres cover 45% of the global ocean (McClain et al. 2004). Assuming that the Ionian Sea is representative of such systems (e.g. Mignot et al. 2014; Barbieux et al. 2019), and extrapolating the estimated relative contribution of the SCM layer to the water column production in the Ionian (F_{SCM} ~16%), then the SCM layer would contribute ~7% of the community production of the water column on a global scale (i.e. F_{SCM} of 16% multiplied by a global spatial occurrence of 45%). In addition, using a global BGC-Argo database, Cornec et al. (2021) estimated that SCMs in oligotrophic subtropical gyres behave as SBM 8–42% of the year, depending on the season. Thus, assuming the Ligurian SCM oligotrophic summer system as a reference for SBM, the contribution of the SCM layer to the

global water column production could seasonally reach 19% (i.e. F_{SCM} of 42% multiplied by a global spatial occurrence of 45%).

We recognize that these estimates are very crude and need to be refined and confirmed in future studies. Yet they suggest that the contribution of the SCM layer to the water column production may be significant globally, although commonly ignored. Our observations are consistent with previous findings in the Mediterranean Sea (Crombet et al. 2011; Marañón et al. 2021) and in other regions of the world ocean (Kemp & Villareal 2013; Mignot et al. 2014), and suggest that stratified oligotrophic systems should no longer be considered as steady oceanic deserts and that their biogeochemical contribution should be accounted for and better quantified to improve global carbon budgets.

4 Conclusions

The present study represents a first attempt to apply the bio-optical diel cycle-based method (Siegel et al. 1989; Claustre et al. 2008) to the c_p and b_{bp} coefficients measured by two BGC-Argo profiling floats. It aims to quantify gross community production in different layers of the water column, the subsurface chlorophyll maximum (SCM) layer in particular, during the oligotrophic summer season in two distinct systems of the Mediterranean, i.e. the Ligurian Sea and the Ionian Sea.

From a methodological point of view, our results indicate that, compared to the c_p coefficient, the diel cycle of the b_{bp} coefficient is not an optimal proxy for the daily POC variations regardless of the water column layer and (Ligurian or Ionian) region under consideration. These results have major implications for use of the methodology with geostationary ocean color missions and standard BGC-Argo profiling floats that yield only the b_{bp} coefficient. The present results thus argue in favor of a frequent implementation onto BGC-Argo floats of transmissometers (c_p sensors), which provide information on a suite of key

a supprimé: , so that we are not confident using the b_{bp}-based gross community production estimates, although it may provide a more robust proxy for the fraction of particulate matter in the smaller size classes

a supprimé: Our results for the surface layer of the Ligurian Sea are consistent with previous studies from moored observations (Kheireddine & Antoine 2014; Barnes & Antoine 2014), and we found they are valid for the entire water column and for both the Ligurian and Ionian Seas.

biogeochemical variables (Claustre et al. 2020), from phytoplankton community composition (Rembauville et al. 2017), to particle flux export (Briggs et al. 2011; Estapa et al. 2013) and, as demonstrated here, biological production (White et al. 2017; Briggs et al. 2018).

Our c_p-based gross community production rates compare consistently with previous estimates from a similar approach applied to oligotrophic waters (Claustre et al. 2008; Gernez et al. 2011; Barnes & Antoine 2014). Nevertheless, these estimates on average decrease by 25% or increase by 37% depending on the used c_p-to-POC relationship, which is not negligible and raises the question of the selection of an empirical bio-optical relationship for converting c_p into POC equivalent. Hence, we recommend POC sampling simultaneously to BGC-Argo floats deployment. This will help to better constrain bio-optical relationships and ultimately improve the reliability of the biomass and production estimates.

Our results indicate that both the Ligurian and Ionian Seas may sustain relatively large levels of gross community production during the oligotrophic summer period, with a substantial contribution by the SCM layer, a feature characteristic of oligotrophic systems that is typically considered as steady and non-productive. Our results also suggest that the contribution of the SCM layer varies broadly depending the considered system, whether seasonally (Ligurian Sea) or permanently (Ionian) oligotrophic. These results agree with previous BGC-Argo-based studies describing the occurrence and functioning of SCM systems in the global ocean (Mignot et al. 2014; Cornec et al. 2021) and Mediterranean Sea (Lavigne et al. 2015; Barbieux et al. 2019), and offer a first attempt to quantify biological production in such systems.

Our study emphases the promising potential of BGC-Argo profiling floats for providing a non-intrusive, high-frequency assessment of POC production within the whole water column, which is critical in particular for applications to stratified oligotrophic environments with recurring or permanent SCMs. The present results, based on data from two Mediterranean environments, should be confirmed in the future through the deployment of "multi-profiling"

a supprimé: These values are also consistent with estimates of primary production either computed from the model of Morel (1991) coupled to the considered BGC-Argo data, or published in the literature, although admittedly higher. This is unsurprising because the present estimates are based on the c_p coefficient, which accounts for both autotrophic and heterotrophic organisms (not just phytoplankton). This nevertheless raises the question of the selection of an empirical bio-optical relationship, which is key to converting c_p into POC equivalent. In the present study

a supprimé: c_p-derived production

a supprimé: bio-optical

a supprimé: In the Ligurian, the SCM behaves as a subsurface biomass maximum (SBM) and appears to respond to episodic abiotic forcing, with increased production rates coinciding with enhanced light availability in response to shoaling isopycnals and SCM. In this system, the particle assemblage is dominated by phytoplankton organisms, mainly nanoflagellates. In contrast, the Ionian SCM layer essentially reflects photoacclimation of phytoplankton cells to prevailing environmental conditions. It does not seem affected by modifications in abiotic forcing, although the phytoplankton assemblage appears to be dominated by diatoms.

a supprimé: More generally, our study suggests that the contribution of the SCM layer to the water column production varies broadly depending the considered system, whether seasonally (~42% in the Ligurian Sea) or permanently (~16% in the Ionian Sea) oligotrophic.

BGC-Argo floats in the broad, remote subtropical gyres. In such systems, biological production is not constant but, instead, shows high temporal heterogeneity (Karl et al. 2003; Claustre et al. 2008) that may be missed by traditional sampling, leading to a potential underestimate of the biogeochemical impact of these systems in global carbon budgets. Implementing such a BGC-Argo-based approach to carbon flux quantification becomes even more important in the perspective of climate change, which is predicted to induce an expansion of stratified oligotrophic gyres and an oligotrophication of the oceans (Sarmiento et al. 2004) as already observed from satellite imagery (Polovina et al. 2008; Signorini et al. 2015).

Author contribution MB, JU and AB designed the work and prepared the manuscript. MB processed the data and conducted the analyses. MB, JU and CR prepared the plots. AM and BG developed the biological production model. AM helped with the implementation of the model and the interpretation of the output data. CR contributed to the analysis of the diel bio-optical variability, interpretation of bio-optical data and the organization of the manuscript. HC contributed to the interpretation of the BGC-Argo data and biological production. HL helped with the interpretation of the bio-optical data and the global extrapolation of the results. VT and FDO contributed to the BGC-Argo float deployments and interpretation of the physical data. AP prepared and tested the BGC-Argo floats prior to deployment and set up the raw data stream. EL and CP developed the BGC-Argo float version used in this study and contributed to float preparation. CS handled BGC-Argo data archiving and distribution. All authors reviewed and approved the manuscript.

Data availability The BGC-Argo profiling float data and metadata used in this paper may be downloaded from the Argo GDAC (http://doi.org/10.17882/42182). All other original data are available from the Argo Global Data Assembly Center (ftp://ftp.ifremer.fr/ifremer/argo).

These data were collected and made freely available by the International Argo Program and the national programs that contribute to it (http://www.argo.ucsd.edu; https://www.ocean-ops.org). The Argo Program is part of the Global Ocean Observing System. The PEACETIME project pigment data are available from the SEANOE archive under the following reference: Guieu et al., Biogeochemical dataset collected during the PEACETIME cruise, SEANOE, https://doi.org/10.17882/75747, 2020. The BOUSSOLE program pigment data may be accessed upon request (http://www.obs-vlfr.fr/Boussole/html/boussole_data/login_form.php).

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Figure captions

Figure 1: Trajectories of the two BGC-Argo profiling floats fLig (WMO6901776) and flon (WMO6902828) deployed respectively in the Ligurian Sea (green) and the Ionian Sea (blue), superimposed onto a 9-km resolution summer climatology of surface chlorophyll *a* concentration (in mg m^{-3}) derived from MODIS Aqua ocean color measurements. The asterisk-shaped symbol indicates the geographic location of the BOUSSOLE site.

Figure 2: Schematic representation of the diel variations of the depth-integrated bio-optical properties converted to POC biomass (B) and the sampling strategies employed in the (a) Ligurian Sea and (b) Ionian Sea. The diamond-shaped symbols indicate schematically the float profile times, labeled with time stamps associated with sunrise (sr), noon (n), sunset (ss) and midnight (m), with the corresponding POC biomass estimated within the considered layer (e.g., $B(t_{sr})$, etc.). The numeric subscripts (+1, +2, +4 or +5) indicate the number of days since the first profile of the summertime time series.

Figure 3: Time series of the vertical distribution of the *Chl* (a and d), b_{bp} (b and e), c_p (d and f), and instantaneous midday PAR (d and h), in the Ligurian Sea (left) and the Ionian Sea (right). The euphotic depth (Z_{eu}; white line), the Mixed Layer Depth (MLD; black line), the depth of the SCM (magenta line), and the depth of the isopycnal 28.85 expressed as σ_t (blue line), are superimposed onto the bio-optical timeseries. The dashed lines indicate the dates at which the c_p and the b_{bp} values in the SCM layer reach a minimum.

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Figure 4: Temporal evolution of *Chl* (a and d), c_p (b and e), and b_{bp} (c and f) in the surface (dark green) and SCM (red) layers for the Ligurian Sea (left) and the Ionian Sea (right). The dashed lines indicate the dates when the values of c_p and b_{bp} in the SCM layer reach a minimum.

Figure 5: Example of the variations of the c_p (a) and b_{bp} (b) coefficients at the daily time scale in the Ionian Sea in the SCM layer during the interval from September 2 to September 6, 2017. The grey shaded area indicates the nighttime.

Figure 6: Comparison of the biological production integrated within the euphotic layer, derived from the diel cycle of c_p (blue) or b_{bp} (yellow) or computed using the bio-optical primary production model of Morel (1991) (purple) for the Ligurian Sea (a) and the Ionian Sea (b).

Figure 7: Temporal evolution of the POC and community production derived from the diel cycle of c_p in the Ligurian Sea (a–b) and the Ionian Sea (c–d) and integrated in three different

layers of the water column: surface (dark green), euphotic (light blue) and SCM (red) layers. The dotted lines indicate the dates when c_p in the SCM layer reaches a minimum.

Figure 8: Depth-interpolated timeseries of the relative contributions (%) to the chlorophyll *a* concentration of the micro- (a and d), nano- (b and e) and picophytoplankton (c and h) derived from HPLC pigment determinations in the Ligurian Sea (BOUSSOLE site; left) and Ionian Sea (PEACETIME cruise; right). The pigment data were collected at the BOUSSOLE site in the same region and at the same time period as the fLig float deployment (see text section 2.1). The fIon float was deployed concurrently to sampling for HPLC pigments at the PEACETIME ION station. Pigment data collected at ION over four days prior to float deployment are shown. As an indication, the depths of the euphotic depth (Z_{eu}; white dashed line), mixed layer (MLD; black dashed line) and SCM (magenta dashed line) derived from the BGC-Argo float measurements, as in Fig. 3, are overlaid onto the pigment data.

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Table 1: POC-to-c_p relationships from the literature, with POC and c_p in units of mg m^{-3} and m^{-1}, respectively.

Reference	Region	Relationship
Marra et al. (1995)	North Atlantic	POC = 367 $c_p(660)$ + 31.2
Claustre et al. (1999)	Equatorial Pacific	POC = 501.81 $c_p(660)$ + 5.33
Oubelkheir et al. (2005)	Mediterranean	POC = 574 $c_p(555)$ – 7.4
Behrenfeld & Boss (2006)	Equatorial Pacific	POC = 585.2 $c_p(660)$ + 7.6
Gardner et al. (2006)	Global Ocean	POC = 381 $c_p(660)$ + 9.4
Stramski et al. (2008)	Pacific and Atlantic, including upwelling	POC = 661.9 $c_p(660)$ – 2.168
Loisel et al (2011)	Mediterranean	POC = 404 $c_p(660)$ + 29.25
Cetinić et al. (2012)	North Atlantic	POC = 391 $c_p(660)$ – 5.8

Table 2: POC-to-b_{bp} relationships from the literature, with POC and b_{bp} in units of mg m^{-3} and m^{-1}, respectively.

Reference	Region	Relationship
Stramski et al. (2008)	Pacific and Atlantic, including upwelling	POC = 71002 $b_{bp}(555)$ – 5.5
Loisel et al (2011)	Mediterranean	POC = 37550 $b_{bp}(555)$ + 1.3
Cetinić et al. (2012)	North Atlantic	POC = 35422 $b_{bp}(700)$ – 14.4

Table 3: Mean and range (%) in relative daily variations ($\widehat{\boldsymbol{m}}\boldsymbol{\Delta}$ and $\widehat{\boldsymbol{r}}\boldsymbol{\Delta}$, respectively) in the diel cycle of c_p and b_{bp} computed for each float over the entire time series, for the two considered regions and in the surface (0-Z_{pd}) and SCM layers of the water column.

		Surface layer		SCM layer	
Region		$\boldsymbol{\Delta c_p}$	$\boldsymbol{\Delta b_{bp}}$	$\boldsymbol{\Delta c_p}$	$\boldsymbol{\Delta b_{bp}}$
Ligurian Sea	$\widehat{\boldsymbol{m}}\boldsymbol{\Delta}$	12.7	-2.3	14.5	3.8
	$\widehat{\boldsymbol{r}}\boldsymbol{\Delta}$	256.7	28.5	194.8	107.8
Ionian Sea	$\widehat{\boldsymbol{m}}\boldsymbol{\Delta}$	0.55	0.23	1.16	0.06
	$\widehat{\boldsymbol{r}}\boldsymbol{\Delta}$	54.4	21.2	102.4	57.3

Table 4: Estimates of primary and community production (in units of gC m^{-2} d^{-1}) from the literature in areas of the Mediterranean Sea comparable, when possible, to the considered study regions.

Primary production					
Method	**Reference**	**Area**	**Period**	**Layer**	**Estimate**
Ocean color-coupled bio-optical model	Morel & André (1991)	Western basin	1981	0–Z_{eu}	0.26
	Antoine et al. (1995)	Whole basin	1979-1981	0–1.5Z_{eu}	0.34
	Bosc et al. (2004)	Western basin	1998-2001	0–1.5Z_{eu}	0.45
	-	Eastern basin	-	-	0.33
	Uitz et al. (2012)	Bloom region	May-Aug 1998-2007	0–1.5Z_{eu}	0.26–0.82
	-	No bloom region	-	-	0.22–0.69
Biogeochemical model	Lacroix & Nival (1998)	Ligurian Sea		0–200 m	0.13
	Allen et al. (2002)	Ligurian Sea		0–Z_{eu}	0.33
	-	Ionian Sea		-	0.14
In-situ ^{14}C measurements	Minas (1970)	Northwestern basin	1961-1965	Surface	0.21
	Magazzu & Decembrini (1995)	Ionian Sea	1983-1992	0–Z_{eu}	0.22
	Turley et al. (2000)	Ligurian Sea	Oct 1997, Apr-May 1998	0–Z_{eu}	0.5
	Marañón et al. (2021)	Ionian Sea	May 2017	0–200 m	0.19

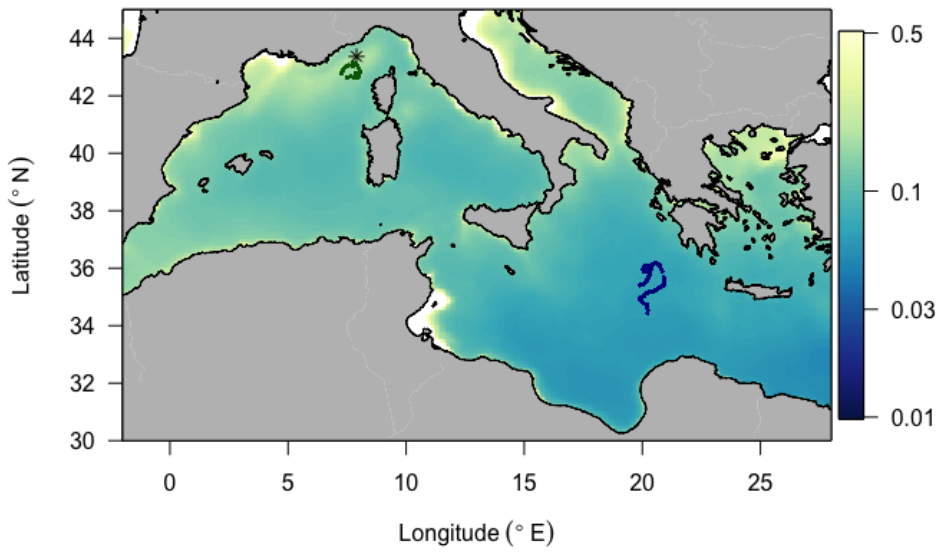
Gross community production					
Method	**Reference**	**Area**	**Period**	**Layer**	**Estimate**
c_p diel cycle-based method	Barnes & Antoine (2014)	Ligurian Sea	May-Aug 2006-2011	0–Z_{eu}	0.8–1.5

Table 5: Comparison of the mean rates ± SD (gC m^{-2} d^{-1}) of the community production integrated within the euphotic layer, derived from the application of the bio-optical diel cycle-based method to the c_p measurements, using different bio-optical relationships from the literature for converting the c_p values into POC biomass.

Reference	Ligurian Sea	Ionian Sea
Marra et al. (1995)	0.89±0.84	0.35±0.09
Claustre et al. (1999)	1.22±1.16	0.48±0.12
Oubelkheir et al. (2005)	1.18±1.13	0.46±0.11
Behrenfeld & Boss (2006)	1.43±1.35	0.56±0.14
Gardner et al. (2006)	0.93±0.88	0.36±0.09
Stramski et al. (2008)	1.62±1.54	0.63±0.16
Loisel et al. (2011)	0.98±0.92	0.38±0.10
Cetinić et al. (2012)	0.96±0.91	0.37±0.09

Table 6: Community production mean rates ± SD (gC m^{-2} d^{-1}) derived from the application of the bio-optical diel cycle-based method to the c_p measurements in the two considered regions. The production rates are integrated within the surface, subsurface maximum (SCM), and euphotic layers.

Variable	Ligurian Sea			Ionian Sea		
	Euphotic	Surface	SCM	Euphotic	Surface	SCM
POC (gC m^{-2} d^{-1})	3.67±1.11	0.36±0.17	3.86 ± 1.20	1.88 ±0.24	0.34±0.14	0.93±0.31
GCP (gC m^{-2} d^{-1})	1.18±1.13	0.29±0.33	0.96±1.28	0.46±0.11	0.11±0.04	0.14± 0.39



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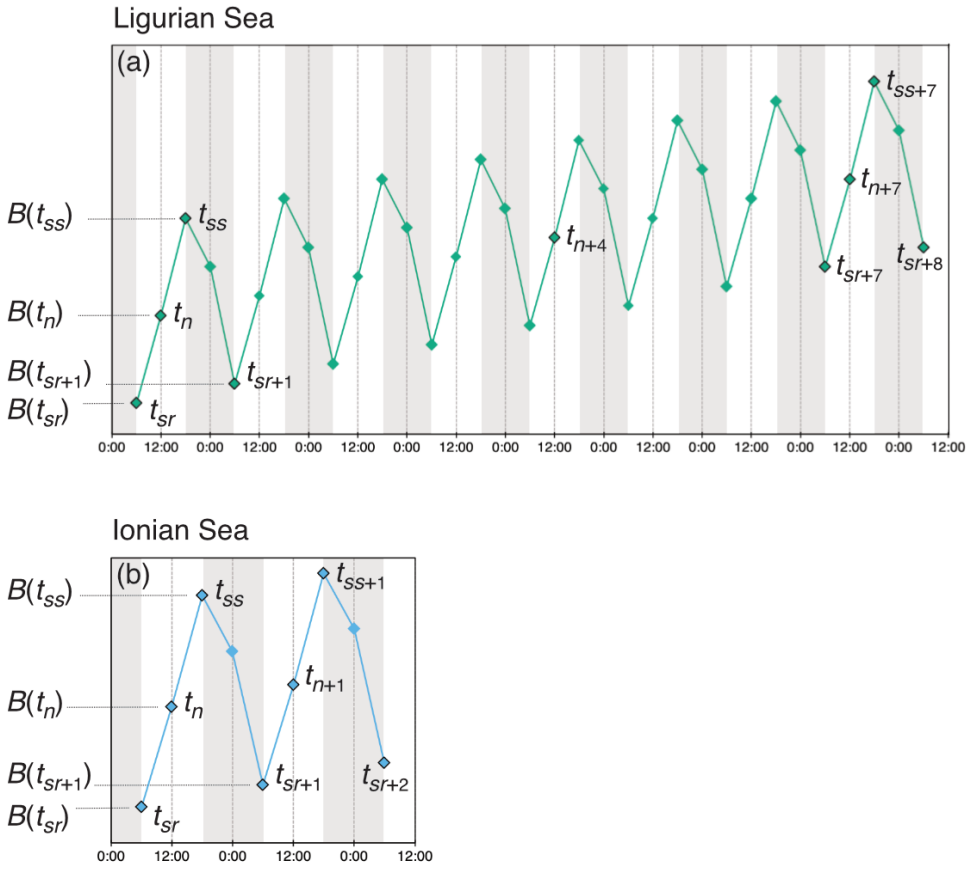

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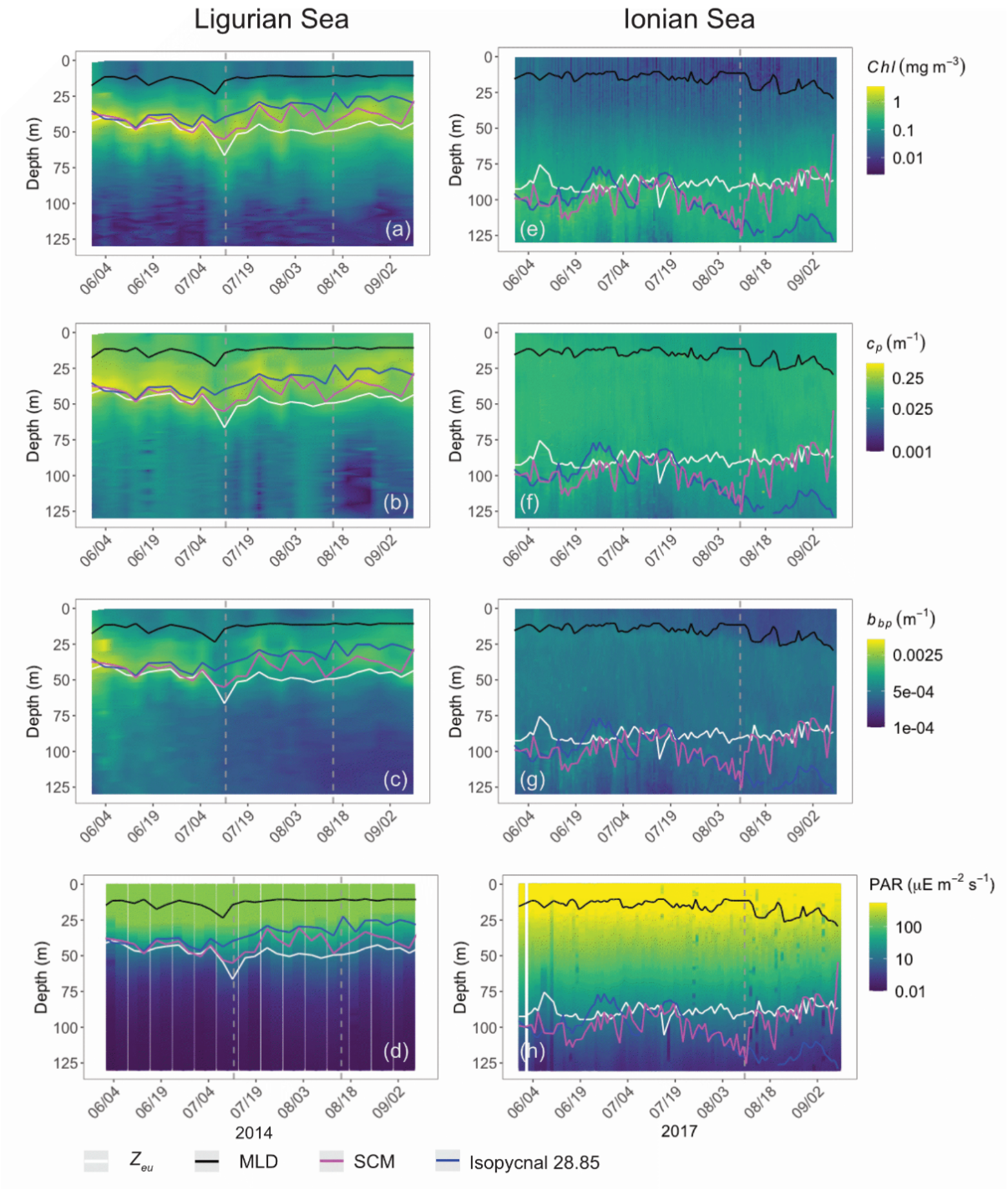

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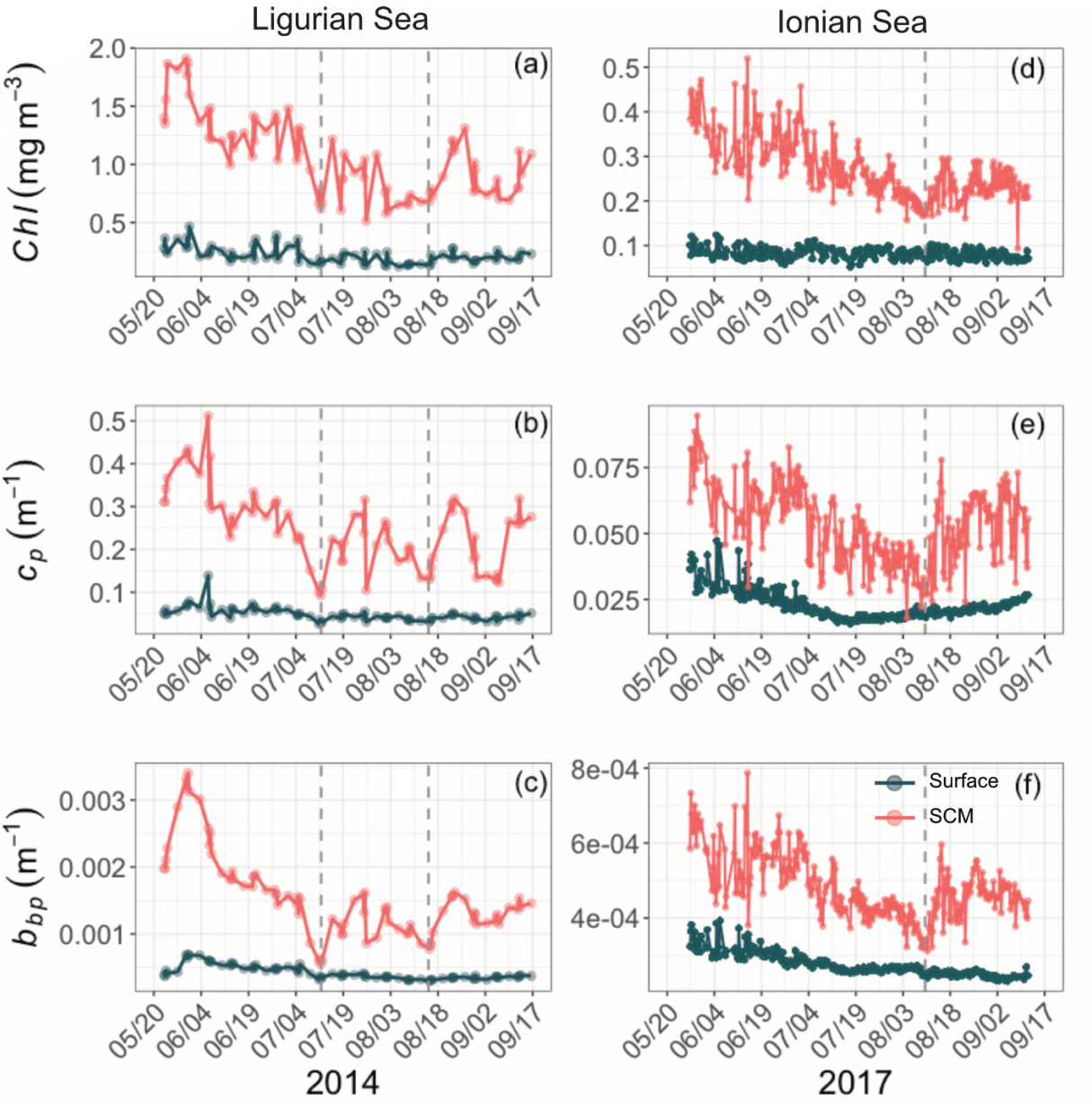

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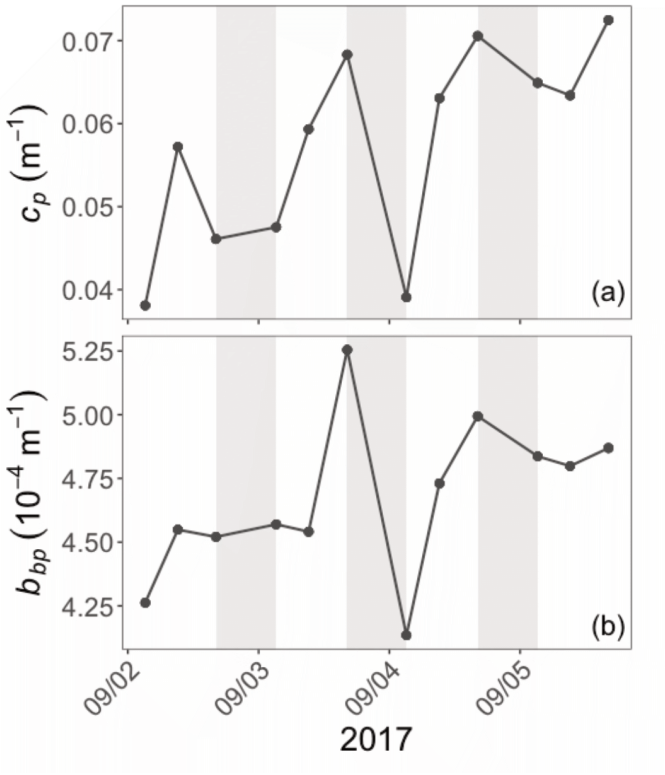

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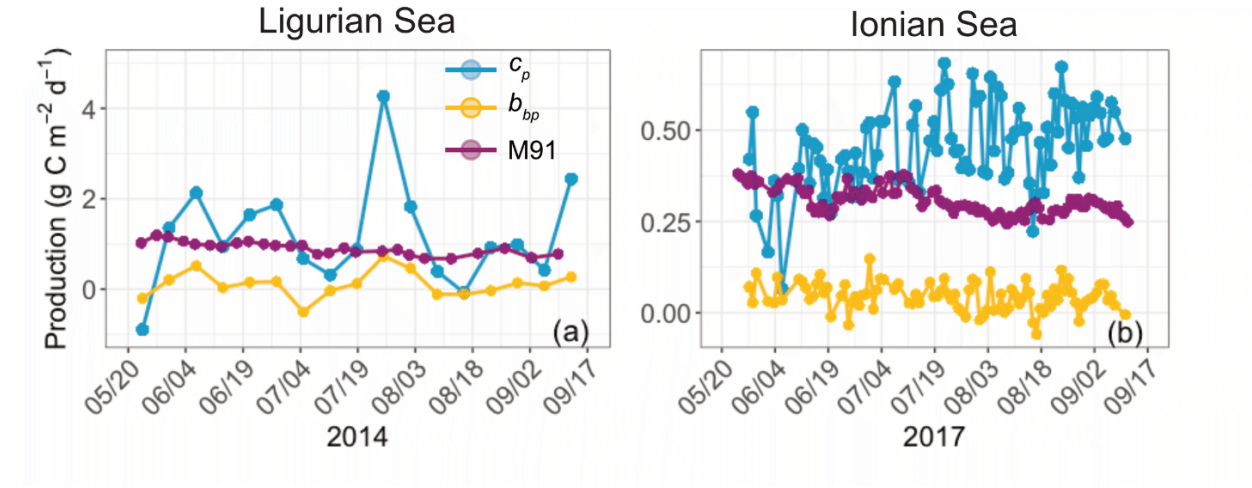

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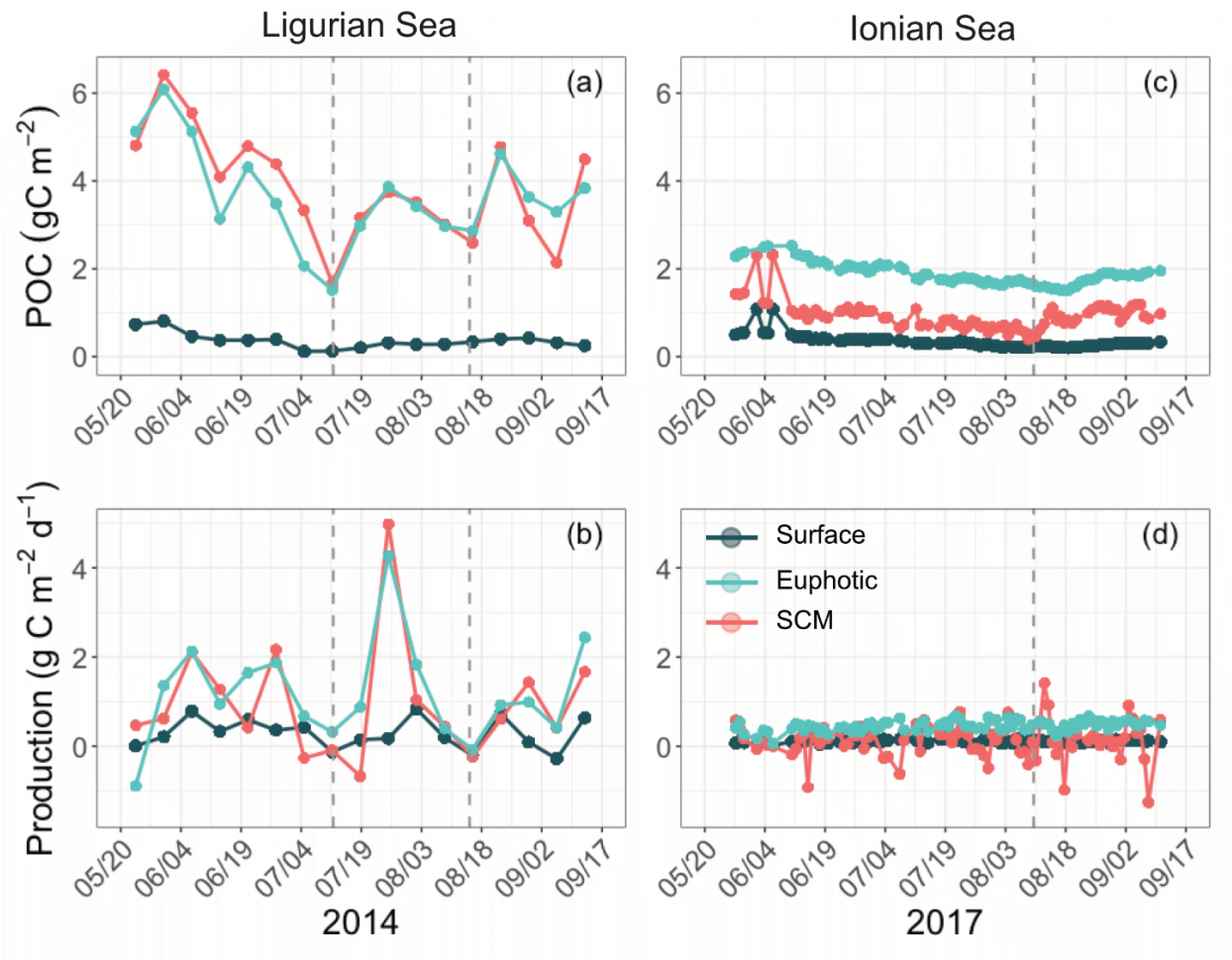

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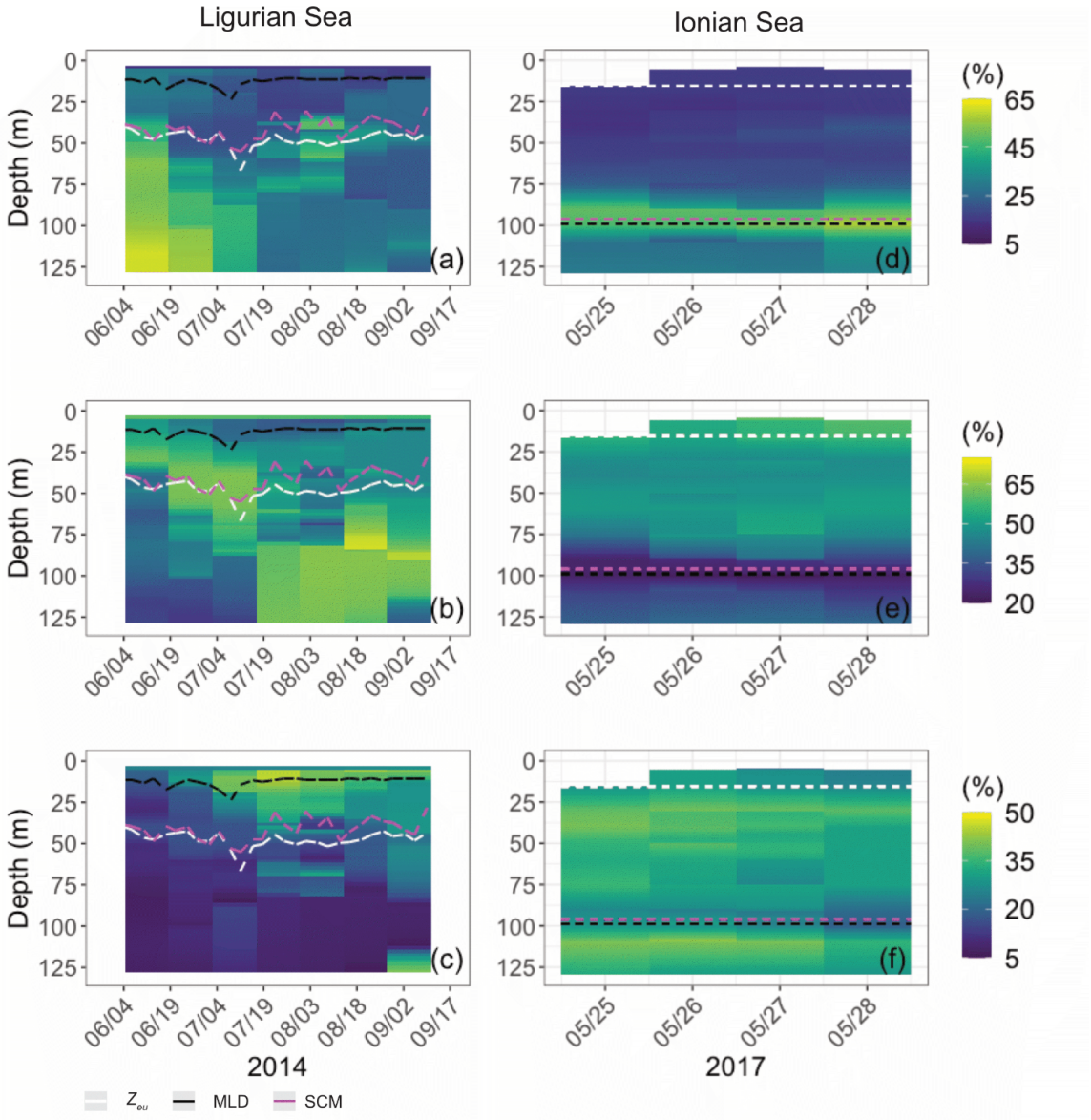

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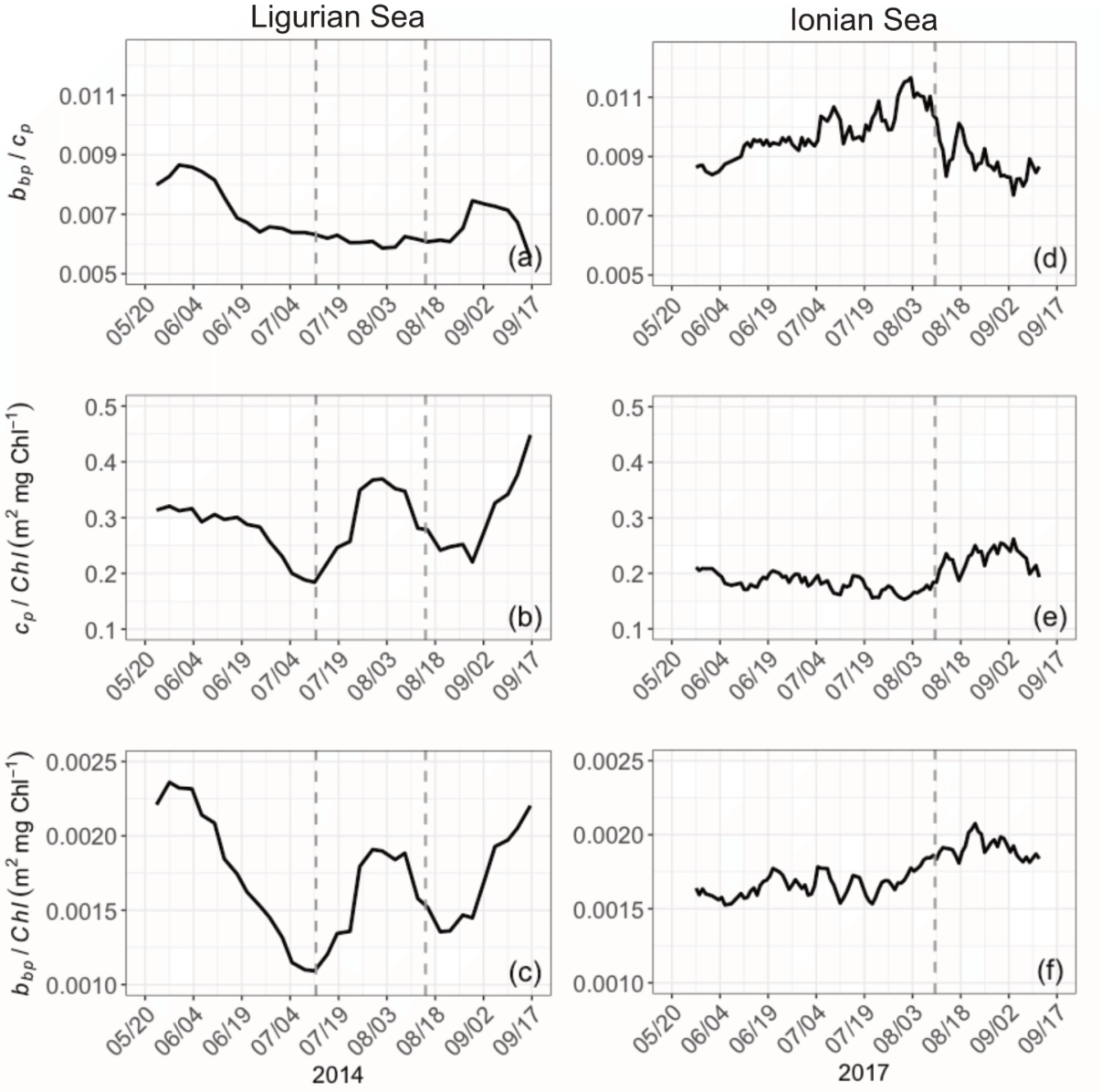

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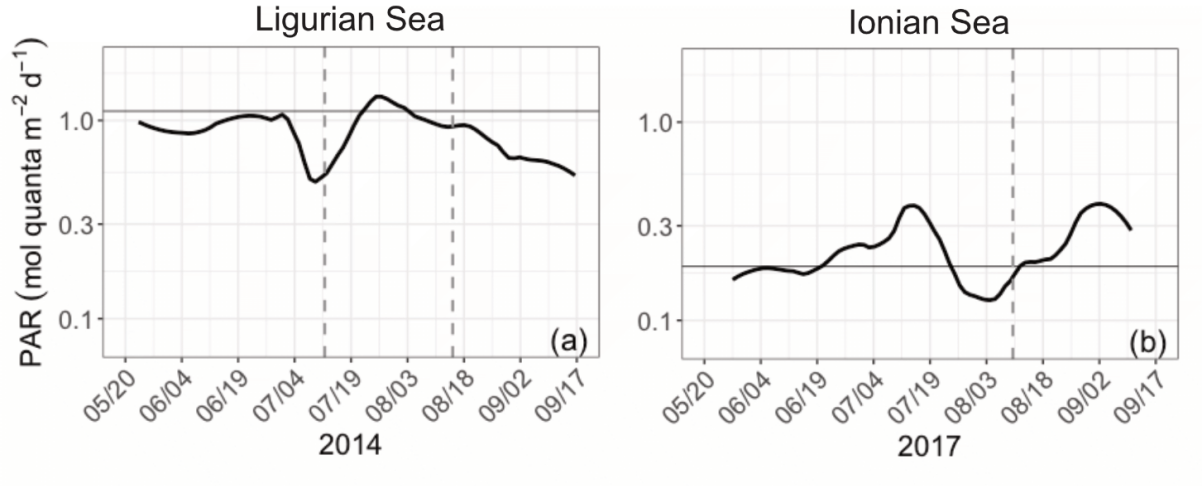

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APPENDIX A

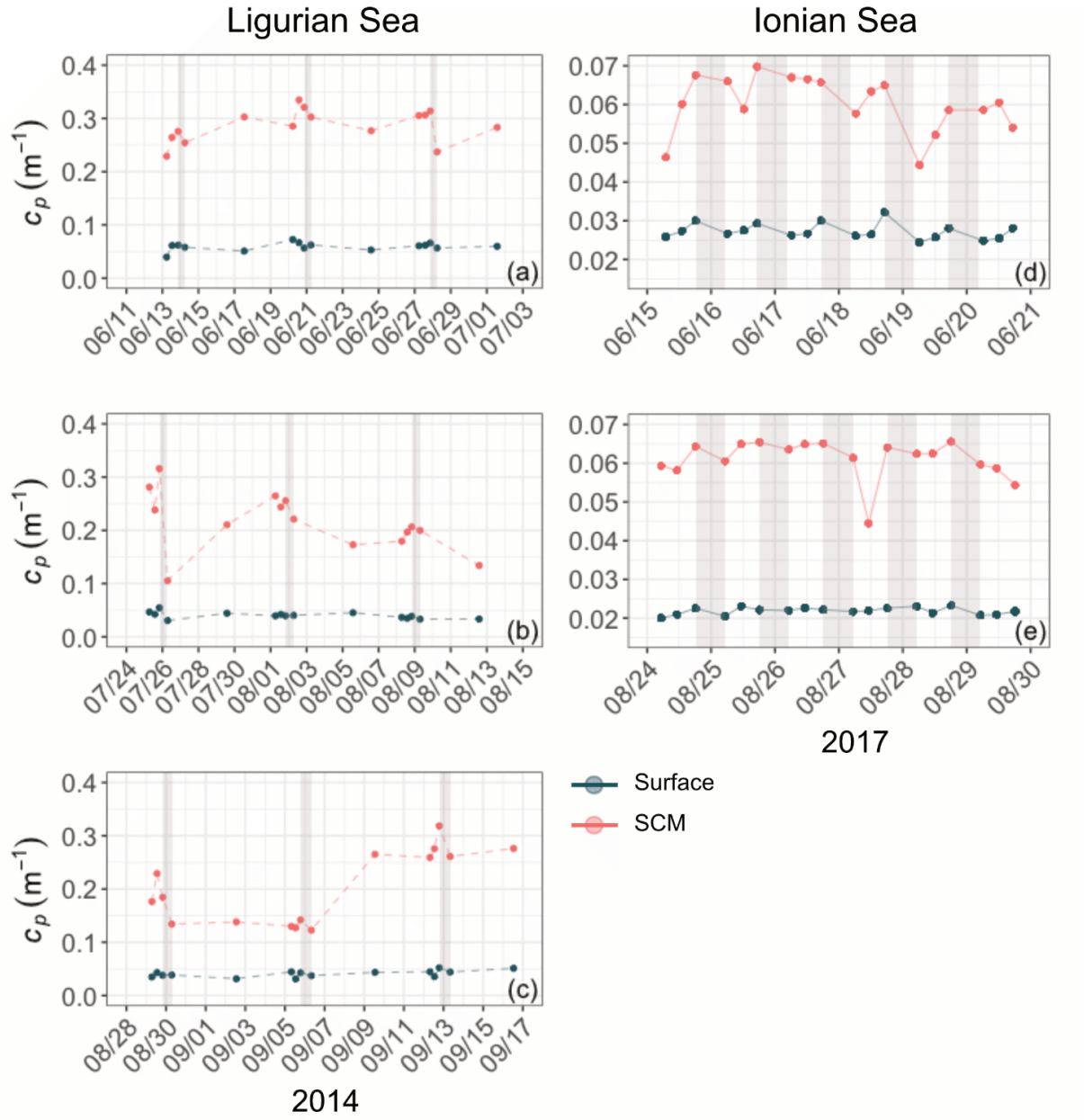

Figure A1: Example of time series of the c_p coefficient in the surface (red) and SCM (dark green) layers, chosen within the time periods indicated by the dashed lines in Figs 3-4, from May 24 to July 14, 2014 (a), July 14 to August 16, 2014 (b), and August 16 to September 13, 2014 for the Ligurian Sea (left), and from May 28 to August 11, 2017 (d) and August 11 to September 11, 2017 (e) for the Ionian Sea (right).

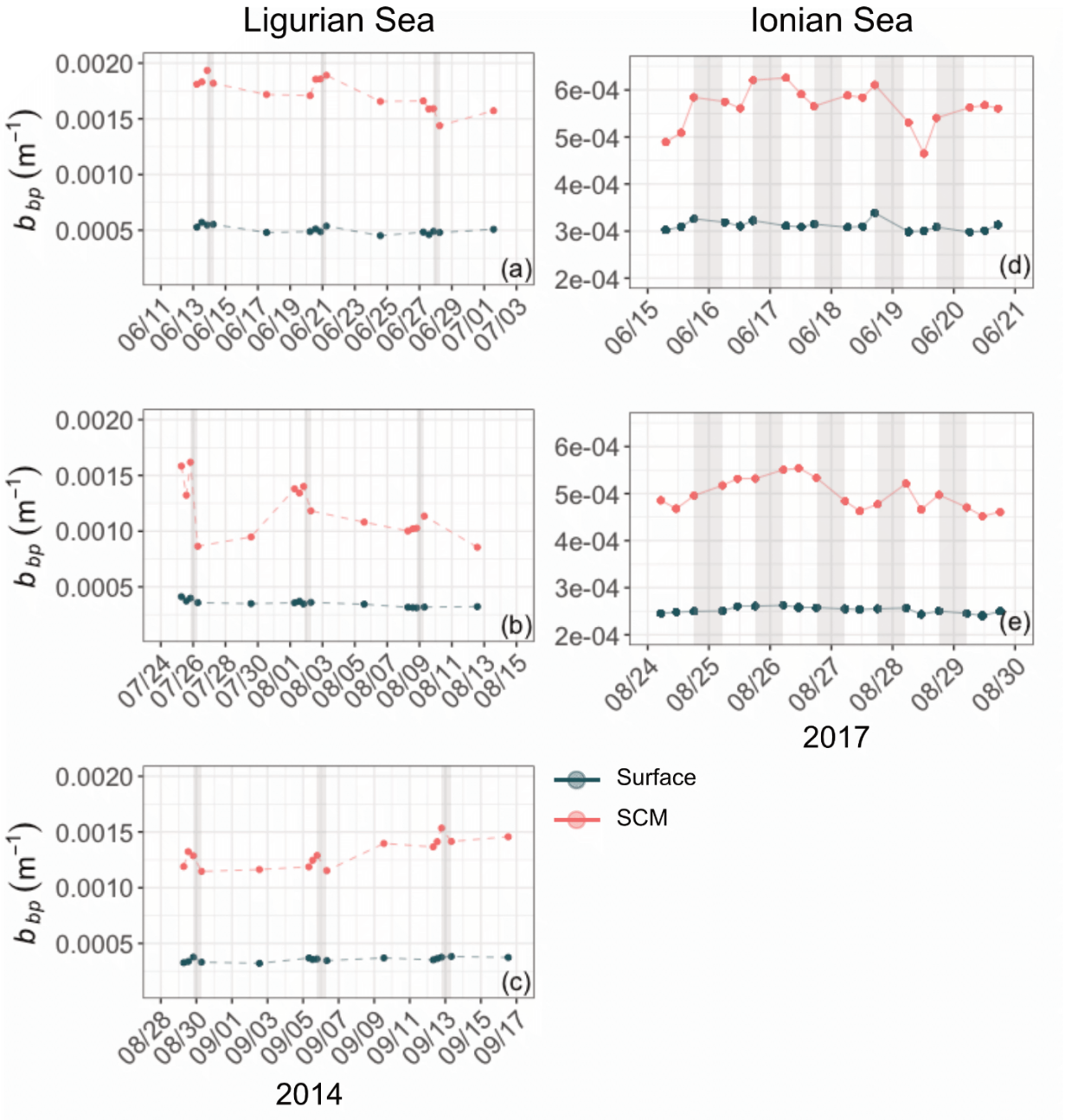

Figure A2: Example of time series of the b_{bp} coefficient in the surface (red) and SCM (dark green) layers, chosen within the time periods indicated by the dashed lines in Figs 3-4, from May 24 to July 14, 2014 (a), July 14 to August 16, 2014 (b), and August 16 to September 13, 2014 for the Ligurian Sea (left), and from May 28 to August 11, 2017 (d) and August 11 to September 11, 2017 (e) for the Ionian Sea (right).

APPENDIX B

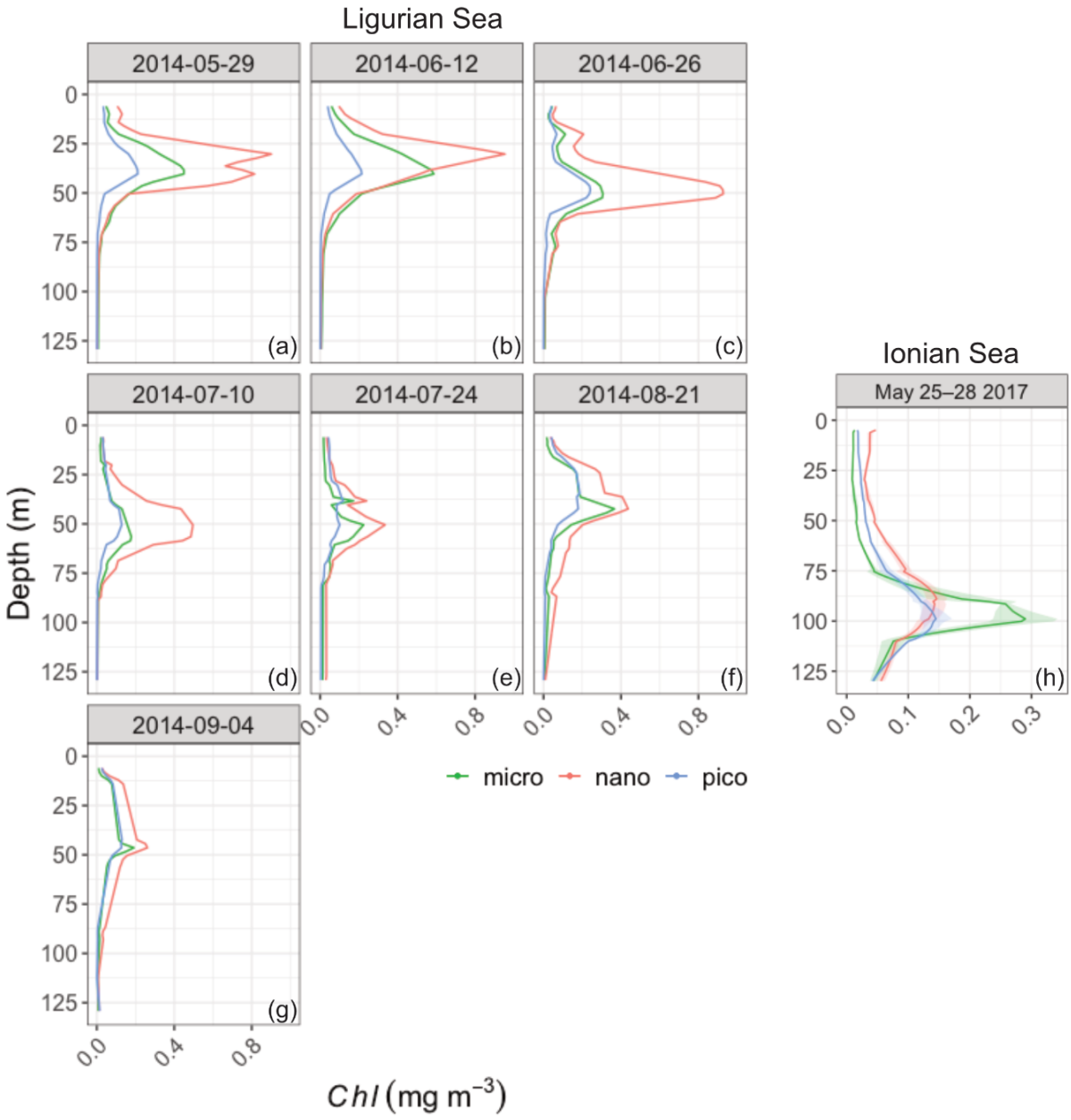

Figure B1: Vertical distribution of the chlorophyll *a* concentration of the micro- (green), nano- (red) and picophytoplankton (blue) derived from HPLC pigment determinations in the Ligurian Sea (BOUSSOLE site; a–h) and the Ionian Sea (PEACETIME cruise; i). For the Ionian Sea the solid line shows the mean value and the shaded area the standard deviation, calculated over a 4-day window (May 25–28, 2017).