



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

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16



17 **Abstract**

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

38



39 1 Introduction

40 Primary production is an essential component of the global ocean carbon cycle (Field et
41 al. 1998). As a major driver of the biological carbon pump, this biogeochemical process plays
42 a critical role in the regulation of the Earth climate (e.g. Sarmiento & Siegenthaler 1992;
43 Falkowski 2012). Hence, quantifying primary production in the ocean stands as a major
44 challenge in the context of climate change. The balance between gross primary production
45 and community respiration in the ocean determines the trophic status of marine systems, i.e.
46 whether the system acts as a source or a sink of carbon (Williams 1993). This balance
47 depends on the considered region and varies substantially according to spatial and temporal
48 scales (Geider et al. 1997; Duarte & Agusti 1998; del Giorgio & Duarte 2002). It is therefore
49 necessary to develop capabilities not only for assessing primary production on a global scale,
50 but also for characterizing and quantifying the biogeochemical functioning of marine
51 ecosystems at smaller spatial and temporal scales (Serret et al. 1999; González et al. 2001 &
52 2002).

53 Traditionally, primary production measurements are based on *in situ* or *in vitro*
54 incubation experiments (i.e. on board the ship, under controlled conditions) coupled with
55 isotopic carbon analysis (Nielsen 1952; Fitzwater et al. 1982; Dandonneau 1993; Barber &
56 Hitling 2002) or measurements of oxygen concentration (Williams & Jenkinson 1982;
57 Williams & Purdie 1991). These methods involve seawater sampling during field campaigns,
58 sample manipulation and subsequent laboratory analyses, which are both time consuming and
59 require strong technical expertise. As a result, the availability of field primary production
60 measurements is relatively limited in terms of spatial and temporal coverage, which hinders
61 the possibility of extrapolation to other systems or to larger space and time scales for
62 modeling purposes.



63 Bio-optical primary production models coupled with ocean color satellite imagery
64 represent another approach for obtaining primary production estimates (Morel 1991;
65 Longhurst et al. 1995; Antoine et al. 1996; Behrenfeld et al. 2002). Such models are
66 extremely valuable for assessing primary production with a large spatial coverage and over a
67 broad range of temporal scales (Sathyendranath et al. 1995; Uitz et al. 2010; Chavez et al.
68 2011). Yet, most of these models suffer from several sources of uncertainties that generate
69 potential errors in the production estimates (e.g. Sarmiento et al. 2004; Saba et al. 2010; Saba
70 et al. 2011). Sources of uncertainties include, in particular, the extrapolation of the satellite
71 chlorophyll product, which is weighted to the upper portion of the euphotic zone, to the
72 entirety of the productive region of the water column not sensed remotely. In addition, the *in*
73 *situ*-based parameterization of phytoplankton photophysiology tends to lack robustness when
74 applied to large (regional or global) scales and over seasonal to interannual time scales.

75 Diel cycles observed in bio-optical properties provide a less-empirical and more
76 mechanistic approach to assess biological production. In a seminal paper published in 1989,
77 Siegel et al. observed the *in situ* diurnal variability of the particulate beam attenuation
78 coefficient (c_p) and used it as a surrogate for the diurnal variations in the abundance of
79 biogenic particles and associated production in the oligotrophic North Pacific Ocean. Several
80 studies subsequently pursued the investigation of the diurnal variability of marine bio-optical
81 properties as a means for determining non-intrusively *in situ* biological production (e.g.
82 Stramska & Dickey 1992; Durand and Olson 1996; Claustre et al. 1999; Claustre 2008;
83 Gernez et al. 2011; White et al. 2017; Briggs et al. 2018).

84 Among this large body of literature, Claustre et al. (2008) carried further the principle
85 of the Siegel et al. (1989) approach for application to the South Pacific Subtropical Ocean.
86 Based upon the generally observed relationship between the c_p coefficient and the stock of
87 particulate organic carbon, POC (e.g. Stramski et al. 1999; Garner et al. 2006), Claustre et al.



88 (2008) assumed that diel variations in c_p reflect diel variations in POC. Thus, the observed
89 daytime increase and nighttime decrease in c_p -derived POC are used to estimate gross
90 community production, community losses and, assuming equivalent day and night losses, net
91 community production (NCP). Because the c_p coefficient is not specific to phytoplankton but
92 includes the POC contribution of both autotrophic and heterotrophic particles, the c_p -based
93 method yields estimate of community production.

94 Two studies (Kheireddine & Antoine 2014; Barnes & Antoine 2014) also attempted to
95 extend this approach to the particulate backscattering coefficient (b_{bp}). The application opens
96 up opportunities for assessing community production from geostationary ocean color satellite
97 observations, from which a nearly continuous daytime b_{bp} coefficient can be retrieved. Both
98 studies focused on surface data obtained from moored observations from the Ligurian Sea
99 (Northwestern Mediterranean) and found weak results for the diel b_{bp} cycle, calling for further
100 investigations.

101 The optics-based approach has proven to be particularly relevant for appraising
102 particulate biological production in stratified oligotrophic systems such as subtropical gyres
103 (e.g. Siegel et al. 1998; Claustre et al. 2008; White et al. 2017). Interestingly, in such systems,
104 the biological production of organic carbon is difficult to quantify and potentially
105 underestimated by ^{14}C incubation methods (Juraneck & Quay 2005; Quay et al. 2010). This
106 might be attributed to an inadequacy of traditional measurement methods for apprehending
107 the spatial and temporal heterogeneity of biological production that may exhibit local or
108 episodic events (Karl et al. 2003; Williams et al. 2004; McGillicuddy 2016). Moreover, in
109 stratified oligotrophic systems, the vertical distribution of phytoplankton is frequently
110 characterized by the presence of a deep chlorophyll maximum (DCM), also referred as
111 subsurface chlorophyll maximum (SCM; e.g. Cullen 1982; Hense & Beckmann 2008; Cullen
112 2014; Mignot et al., 2014). SCMs are not necessarily resolved by *in situ* discrete sampling and



113 cannot be observed from ocean color satellites that are limited to the surface ocean. They are
114 typically attributed to the photoacclimation of phytoplankton cells to low light conditions
115 (Kiefer et al. 1976; Cullen 1982; Fennel & Boss 2003; Letelier et al., 2004; Dubinsky &
116 Stambler 2009). Yet, SCMs resulting from an actual increase in phytoplankton (carbon)
117 biomass, and so referred to as subsurface biomass maximum (SBM), have also been observed
118 episodically and/or seasonally in oligotrophic regions of the global ocean (Beckmann &
119 Hense 2007; Mignot et al. 2014; Barbieux et al. 2019; Cornec et al. 2021). Considering the
120 large (45%) surface areas covered by stratified oligotrophic regions in the global ocean
121 (McClain et al. 2004), improving the quantification of biological production of organic carbon
122 and characterizing the contribution of SCMs to the water-column production in such regions
123 are critical. For this purpose, *in situ* diel-resolved measurements with high spatio-temporal
124 resolution in the entire water column represent an intriguing opportunity.

125 In this study, we exploit summertime observations acquired by two BioGeoChemical-
126 Argo (BGC-Argo) profiling floats deployed in contrasted systems of the Mediterranean Sea.
127 This offers a unique opportunity for pursuing the exploration of the bio-optical diel cycle-
128 based approach to biological production in oligotrophic environments. One of the two BGC-
129 Argo floats was deployed in the Ligurian Sea in the vicinity of the BOUSSOLE fixed
130 mooring (BOUée pour l'acquiSition d'une Série Optique à Long termE; Antoine et al. 2008).
131 This area is representative of a seasonally stratified oligotrophic system, with a potentially
132 productive SCM (e.g. Mignot et al. 2014; Barbieux et al. 2019) that follows a recurrent spring
133 bloom. The second float was deployed in the Ionian Sea (Central Mediterranean) as part of
134 the PEACETIME (ProcEss studies at the Air-sEa Interface after dust deposition in the
135 MEDiterranean sea) project (Guieu et al. 2020). The Ionian Sea is a nearly permanent
136 oligotrophic system (e.g. Lavigne et al. 2015) with an SCM induced mostly by
137 photoacclimation (e.g. Mignot et al. 2014; Barbieux et al. 2019).



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

149 **2 Data and methods**

150 **2.1 Study region**

151 The Mediterranean Sea provides a unique environment for investigating the
152 biogeochemical functioning of oligotrophic systems that exhibit either a seasonal or
153 permanent SCM. The Mediterranean is a deep ocean basin characterized by a West-to-East
154 gradient in nutrients and chlorophyll *a* concentration (e.g. Dugdale & Wilkerson 1988;
155 Bethoux et al. 1992; Antoine et al. 1995; Bosc et al. 2004; D’Ortenzio & D’Alcalà 2009)
156 associated with a deepening of the SCM (Lavigne et al. 2012; Barbieux et al. 2019). The
157 Ionian Sea in the eastern Mediterranean is defined as permanently oligotrophic, with the SCM
158 settled at depth over the whole year. This system represents the oligotrophic end-member type
159 of SCM (Barbieux et al. 2019), much like the subtropical South Pacific Ocean Gyre. By
160 contrast, the Ligurian Sea in the western Mediterranean is seasonally productive as akin to a
161 temperate system (e.g. Casotti et al. 2003; Marty & Chiavérini 2010; Siokou-Frangou et al.



162 2010; Lavigne et al. 2015). The mixed layer deepens significantly during the winter period,
163 inducing seasonal renewal of nutrients in the surface layer that supports the spring bloom
164 (Marty et al. 2002; Lavigne et al. 2013; Pasqueron de Fommervault et al. 2015; Mayot et al.
165 2016). After the seasonal bloom, the SBM intensifies throughout the summer and into early
166 fall. This system represents the temperate end-member type of SCM.

167 We deployed BGC-Argo floats programmed for “multi-profile” sampling in each of
168 these two regions (Fig. 1). The Ligurian Sea float (hereafter noted fLig, WMO: 6901776),
169 was deployed in the vicinity of the BOUSSOLE fixed mooring (7°54'E, 43°22'N) during one
170 of the monthly cruises of the BOUSSOLE program (Antoine et al. 2008). We used the fLig
171 float measurements acquired during the time period May 24 to September 13, 2014. The
172 Ionian Sea float (hereafter noted fIon, WMO: 6902828) was deployed as part of the
173 PEACETIME project (Guieu et al. 2020). We used the fIon float measurements acquired
174 during the time period May 28 to September 11, 2017. Thus, although collected in different
175 years, the data sets arise from similar seasonal contexts.

176 **2.2 BGC-Argo multi-profiling floats and data processing**

177 The BGC-Argo floats used in this study are “PROVOR CTS-4” (nke Instrumentation,
178 Inc.). They were both equipped with the following sensors and derived data products: (1) a
179 CTD sensor for depth, temperature and salinity; (2) a “remA” combo sensor that couples a
180 SATlantic OCR-504 (for downwelling irradiance at three wavelengths in addition to
181 photosynthetic available radiation, PAR) and a WET Labs ECO Puck Triplet (for both
182 chlorophyll *a* (excitation/emission wavelengths of 470 nm/695 nm) and colored dissolved
183 organic matter (CDOM; 370 nm/460 nm) fluorescence, and particulate backscattering
184 coefficient at 700 nm); and (3) a WET Labs C-Rover (for particulate beam attenuation
185 coefficient at 660 nm, 25-cm pathlength). Data were collected along water column profiles
186 from 1000 m up to the surface with a vertical resolution of 10 m between 1000 and 250 m, 1



187 m between 250 and 10 m, and 0.2 m between 10 m and the surface. First, the BGC-Argo raw
188 counts were converted into geophysical units by applying factory calibration. Second, we
189 applied corrections following the BGC-Argo QC procedures (Schmechtig et al. 2015, 2016;
190 Organelli et al. 2017).

191 Factory-calibrated chlorophyll fluorescence requires additional corrections for
192 determining the chlorophyll *a* concentration (Chl). Values collected during daylight hours
193 were corrected for non-photochemical quenching following Xing et al. (2012). A global
194 analysis of factory-calibrated chlorophyll fluorescence measured with WET Labs ECO
195 sensors relative to concurrent chlorophyll *a* concentrations, determined by High Performance
196 Liquid Chromatography (HPLC), yielded a global overestimate bias of 2 (Roesler et al. 2017),
197 with statistically significant regional biases varying between 0.5 and 6. In the Mediterranean
198 Sea, the regional variations of the fluorescence-to-Chl ratio are known to be very small
199 (Taillandier et al. 2018), hence the bias correction factor of 2 was applied to BGC-Argo
200 fluorescence data from both the Ligurian and Ionian regions, consistently with the processing
201 performed at the Coriolis Data Center.

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

$$205 \quad b_{bp}(700) = 2 \pi \chi [(\beta b_{bp} - Darkb_{bp}) \times Scaleb_{bp} - \beta sw] \quad (1)$$

206 where $\chi = 1.076$ is the empirical weighting function that converts particulate volume
207 scattering function at 124° to total backscattering coefficient (Sullivan et al. 2013); βb_{bp} is
208 the raw observations from the backscattering meter (digital counts); $Darkb_{bp}$ (digital counts)
209 and $Scaleb_{bp}$ ($m^{-1} sr^{-1} count^{-1}$) are the calibration coefficients provided by the manufacturer;
210 and βsw is the contribution to the Volume Scattering Function (VSF) by the pure seawater at



211 the 700 nm measurement wavelength that is a function of temperature and salinity (Zhang et
212 al. 2009).

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

$$216 \quad c = -\frac{1}{x} \ln \frac{T}{100} \quad (2)$$

217 where x is the transmissometer pathlength (25 cm). The beam attenuation coefficient c is the
218 sum of the absorption and scattering by seawater and its particulate and dissolved
219 constituents. At 660 nm, the contribution of CDOM (c_{cdom}) can be considered negligible in
220 oligotrophic waters because, although its absorption in the blue is comparable to that of
221 particulate material (Organelli et al. 2014), the c_{cdom} spectrum decays exponentially towards
222 near zero in the red (Bricaud et al. 1981), and because it is comprised of dissolved molecules
223 and colloids, its scattering is negligible (Boss and Zaneveld 2003). Meanwhile $c_w(660)$ for
224 pure water is constant and removed in the application of the factory calibration; effects due to
225 dissolved salt are accounted for according to Zhang et al. (2009). Hence, at a wavelength of
226 660 nm, the particle beam attenuation coefficient, c_p (m^{-1}), is retrieved by subtracting the
227 seawater contribution to c . The biofouling-induced increasing signal observed in clear deep
228 waters and resulting in a drift in c_p values with time, is corrected as follows. For each profile,
229 a median c_p value, used as an “offset”, is computed from the c_p values acquired between 300
230 m and the maximum sampled depth, and subtracted from the entire profile.

231 Using the solar noon Photosynthetically Available Radiation (PAR) measurements, we
232 computed the euphotic layer depth (Z_{eu}) as the depth at which the PAR is reduced to 1% of its
233 value just below the surface (Gordon & McCluney 1975) and the penetration depth (Z_{pd} ; also
234 known as the e-folding depth or first attenuation depth) as $Z_{eu} / 4.6$. We define the surface



235 layer from 0 m to Z_{pd} . We also define the SCM layer as in Barbieux et al. (2019), whereby a
236 Gaussian model is fit to each Chl vertical profile in order to determine the depth interval of
237 the full width half maximum of the SCM. Finally, the Mixed Layer Depth (MLD) is derived
238 from the float CTD data as the depth at which the potential density difference relative to the
239 surface reference value is 0.03 kg m^{-3} (de Boyer Montégut et al. 2004).

240 Unlike the majority of BGC-Argo floats that collect profile measurements every 10
241 days, the two platforms used in this study sampled the water column 4 profiles per day, albeit
242 with slightly different regimes (Fig. 2). The fLig float cycle commences with the first profile
243 at solar noon (t_n), a second at sunset the same day (t_{ss}), a third profile at sunrise the next day
244 (t_{sr+1}), and a last one at solar noon the next day (t_{n+1}). The sampling cycle is repeated every
245 four days. The fIon cycle is performed over a single 24-hour period; it begins at sunrise (t_{sr}),
246 followed by a second profile at solar noon (t_n), a third at sunset (t_{ss}) and a last night profile at
247 approximately midnight (t_m). For this float, the sampling cycle is repeated each day.

248 2.3 Characterization of the diel cycle of the bio-optical properties

249 In order to characterize the amplitude and variability of the diel cycle of the c_p and b_{bp}
250 coefficients, we use the metrics defined by Kheireddine & Antoine (2014). We compute the
251 relative daily variation $\tilde{\Delta}c_p$ and $\tilde{\Delta}b_{bp}$ (expressed as % change) for each float and each day of
252 observation, from sunrise to sunrise (fIon) as follows:

$$253 \quad \tilde{\Delta}c_p = 100 \left(\frac{c_p(t_{sr})}{c_p(t_{sr+1})} - 1 \right) \quad (3)$$

$$254 \quad \tilde{\Delta}b_{bp} = 100 \left(\frac{b_{bp}(t_{sr})}{b_{bp}(t_{sr+1})} - 1 \right) \quad (4)$$

255 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
256 $b_{bp}(t_{sr+1})$ the values at sunrise the next day. Comparable computations for fLig were made



257 from noon (t_n) to noon (t_{n+1}). Then the mean and range in relative daily variations ($\widetilde{m\Delta}$ and $\widetilde{r\Delta}$,
258 respectively) are computed for each float over the entire time series.

259 **2.4 Principle of the bio-optical diel cycle-based approach to biological production**

260 In this study we considered two distinct bio-optical properties, i.e. the c_p coefficient
261 (Siegel et al. 1989; Claustre et al. 2008) and the b_{bp} coefficient (Barnes & Antoine 2014;
262 Kheireddine & Antoine 2014). To first order, c_p and b_{bp} are linearly correlated to, and thus
263 may be used as a proxy for, the stock of POC (e.g. Oubelkheir et al. 2005; Gardner et al.
264 2006; Cetinić et al. 2012). Both of these bio-optical proxies have been shown to exhibit a
265 diurnal cycle (e.g. Oubelkheir & Sciandra 2008; Loisel et al. 2011; Kheireddine & Antoine
266 2014).

267 The daily solar cycle is a major driver of biological activity in all oceanic euphotic
268 zones (e.g. Oubelkheir & Sciandra 2008), which influences the abundance of microorganisms
269 (Jacquet et al. 1998; Vaulot & Marie 1999; Brunet et al. 2007) and therefore, the magnitude
270 of the c_p and b_{bp} coefficients. To first order, the diurnal increase in c_p or b_{bp} may be attributed
271 to an increase in particle biomass, resulting from an increase in particle abundance and/or
272 size, both associated with cell division. To second order, the diurnal increase in c_p or b_{bp} may
273 be caused by variations in particle shape and refractive index (Stramski & Reynolds 1993;
274 Durand & Olson 1996; Claustre et al. 2002; Durand et al. 2002). The night decrease in c_p or
275 b_{bp} may be explained by a decrease in particle abundance due to particle aggregation and
276 sinking or grazing (Cullen et al. 1992), changes in particle size and/or refractive index
277 associated with cell division, or microorganism respiration.

278 The bio-optical diel cycle-based approach used in this study relies on a modified version
279 of Claustre et al. (2008). Following this approach, the observed daytime increase and
280 nighttime decrease in c_p -derived (or b_{bp} -derived) POC are used to estimate gross community



281 production. For this purpose, the c_p and b_{bp} coefficients, measured *in situ* by the BGC-Argo
282 profiling floats, are converted into POC equivalent using a constant c_p -to-POC (or b_{bp} -to-
283 POC) relationship from the literature (see below). By definition, the c_p and b_{bp} coefficients
284 target particles so that the dissolved biological matter is not accounted for by the present
285 method.

286 **2.5 Bio-optical properties-to-POC relationships**

287 The conversion of c_p and b_{bp} into POC relies on the use of empirical proxy relationships
288 and assumptions concerning the variations in those relationships. First, as in Claustre et al.
289 (2008), we assume that the c_p - or b_{bp} -to-POC relationship remains constant on a daily
290 timescale, consistently with previous works (Stramski & Reynolds 1993; Cullen & Lewis
291 1995), so that observed variations in the optical coefficients can be interpreted as variations in
292 POC. Second, the specific proxy value is not constant, as many empirical relationships
293 between POC and c_p (e.g. Claustre et al. 1999; Oubelkheir et al. 2005; Gardner et al. 2006;
294 Loisel et al. 2011) or b_{bp} (e.g. Stramski et al. 2008; Loisel et al. 2011; Cetinić et al. 2012)
295 have been proposed for specific regions (Tables 1 and 2). In the present study, we used the
296 relationships from Oubelkheir et al. (2005) and Loisel et al. (2011) for c_p and b_{bp} ,
297 respectively. Both relationships were established from *in situ* measurements collected in the
298 Mediterranean Sea and produce c_p - or b_{bp} -derived POC values falling in the middle of the
299 range of all the POC values resulting from the different bio-optical relationships taken from
300 the literature (Tables 1 and 2).

301 **2.6 Estimating biological production from the diel cycle of POC**

302 **2.6.1 Hypotheses**

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



$$305 \quad \frac{\partial b(z,t)}{\partial t} = \mu(z,t) b(z,t) - l(z,t) b(z,t), \quad (5)$$

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

315 2.6.2 Calculation of the loss rate

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

$$317 \quad \frac{\partial b(z,t)}{\partial t} = l b(z,t). \quad (6)$$

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

$$320 \quad \frac{\partial B(t)}{\partial t} = -l B(t), \quad (7)$$

321 with $B(t) = \int_{z_2}^{z_1} b(z,t) dz$, the POC integrated within a given layer of the water column,
322 comprised between the depths z_1 and z_2 (in $gC \ m^{-2}$). In this respect, we consider three
323 different layers: the euphotic layer extending from $z_1 = 0$ m to $z_2 = Z_{eu}$; the surface layer
324 extending from $z_1 = 0$ m to $z_2 = Z_{pd}$; and the SCM layer extending from $z_1 = Z_{SCM} - Z_{SCM,1/2}$
325 and $z_2 = Z_{SCM} + Z_{SCM,1/2}$, with Z_{SCM} the depth of the SCM and $Z_{SCM,1/2}$ the depth at which Chl
326 is half of the SCM value.



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

$$329 \quad l = \frac{\ln\left(\frac{B_{SS}}{B_{SR+1}}\right)}{t_{SR+1} - t_{SS}}, \quad (8)$$

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

332 2.6.3 Calculation of the production rate

333 The daily and depth-integrated production of particles, P (in units of $\text{gC m}^{-2} \text{d}^{-1}$), is
334 defined as:

$$335 \quad P = \int_{t_{SR}}^{t_{SR+1}} \int_{z_2}^{z_1} \mu(z, t) b(z, t) dz dt, \quad (9)$$

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

$$338 \quad P = \int_{t_{SR}}^{t_{SR+1}} \int_{z_2}^{z_1} \left(\frac{\partial b(z, t)}{\partial t} + l b(z, t) \right) dz dt, \quad (10)$$

339 which yields:

$$340 \quad P = B_{t_{SR+1}} - B_{t_{SR}} + l \int_{t_{SR}}^{t_{SR+1}} B(t) dt. \quad (11)$$

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

$$342 \quad P = B_{t_{SR+1}} - B_{t_{SR}} + l \sum_{i=1}^j (t_{i+1} - t_i) \frac{B_{i+1} + B_i}{2}, \quad (12)$$

343 with l calculated from Eq. (8) and the index i corresponding to the different measurement time
344 steps over the course of the diel cycle (t_n , t_{SS} , t_{SR+1} , and t_{n+1} for the Ligurian Sea, and t_{SR} , t_n , t_{SS} ,
345 and t_m for the Ionian Sea; Fig. 2).

346 In brief, Eq. (12) is applied to the time series of the BGC-Argo floats by using b_{bp} and
347 c_p converted into POC equivalents, integrated within the euphotic, surface, and SCM layers to



348 compute c_p - and b_{bp} -derived estimates of gross community production, P , in all three layers of
349 the water column.

350 **2.7 Primary production model**

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

358 **2.8 Phytoplankton pigments and community composition**

359 During the BOUSSOLE cruises conducted in 2014 (cruises #143 to #154) and the
360 PEACETIME cruise, discrete seawater samples were taken at 10–12 depths within the water
361 column from Niskin bottles mounted on a CTD-rosette system and then filtered under low
362 vacuum onto Whatman GF/F filters (0.7- μ m nominal pore size, 25-mm diameter). The filters
363 were flash-frozen in liquid nitrogen and stored at -80°C until analysis by HPLC following the
364 protocol of Ras et al. (2008). The concentrations of phytoplankton pigments resulting from
365 these analyses were used to estimate the composition of the phytoplankton assemblage. For
366 this purpose, we used the diagnostic pigment-based approach (Claustre et al. 1994; Vidussi et
367 al. 2001; Uitz et al. 2006) with the coefficients of Di Cicco et al. (2017) to account for the
368 specificities of Mediterranean phytoplankton communities. This approach yields the relative
369 contribution to chlorophyll a biomass of major taxonomic groups merged into three size
370 classes (micro-, nano and picophytoplankton).



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

381 **3 Results and discussion**

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

388 **3.1 Biogeochemical and bio-optical context in the study regions**

389 Both study regions are characterized by either seasonal or persistent oligotrophy, with
390 mean surface Chl values ranging within 0.08–0.22 mg m⁻³ (Fig. 3), and a stratified water
391 column with a consistently shallow MLD (<30 m). They do exhibit very different euphotic
392 zones, with a mean Z_{eu} of 47±5 m and 89±4 m in the Ligurian and Ionian Seas, respectively.
393 Both regions also display a SCM, the depth of which co-occurs with Z_{eu} and the isopycnal
394 28.85 (i.e. the isoline of potential density 28.85 kg m⁻³) over the considered time series,



395 except for the last month of observation in the Ionian Sea. In the Ligurian Sea, the SCM is
396 intense (1.06 ± 0.34 mg Chl m^{-3} ; Fig. 3a), relatively shallow (41 ± 7 m), and associated with the
397 subsurface c_p and b_{bp} maxima (0.27 ± 0.09 and 0.0015 ± 0.0006 m^{-1} , respectively; Fig. 3b–c).
398 The Chl, and c_p values are 5 times larger in the SCM layer than at surface, and the b_{bp} values
399 3.6 times larger. In contrast, in the Ionian Sea, the SCM is associated with lower values of Chl
400 (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).
401 Compared to the Ligurian Sea SCM, the Ionian Sea SCM is located twice as deep (97 ± 11 m)
402 and is uncoupled from any c_p and b_{bp} maxima that occur at shallower depth. Hence, the
403 selected regions are representative of two contrasted SCM systems with distinct degree of
404 oligotrophy, consistent with our expectations (e.g. D’Ortenzio & Ribera D’Alcalà 2009;
405 Barbieux et al. 2019). These observations indeed suggest that the Ligurian Sea SCM mirrors
406 an increase in phytoplankton carbon biomass (SBM) likely resulting from favorable light and
407 nutrient conditions, whereas the Ionian SCM is induced by photoacclimation of
408 phytoplankton cells.

409 Although the summer period is typically considered stable, some temporal variations
410 are observed over the time series that are more pronounced in the SCM layer than at surface.
411 In the Ligurian Sea SCM, the Chl, c_p and b_{bp} exhibit similar temporal evolution, with
412 relatively high values in late May 2014, followed by a marked decrease until mid-July (Figs.
413 4a–c). Then we observe two minima in Chl, c_p and b_{bp} that delineate a second peak between
414 July 14 and August 16, 2014 (as indicated by the dashed lines in Fig. 4a–c). In the Ionian Sea
415 SCM, the Chl, c_p and b_{bp} values all decrease from late May until a minimum is reached on
416 August 11, 2017 (dashed line in Figs. 4d–e) and a second increase is recorded later in the
417 season. These temporal patterns are further discussed (Section 3.4).



418 3.2 Assessment of the method

419 3.2.1 Analysis of the diel cycle of the b_{bp} coefficient

420 Diel cycles, characterized by a daytime increase and a nighttime decrease, are observed in
421 both c_p and b_{bp} time series in all three layers of the water column (Fig. 5). In the surface layer
422 of the Ligurian Sea, the diel cycles of c_p and b_{bp} exhibit, respectively, mean relative daily
423 variation ($\widetilde{m\Delta}$) of 12.7% and 2.3%, and a range in relative daily variations ($\widetilde{r\Delta}$) of 256.7% and
424 28.5% (Table 3). These values are of the same order of magnitude as those reported by
425 Kheireddine & Antoine (2014), acquired from the BOUSSOLE surface mooring in the same
426 area and during the oligotrophic season (from -5% to 25% for c_p and from -2% to 10% for
427 b_{bp}). Interestingly, the diel cycle of the c_p coefficient appears systematically more pronounced
428 than that of b_{bp} , with larger values of $\widetilde{m\Delta}$ and $\widetilde{r\Delta}$, regardless of the considered region and layer
429 of the water column (Table 3).

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



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

450 We now consider the integrated euphotic zone gross community production estimates
451 derived from the bio-optical diel cycle-based method (Fig. 6). We compare the c_p - and b_{bp} -
452 based estimates with primary production estimates computed with the model of Morel (1991).
453 The b_{bp} -derived production rates underestimate those derived from c_p in both regions by about
454 a factor of ten, with respective mean values of $0.11 \pm 0.28 \text{ gC m}^{-2} \text{ d}^{-1}$ and $1.18 \pm 1.13 \text{ gC m}^{-2} \text{ d}^{-1}$
455 in the Ligurian Sea, and $0.04 \pm 0.04 \text{ gC m}^{-2} \text{ d}^{-1}$ and $0.46 \pm 0.11 \text{ gC m}^{-2} \text{ d}^{-1}$ in the Ionian Sea. In
456 addition, the b_{bp} -derived production is much lower than the primary production computed
457 with the model of Morel (1991), which has mean values of $0.91 \pm 0.14 \text{ gC m}^{-2} \text{ d}^{-1}$ in the
458 Ligurian Sea and $0.31 \pm 0.04 \text{ gC m}^{-2} \text{ d}^{-1}$ in the Ionian Sea. The significantly lower community
459 production rates are a direct effect of the dampened relative daily amplitude of the b_{bp} diel
460 cycle (Table 3), and the sensitivity of b_{bp} to the smaller heterotrophic and detrital particulate
461 matter. These bio-optical diel cycle-based method, whether applied to c_p or b_{bp} , yields an
462 estimate of the community production, i.e. that associated with the accumulation of
463 phytoplankton *and* bacteria biomass, which is necessarily larger than the primary (photo-
464 autotrophic) production rates from the Morel (1991) model. These questionable low values of
465 community production, along with the observation of a weak daily variability in b_{bp} , support
466 the idea that the diel cycle of b_{bp} may not be a reliable index for total community production
467 rates, consistently with previous studies (Kheireddine & Antoine 2014; Barnes & Antoine



468 2014). However, the utility of a b_{bp} -derived community production may be revealed in
469 elucidating rates for distinct size-based groups of organisms, such as picoplankton. A better
470 understanding of the specific size range that dominates the diel cycle in b_{bp} will be important
471 to understand. Yet, for our purposes, we disregard the b_{bp} -based estimates and focus our
472 analysis on the c_p -derived gross community production estimates.

473 **3.2.2 Community production derived from the c_p coefficient**

474 The c_p -derived estimates of gross community production, integrated within the euphotic
475 layer, compare favorably with those found in the literature for similar Mediterranean areas
476 (see Table 4 and references therein). The c_p -based estimates show a 2.5-fold difference
477 between the Ligurian Sea and the Ionian Sea (mean of $1.18 \text{ gC m}^{-2} \text{ d}^{-1}$ and $0.46 \text{ gC m}^{-2} \text{ d}^{-1}$,
478 respectively; Table 6). In comparison, water column-integrated primary production values,
479 either inferred from satellite observations and biogeochemical models or measured *in situ*,
480 vary within the range $0.13\text{--}1 \text{ gC m}^{-2} \text{ d}^{-1}$ and $0.14\text{--}0.69 \text{ gC m}^{-2} \text{ d}^{-1}$ for the Western (or
481 Ligurian) and Eastern (or Ionian) region, respectively (Table 4). As expected, our c_p -based
482 community production rates are larger than published primary production rates. The present
483 c_p -derived values also compare favorably with gross community production estimates inferred
484 from a similar approach applied to bio-optical measurements from the BOUSSOLE mooring
485 in the Ligurian Sea ($0.8\text{--}1.5 \text{ gC m}^{-2} \text{ d}^{-1}$ in May–August; Barnes & Antoine 2014) and along an
486 oligotrophic gradient in the South Pacific Subtropical Ocean ($0.85 \text{ gC m}^{-2} \text{ d}^{-1}$; Claustre et al.
487 2008).

488 The empirical relationships linking the c_p (or b_{bp}) coefficient to POC are known to exhibit
489 regional and seasonal variability in response to changes in the composition of the particle
490 assemblage and associated changes in particle size, shape and type, i.e. biogenic or mineral
491 (e.g. Stramski et al. 2004; Neukermans et al. 2012; Slade & Boss 2015). Hence, the choice of
492 such relationships strongly affects the conversion of the measured daily bio-optical variability



493 into POC fluxes. For the time period and study regions here, the c_p -based community
494 production varies by a factor of 2, depending on the selected bio-optical relationship, so that
495 c_p -based estimates vary between $0.89 \pm 0.84 \text{ gC m}^{-2} \text{ d}^{-1}$ and $1.62 \pm 1.54 \text{ gC m}^{-2} \text{ d}^{-1}$ in the
496 Ligurian Sea, and between $0.35 \pm 0.09 \text{ gC m}^{-2} \text{ d}^{-1}$ and $0.63 \pm 0.16 \text{ gC m}^{-2} \text{ d}^{-1}$ in the Ionian Sea.
497 The minimal and maximal values are obtained with the bio-optical relationships from Marra
498 et al. (1995) and Stramski et al. (2008), respectively (Table 5). Compared to the reference
499 value obtained using the Oubelkheir et al. (2005) relationship, the c_p -based estimates are 25%
500 lower and 37% higher using the relationships of Marra et al. (1995) and Stramski et al.
501 (2008), respectively.

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

509 **3.3 Regional and vertical variability of production**

510 The temporal evolution of the c_p -derived POC biomass integrated within the three
511 distinct layers of the water column is presented for the two study regions in Fig. 7. The
512 integrated POC concentration values follow similar temporal trends as reported for c_p (Figs.
513 3–4). In the Ligurian Sea, the euphotic layer-integrated POC varies between 1.5 and 6.0 gC
514 m^{-2} (mean of $3.7 \pm 1.1 \text{ gC m}^{-2}$; Fig. 7a and Table 6). There was a decrease from late May to
515 mid-July (6.0 to 1.5 gC m^{-2}) followed by a moderate peak (3.9 gC m^{-2}) between mid-July and
516 mid-August (as bounded by the dashed lines in Fig. 5). The c_p -based community production
517 did exhibit large variability over the time period (Fig. 7b and Table 6), but interestingly, the



518 moderate POC peak observed in the core of the oligotrophic season (between mid-July and
519 mid-August) is associated with the maximum production rate of the time series ($4.3 \text{ gC m}^{-2} \text{ d}^{-1}$).
520 ¹).

521 In the Ionian Sea, the POC biomass integrated within the euphotic zone is much lower
522 than in the Ligurian Sea and remains more stable over the time period ($1.9 \pm 0.24 \text{ gC m}^{-2}$; Fig.
523 7c and Table 6). As with POC, the community production is much lower in the Ionian Sea
524 than in the Ligurian Sea, but still exhibits substantial variability with values ranging within
525 $0.06\text{--}0.68 \text{ gC m}^{-2} \text{ d}^{-1}$ (Fig. 7d). These results are consistent with multiple studies reporting a
526 large difference in the trophic status and productivity of the Ligurian and Ionian Seas, on
527 seasonal and annual timescales (D'Ortenzio & Ribera d'Alcala, 2009; Siokou-Frangou et al.
528 2010; Lavigne et al. 2013; Mayot et al. 2016). Our results confirm this difference, yet on a
529 monthly timescale during the oligotrophic summer period.

530 The gross community production estimates integrated over different layers of the
531 water column reveal distinct patterns. In the Ligurian Sea, both the euphotic and SCM layers
532 show large production rates ($0.96 \pm 1.3 \text{ gC m}^{-2} \text{ d}^{-1}$), with production in the SCM layer
533 frequently equaling or overtaking on the production in the euphotic layer (Fig. 7b). This is
534 particularly striking in late July, when the production peak is actually associated with a large
535 enhancement of the production in the SCM layer ($4.9 \text{ gC m}^{-2} \text{ d}^{-1}$). In contrast, the surface
536 layer shows reduced production rates ($0.29 \pm 0.33 \text{ gC m}^{-2} \text{ d}^{-1}$), a pattern also observed in the
537 Ionian Sea ($0.11 \pm 0.04 \text{ gC m}^{-2} \text{ d}^{-1}$). In the Ionian Sea, the production is maximal in the
538 euphotic zone, and very variable and occasionally larger in the SCM layer ($0.14 \pm 0.39 \text{ gC m}^{-2}$
539 d^{-1} ; Fig. 7d). The bio-optical diel cycle-based method produces several occurrences of
540 negative values in the SCM layer, indicating that the quasi-1-D assumption is occasionally not
541 satisfied in the lower part of the euphotic layer. This could arise when physical processes that
542 transport particles are larger than local growth and loss of POC.



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

550 **3.4 Production in the SCM layer in relation with the biotic and abiotic context**

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

553 **3.4.1 Phytoplankton and particulate assemblage**

554 The pigment data collected during the BOUSSOLE and PEACETIME cruises
555 concomitantly with the deployments of the fLig and fIon floats, respectively, are used as
556 proxies for phytoplankton community structure (Fig. 8). In the Ligurian Sea,
557 nanophytoplankton (mainly prymnesiophytes) appear as dominant contributors to the
558 phytoplankton assemblage both in the surface layer ($48\pm 8\%$; Fig. 8b) and SCM layer
559 ($54\pm 10\%$). Picophytoplankton (prokaryotes and small chlorophytes) and microphytoplankton
560 (diatoms and dinoflagellates) are present in moderate proportions, with $30\pm 11\%$ and $22\pm 5\%$
561 in the upper layer, and $19\pm 7\%$ and $27\pm 9\%$ in the SCM layer, respectively (Figs. 8a and 8c).
562 No marked community change is observed during the timeseries. In the Ionian Sea, the
563 surface layer displays large contribution of nanophytoplankton ($56\pm 2\%$; Fig. 8e) and, to a
564 lesser extent, picophytoplankton ($29\pm 3\%$; Fig. 8d). However, the SCM level is characterized
565 by an enhanced contribution of microphytoplankton (diatoms) to the algal assemblage
566 ($49\pm 5\%$; Fig. 8f), as discussed in Marañón et al. (2021). The Ionian PEACETIME data was



567 limited to the period from May 25 to 28, 2017, and thus it was not possible to determine
568 whether the composition of phytoplankton communities evolved with time. Although not
569 characterized by the prokaryotic populations (*Synechococcus* and *Prochlorococcus*) that
570 typically prevail in stratified oligotrophic environments, our observations are consistent with
571 previous studies reporting enhanced contributions of nanophytoplankton (e.g. Gitelson et al.
572 1996; Vidussi et al. 2001) and the occurrence of diatoms at depth (Siokou-Frangou et al.
573 2010; Crombet et al. 2011; Marañón et al. 2021) in the Mediterranean Sea.

574 Bio-optical properties and their ratios provide indication about variations in the
575 constituents (algal or nonalgal) and size of the particulate pool, the composition of the
576 phytoplankton assemblage and the physiological status of phytoplankton cells (e.g. Geider
577 1987; Ulloa et al. 1994; Stramski et al. 2004; Loisel et al. 2007). Here we consider the bio-
578 optical ratios b_{bp} / c_p , c_p / Chl , and b_{bp} / Chl in the SCM layer (Fig. 9). The b_{bp} / c_p ratio, while
579 at slightly different wavelengths (700 nm and 660 nm, respectively) are at absorption minima
580 and thus this ratio is comparable to the backscattering ratio b_{bp} / b_p . The b_{bp} / b_p ratio is a
581 demonstrated proxy for determining relative constituent composition (Twardowski et al.
582 2001), with phytoplankton exhibiting lower ratios than nonalgal particles (approximately
583 0.5% and 1%, respectively; Boss et al. 2004; Whitmire et al. 2007; Westberry et al. 2010).
584 The b_{bp} / Chl and c_p / Chl ratios are both proxies for the POC / Chl ratio (e.g. Claustre et al.
585 1999; Oubelkheir et al. 2005; Behrenfeld et al. 2015; Álvarez et al. 2016), and thus an
586 indicator of the contribution of phytoplankton to the whole organic pool. The variations are
587 also interpreted as changes in the composition of phytoplankton communities (e.g.
588 Sathyendranath et al. 2009) and their acclimation to the light-nutrient regime (e.g. Geider et
589 al. 1987; Geider et al. 1997; Cloern 1999) if one assumes that nonalgal particles are negligible
590 (e.g., as indicated by the backscattering ratio) or not varying in concentration. The differences
591 between the b_{bp} / Chl and c_p / Chl ratios lie in the fact that they are sensitive to different



592 particle size ranges (Roesler and Boss 2008) and, thus, when they are not correlated, one can
593 qualitatively discern differing dynamics across the phytoplankton size spectrum.

594 The b_{bp} / c_p ratio is very different between the Ligurian and Ionian Seas, with significantly
595 lower values in the Ligurian Sea (0.0068 ± 0.0009 or $0.68 \pm 0.09\%$, and 0.0095 ± 0.0009 or
596 $0.95 \pm 0.09\%$; Fig. 9). These ratios indicate that, in the general sense, the Ligurian Sea SCM is
597 more phytoplankton dominated than the Ionian Sea SCM, which tends towards nonalgal
598 particles. In the Ligurian Sea, the b_{bp} / c_p ratio remains < 0.0087 (0.87%) and reaches a
599 minimum of 0.0055 (0.55%) over the period coinciding with the production event from mid-
600 July to mid-August (Fig. 9a), consistent with phytoplankton dominance. In contrast, in the
601 Ionian Sea SCM, the b_{bp} / c_p ratio increases from 0.0085 (0.85%) in late May, peaking at
602 nearly 0.012 (1.2%) in early August, and then decreasing back to 0.0085 (0.85%) in
603 September (Fig. 9b). The tendency towards a ratio of 1% in the core of the oligotrophic
604 season, evidences the increased proportion of nonalgal particles to the bulk pool as previously
605 observed in oligotrophic environments (Yentsch & Phinney 1989; Stramski et al. 2004; Loisel
606 et al. 2007).

607 The c_p and b_{bp} to Chl ratios exhibit not only different temporal patterns between the
608 Ligurian and Ionian Sea SCMs, they also exhibit different relative values. The c_p / Chl ratio in
609 the Ligurian Sea SCM is higher than that of the Ionian Sea, ranging from 0.18 to $0.45 \text{ m}^2 \text{ mg}$
610 Chl^{-1} , compared to 0.15 to $0.26 \text{ m}^2 \text{ mg Chl}^{-1}$, respectively. In contrast, although the b_{bp} / Chl
611 ratio in the Ligurian Sea SCM ranges from 0.0011 to $0.0023 \text{ m}^2 \text{ mg Chl}^{-1}$, and the Ionian Sea
612 from 0.0015 to $0.0021 \text{ m}^2 \text{ mg Chl}^{-1}$, they have essentially identical mean values over the time
613 series (0.0017 ± 0.0006 and 0.0017 ± 0.0001 , respectively). This suggests that the POC in the
614 smaller size fractions are more similar in their respective SCM than in their larger size
615 fractions.



616 Temporally, the Ligurian Sea SCM exhibits significantly more temporal variations in both
617 ratios compared to the Ionian Sea SCM, and the temporal variations are highly correlated.
618 Both the c_p / Chl and b_{bp} / Chl ratios in the Ligurian Sea SCM exhibit a peak at the start of the
619 time series in late May that decreases to mid-July, followed by a second peak during the
620 period coinciding with the production episode from mid-July to mid-August, and then a third
621 increase until the end of the time series (Figs. 9b–c). In contrast, both ratios in the Ionian Sea
622 SCM exhibit significantly reduced temporal variability (Figs. 9e–f), with a weak increase is
623 observed starting in early August.

624 Despite differing temporal variability, the b_{bp} / Chl ratio in both Seas remains moderate to
625 low ($<0.0025 \text{ m}^2 \text{ mg Chl}^{-1}$; Figs. 9c and 9f, consistent with global SCM values (Barbieux et
626 al., 2018). The enhanced b_{bp} / Chl values observed in the Ligurian Sea SCM in early May, late
627 July and late August suggest an increased contribution of small (pico- and nano-sized)
628 phytoplankton (Cetinić et al. 2012; Cetinić et al. 2015). Yet, the BOUSSOLE pigment data do
629 not reveal pronounced changes in the phytoplankton assemblage. Low-light conditions
630 typically prevailing in the SCM layer are usually associated with low values of the c_p / Chl
631 and b_{bp} / Chl ratios (e.g. (Behrenfeld & Boss 2003; Westberry et al., 2008; Barbieux et al.
632 2019), caused by photoacclimation by which phytoplankton organisms increase their
633 intracellular Chl. Nevertheless, the temporal variability in the c_p / Chl and b_{bp} / Chl values
634 may be resulting from fluctuations in the light conditions at the SCM in the Ligurian Sea. In
635 the Ionian Sea, the invariant low c_p / Chl and b_{bp} / Chl values are consistent with both
636 photoacclimation of phytoplankton to low-light conditions and a diatom-dominated
637 phytoplankton assemblage (Cetinić et al. 2015; Barbieux et al. 2018). The relatively stable
638 ratios observed in this region suggest a relative steadiness in the composition of the
639 phytoplankton assemblage over the considered period.



640 **3.4.2 Relation to abiotic conditions**

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

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



665 Considering the large contribution of diatoms at the SCM, one may conclude that the low, yet
666 non-negligible, production levels estimated in the SCM layer are supported by diatoms. This
667 result supports previous findings indicating that, contrary to the classic view of diatoms
668 thriving essentially in dynamic eutrophic conditions, these organisms have the ability to
669 maintain in stratified oligotrophic environments, including in deep layers under low light-
670 nutrient conditions (Kemp & Villareal 2013; Kemp & Villareal, 2018).

671 **3.5 Contribution of the SCM to the water column production**

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

679 Subtropical stratified oligotrophic gyres cover 45% of the global ocean (McClain et al.
680 2004). Assuming that the Ionian Sea is representative of such systems (e.g. Mignot et al.
681 2014; Barbieux et al. 2019), and extrapolating the estimated relative contribution of the SCM
682 layer to the water column production in the Ionian (F_{SCM} ~16%), then the SCM layer would
683 contribute ~7% of the community production of the water column on a global scale (i.e. F_{SCM}
684 of 16% multiplied by a global spatial occurrence of 45%). In addition, using a global BGC-
685 Argo database, Cornec et al. (2021) estimated that SCMs in oligotrophic subtropical gyres
686 behave as SBM 8–42% of the year, depending on the season. Thus, assuming the Ligurian
687 SCM oligotrophic summer system as a reference for SBM, the contribution of the SCM layer
688 to the global water column production could seasonally reach 19% (i.e. F_{SCM} of 42%
689 multiplied by a global spatial occurrence of 45%).



690 We recognize that these estimates are very crude and need to be refined and confirmed
691 in future studies. Yet they suggest that the contribution of the SCM layer to the water column
692 production may be significant globally, although commonly ignored. Our observations are
693 consistent with previous findings (Crombet et al. 2011; Kemp & Villareal 2013; Mignot et al.
694 2014), and suggest that stratified oligotrophic systems should no longer be considered as
695 steady oceanic deserts and that their biogeochemical contribution should be accounted for and
696 better quantified to improve global carbon budgets.

697 **4 Conclusions**

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

704 From a methodological point of view, our results indicate that, compared to the c_p
705 coefficient, the diel cycle of the b_{bp} coefficient is not an optimal proxy for the daily POC
706 variations, so that we are not confident using the b_{bp} -based gross community production
707 estimates, although it may provide a more robust proxy for the fraction of particulate matter in
708 the smaller size classes. Our results for the surface layer of the Ligurian Sea are consistent
709 with previous studies from moored observations (Kheireddine & Antoine 2014; Barnes &
710 Antoine 2014), and we found they are valid for the entire water column and for both the
711 Ligurian and Ionian Seas. These results have major implications for use of the methodology
712 with geostationary ocean color missions and standard BGC-Argo profiling floats that yield
713 only the b_{bp} coefficient. The present results thus argue in favor of a frequent implementation



714 onto BGC-Argo floats of transmissometers (c_p sensors), which provide information on a suite
715 of key biogeochemical variables (Claustre et al. 2020), from phytoplankton community
716 composition (Rembauville et al. 2017), to particle flux export (Briggs et al. 2011; Estapa et al.
717 2013) and, as demonstrated here, biological production (White et al. 2017; Briggs et al. 2018).

718 Our c_p -based gross community production rates compare consistently with previous
719 estimates from a similar approach applied to oligotrophic waters (Claustre et al. 2008; Gernez
720 et al. 2011; Barnes & Antoine 2014). These values are also consistent with estimates of
721 primary production either computed from the model of Morel (1991) coupled to the
722 considered BGC-Argo data, or published in the literature, although admittedly higher. This is
723 unsurprising because the present estimates are based on the c_p coefficient, which accounts for
724 both autotrophic and heterotrophic organisms (not just phytoplankton). This nevertheless
725 raises the question of the selection of an empirical bio-optical relationship, which is key to
726 converting c_p into POC equivalent. In the present study, the c_p -derived production estimates
727 on average decrease by 25% or increase by 37% depending on the used bio-optical
728 relationship, which is not negligible. Hence, we recommend POC sampling simultaneously to
729 BGC-Argo floats deployment. This will help to better constrain bio-optical relationships and
730 ultimately improve the reliability of the biomass and production estimates.

731 Our results indicate that both the Ligurian and Ionian Seas may sustain relatively large
732 levels of gross community production during the oligotrophic summer period, with a
733 substantial contribution by the SCM layer, a feature characteristic of oligotrophic systems that
734 is typically considered as steady and non-productive. In the Ligurian, the SCM behaves as a
735 subsurface biomass maximum (SBM) and appears to respond to episodic abiotic forcing, with
736 increased production rates coinciding with enhanced light availability in response to shoaling
737 isopycnals and SCM. In this system, the particle assemblage is dominated by phytoplankton
738 organisms, mainly nanoflagellates. In contrast, the Ionian SCM layer essentially reflects



739 photoacclimation of phytoplankton cells to prevailing environmental conditions. It does not
740 seem affected by modifications in abiotic forcing, although the phytoplankton assemblage
741 appears to be dominated by diatoms. These results agree with previous BGC-Argo-based
742 studies describing the occurrence and functioning of SCM systems in the global ocean
743 (Mignot et al. 2014; Cornec et al. 2021) and Mediterranean Sea (Lavigne et al. 2015;
744 Barbieux et al. 2019), and offer a first attempt to quantify biological production in such
745 systems. More generally, our study suggests that the contribution of the SCM layer to the
746 water column production varies broadly depending the considered system, whether seasonally
747 (~42% in the Ligurian Sea) or permanently (~16% in the Ionian Sea) oligotrophic.

748 Our study emphasizes the promising potential of BGC-Argo profiling floats for providing
749 a non-intrusive, high-frequency assessment of POC production within the whole water
750 column, which is critical in particular for applications to stratified oligotrophic environments
751 with recurring or permanent SCMs. The present results, based on data from two
752 Mediterranean environments, should be confirmed in the future through the deployment of
753 “multi-profiling” BGC-Argo floats in the broad, remote subtropical gyres. In such systems,
754 biological production is not constant but, instead, shows high temporal heterogeneity (Karl et
755 al. 2003; Claustre et al. 2008) that may be missed by traditional sampling, leading to a
756 potential underestimate of the biogeochemical impact of these systems in global carbon
757 budgets. Implementing such a BGC-Argo-based approach to carbon flux quantification
758 becomes even more important in the perspective of climate change, which is predicted to
759 induce an expansion of stratified oligotrophic gyres and an oligotrophication of the oceans
760 (Sarmiento et al. 2004) as already observed from satellite imagery (Polovina et al. 2008;
761 Signorini et al. 2015).

762



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

775

776 *Data availability* The BGC-Argo profiling float data and metadata used in this paper may
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778 are available from the Argo Global Data Assembly Center (<ftp://ftp.ifremer.fr/ifremer/argo>).
779 These data were collected and made freely available by the International Argo Program and
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781 [ops.org](https://www.ocean-ops.org)). The Argo Program is part of the Global Ocean Observing System. The
782 PEACETIME project pigment data are available from the SEANOE archive under the
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785 data may be accessed upon request ([http://www.obs-](http://www.obs-vlfr.fr/Boussole/html/boussole_data/login_form.php)
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802

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Figure captions

Figure 1: Trajectories of the two BGC-Argo profiling floats fLig (WMO6901776) and fIon (WMO6902828) deployed respectively in the Ligurian Sea (green) and the Ionian Sea (blue).

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 Chl (a and d), b_{bp} (b and e) and c_p (d and f) in the Ligurian Sea (left) and the Ionian Sea (right). The Mixed Layer Depth (MLD; black line), the isopycnal 28.85, expressed as σ_t (blue line), the euphotic depth (Z_{eu} ; white line) and the depth of the SCM (magenta 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.

Figure 4: Temporal evolution of Chl (a and d), c_{bp} (b and e), and b_{bp} (c and f) in the surface (red) and SCM (dark green) 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 time series 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 the 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 on May 24, 2014 (see text section 2.1). The fION float was deployed concurrently to sampling for HPLC pigments at the PEACETIME ION station on May 28, 2017. Pigment data collected at ION over four days prior to float deployment are shown.

Figure 9: Temporal evolution of the bio-optical ratios of b_{bp} / c_p (a), c_p / Chl (b) and b_{bp} / Chl (c) in the SCM layer for the Ligurian Sea (left) and the Ionian Sea (right). The dotted lines indicate the dates when the values of c_p in the SCM layer reach a minimum.

Figure 10: Time series of the daily-integrated photosynthetically available radiation (PAR) at the SCM level in the Ligurian Sea (a) and the Ionian Sea (b). The horizontal grey line shows the median of each time series. The dotted lines indicate the dates at which the values of c_p in the SCM layer reach a minimum.



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



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	$\text{POC} = 71002 b_{bp}(555) - 5.5$
Loisel et al (2011)	Mediterranean	$\text{POC} = 37550 b_{bp}(555) + 1.3$
Cetinić et al. (2012)	North Atlantic	$\text{POC} = 35422 b_{bp}(700) - 14.4$



Table 3: Mean and range (%) in relative daily variations ($\widetilde{m}\Delta$ and $\widetilde{r}\Delta$, 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 different layers of the water column, i.e. surface (0- Z_{pd}), SCM (SCM), and euphotic (0- Z_{eu}) layers.

Region		Surface layer		SCM layer		Euphotic layer	
		$\widetilde{\Delta}c_p$	$\widetilde{\Delta}b_{bp}$	$\widetilde{\Delta}c_p$	$\widetilde{\Delta}b_{bp}$	$\widetilde{\Delta}c_p$	$\widetilde{\Delta}b_{bp}$
Ligurian Sea	$\widetilde{m}\Delta$	12.7	-2.3	14.5	3.8	-134.9	1.1
	$\widetilde{r}\Delta$	256.7	28.5	194.8	107.8	2603.1	20.5
Ionian Sea	$\widetilde{m}\Delta$	0.55	0.23	1.16	0.06	0.39	0.21
	$\widetilde{r}\Delta$	54.4	21.2	102.4	57.3	55.9	24.9



Table 4: Estimates of primary and community production (in units of $\text{gC m}^{-2} \text{d}^{-1}$) 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	0-1.5 Z_{eu}	0.34
	Bosc et al. (2004)	Western basin	1998-2001	0-1.5 Z_{eu}	0.45
	-	Eastern basin	-	-	0.33
	Uitz et al. (2012)	Bloom region	May-Aug 1998-2007	0-1.5 Z_{eu}	0.26–0.82
	-	No blom 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
	Marañon 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 \pm SD ($\text{gC m}^{-2} \text{d}^{-1}$) 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 \pm 0.84	0.35 \pm 0.09
Claustre et al. (1999)	1.22 \pm 1.16	0.48 \pm 0.12
Oubelkheir et al. (2005)	1.18 \pm 1.13	0.46 \pm 0.11
Behrenfeld & Boss (2006)	1.43 \pm 1.35	0.56 \pm 0.14
Gardner et al. (2006)	0.93 \pm 0.88	0.36 \pm 0.09
Stramski et al. (2008)	1.62 \pm 1.54	0.63 \pm 0.16
Loisel et al. (2011)	0.98 \pm 0.92	0.38 \pm 0.10
Cetinić et al. (2012)	0.96 \pm 0.91	0.37 \pm 0.09



Table 6: Community production mean rates \pm SD ($\text{gC m}^{-2} \text{d}^{-1}$) 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, and euphotic layers.

Variable	Ligurian Sea			Ionian Sea		
	Euphotic	Surface	SCM	Euphotic	Surface	SCM
POC ($\text{gC m}^{-2} \text{d}^{-1}$)	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 ($\text{gC m}^{-2} \text{d}^{-1}$)	1.18 ± 1.13	0.29 ± 0.33	0.96 ± 1.28	0.46 ± 0.11	0.11 ± 0.04	0.14 ± 0.39

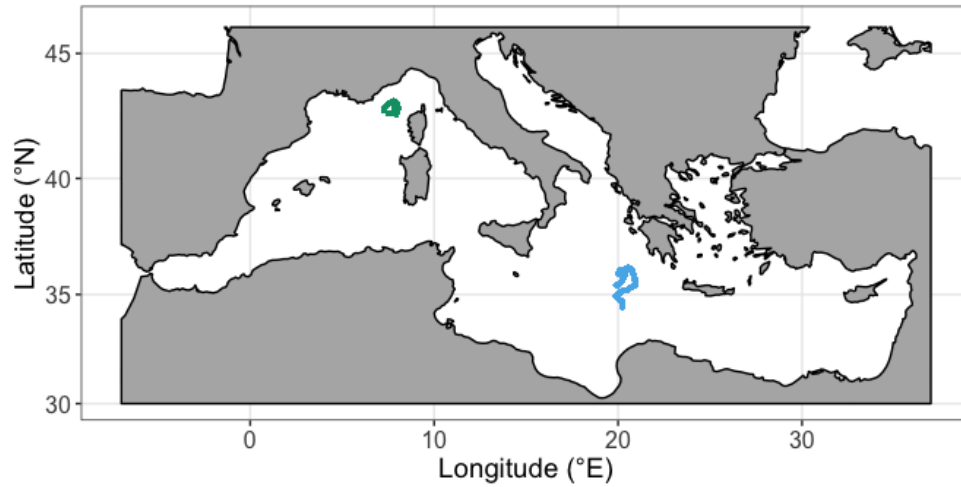


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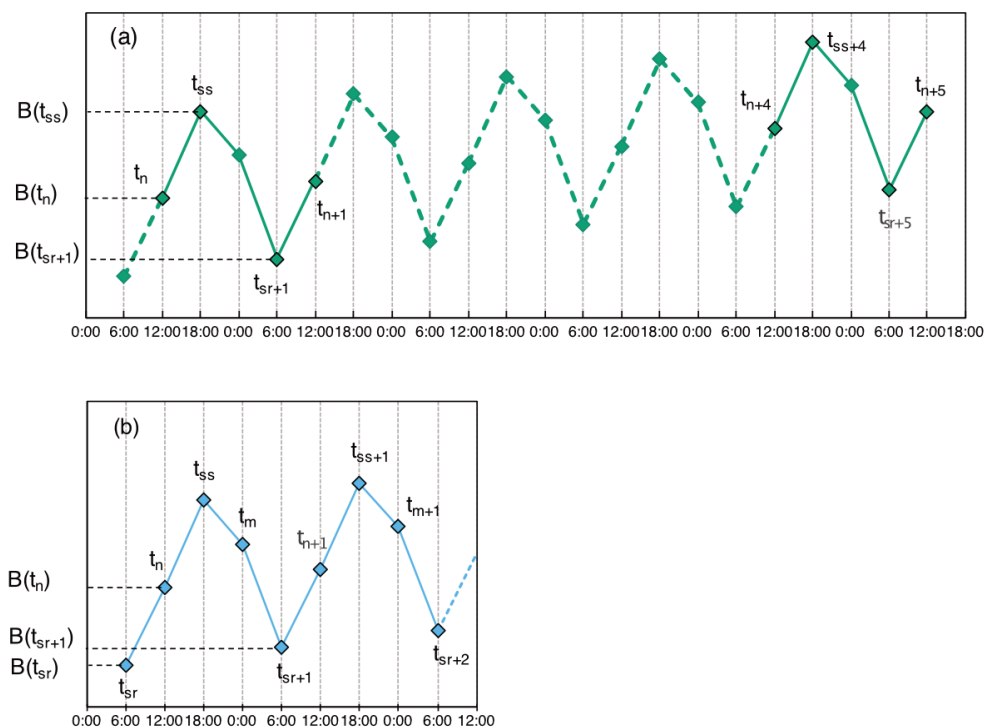


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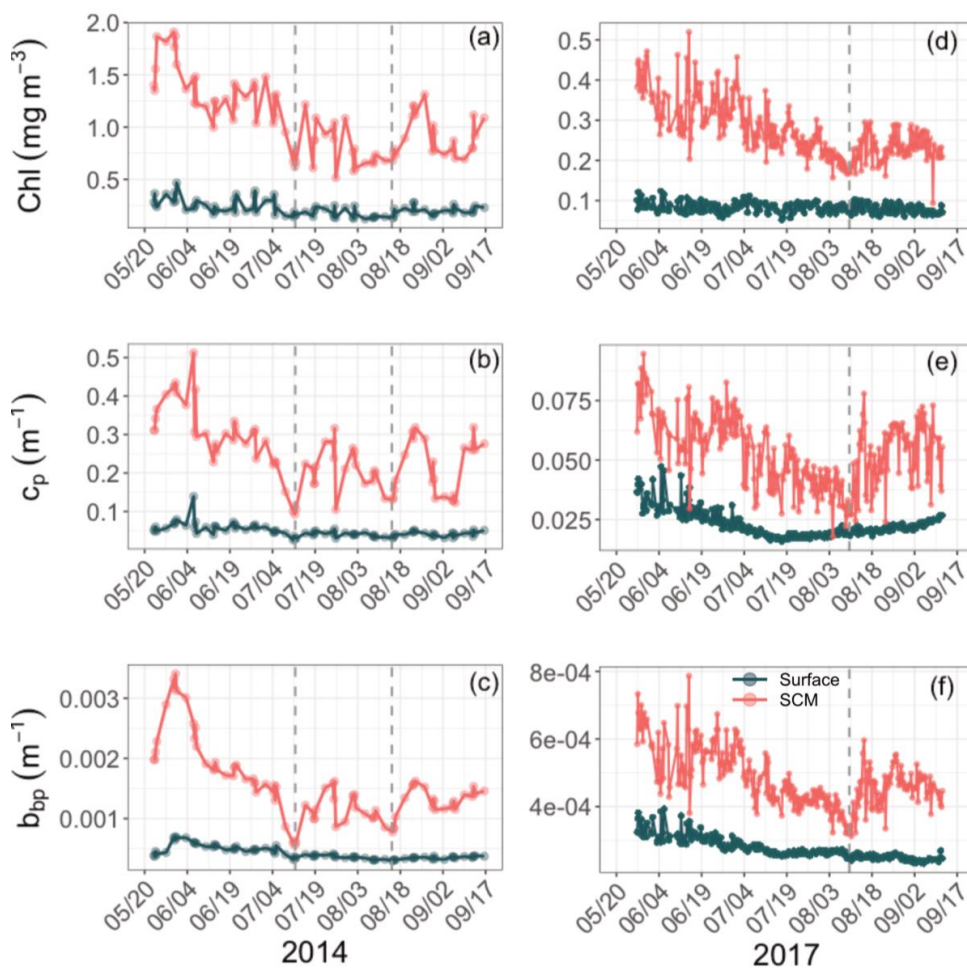


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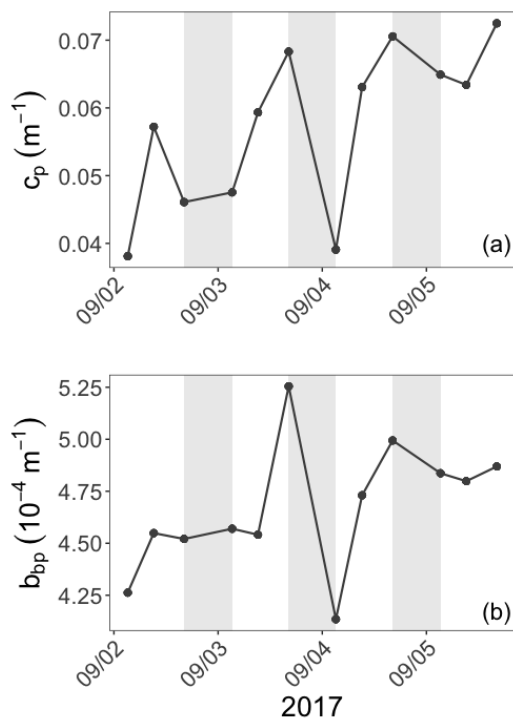


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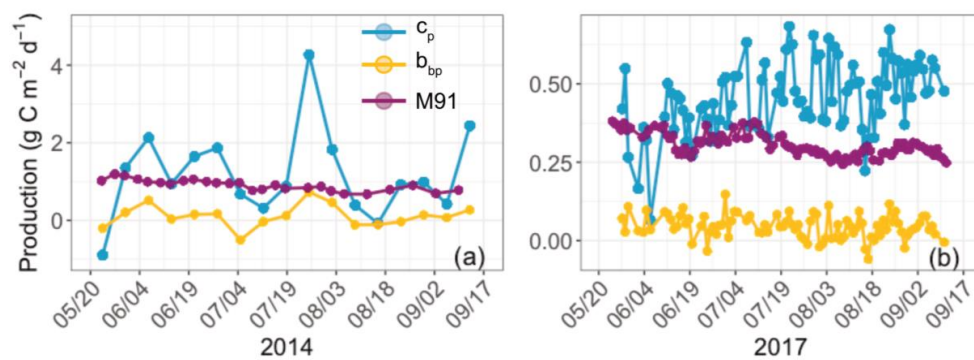


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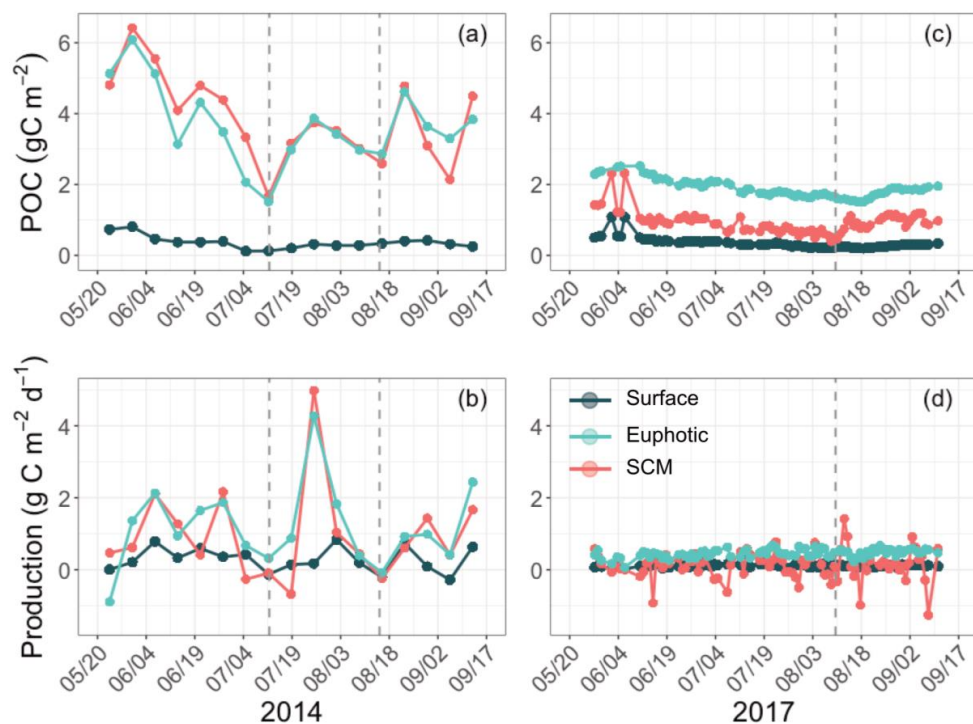


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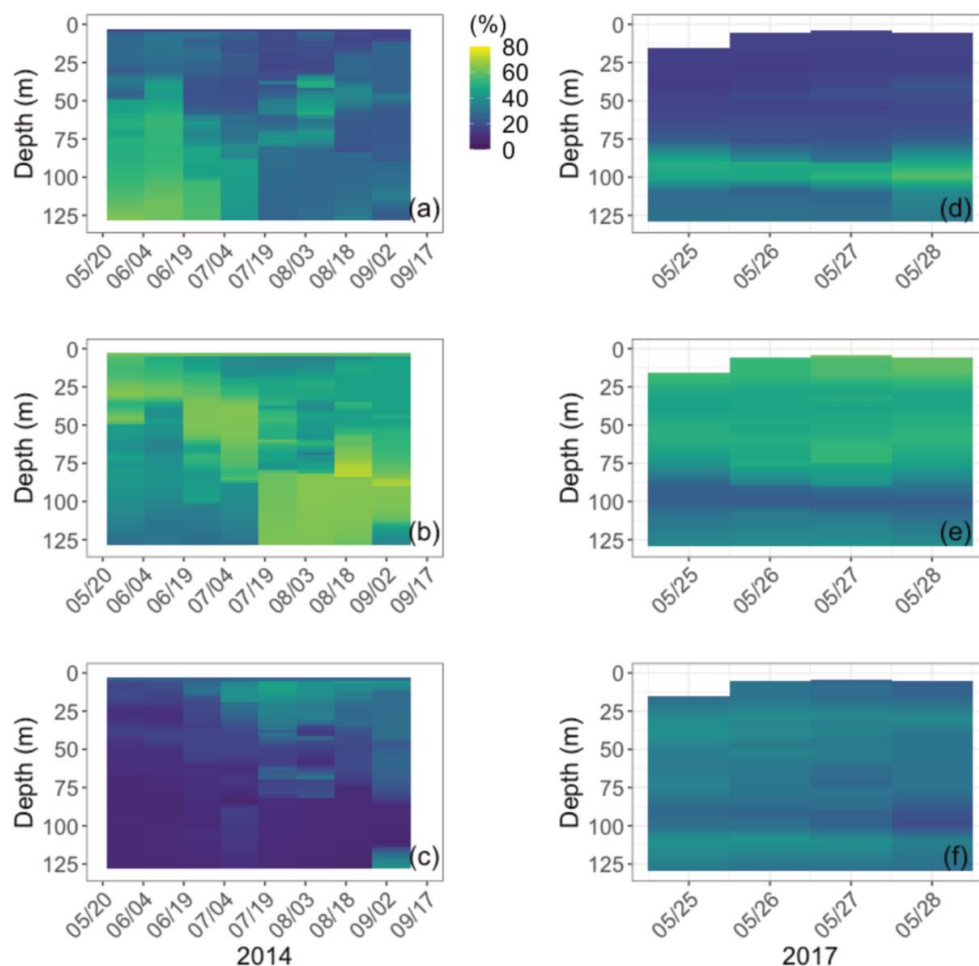


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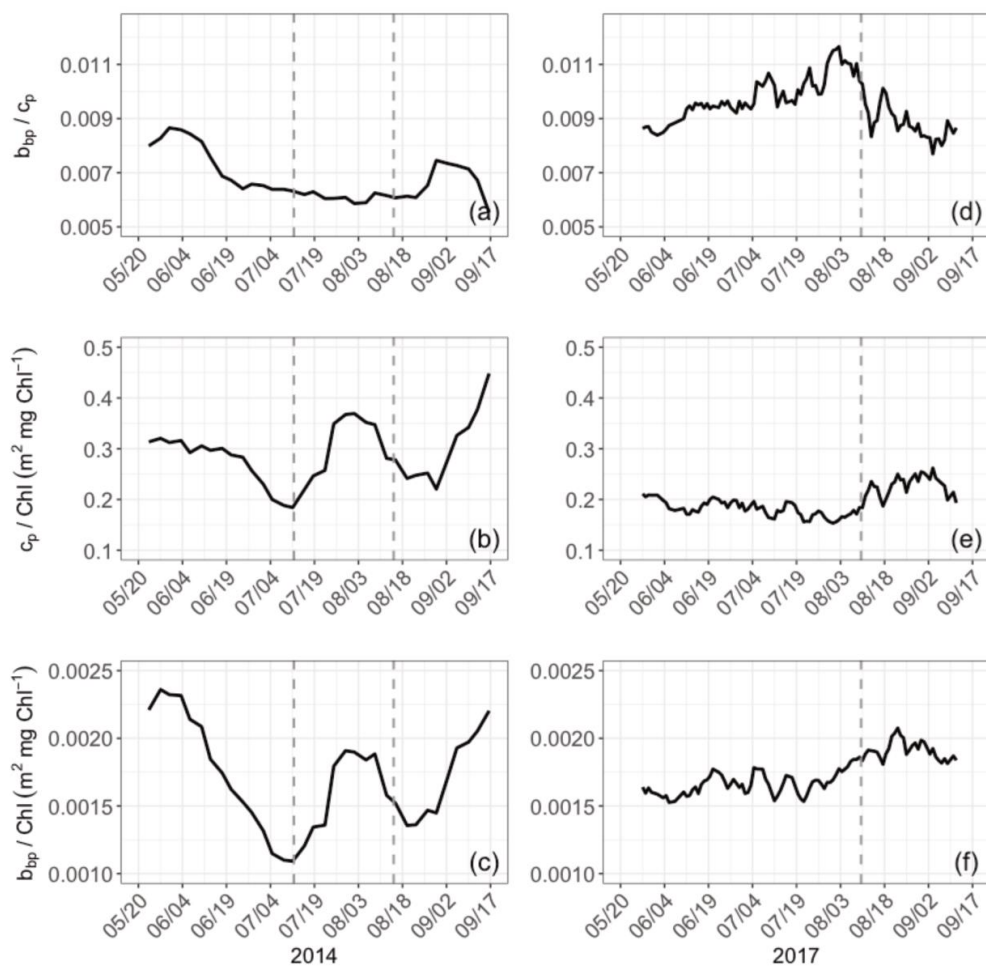


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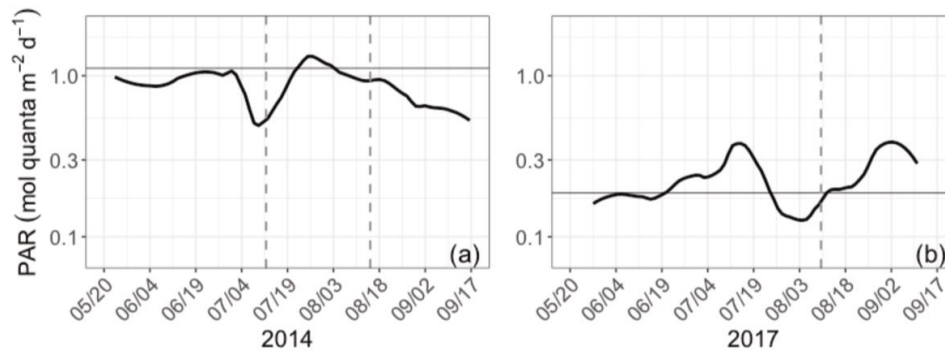


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