Inter-annual variations over a decade of primary production of the seagrass *Posidonia oceanica*

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**Abstract**

We acquired quasi-continuous measurements of community gross primary production (GPP) by mass balance of O₂ measured on a mooring, from August 2006 to October 2016 over a *Posidonia oceanica* meadow (10 m depth) in the Bay of Revellata (Corsica). Over the 2006–2016 period, annual GPP averaged 88 molO₂ m⁻² yr⁻¹ and ranged from 61 to 108 molO₂ m⁻² yr⁻¹. The 2 yr with the lowest annual GPP (2007 and 2015) were characterized by a low occurrence of fall–winter storms, probably leading to the accumulation of leaf litter in fall and early winter; we hypothesize this might have led to occultation of benthic macro-algae. Among the other years, the inter-annual variability of GPP was related to changes during the February–August period, as GPP was repeatable among years during the September–January period. For the February–August period, inter-annual variations of GPP were correlated to chlorophyll *a* (Chl *a*), solar radiation (SR) and water temperature. Computed phytoplankton GPP corresponded to a small fraction of community GPP, so the relation between GPP and Chl *a* probably reflected inter-annual variations of a common driver that we hypothesize to be nutrient inputs. The correlation of GPP with SR shows that light availability contributed to inter-annual variations of the development of *P. oceanica*. The positive relation between GPP and temperature was consistent with the fact that the observed temperatures in the Bay of Revellata were during the study period within the comfort range for the growth of *P. oceanica*, despite an increase of water temperature of 0.7°C.

*Posidonia oceanica* is a marine phanerogam (magnoliophyta) endemic of the Mediterranean Sea that forms vast and lush meadows, and ranks among the most productive ecosystems on Earth (Duarte and Chiscano 1999; Duarte et al. 2010). There is a large uncertainty in the estimation of the total surface area occupied by *P. oceanica* meadows (Bonacorsi et al. 2013), that range between 25,000 km² and 50,000 km² corresponding to 1–2% of the total surface area of the Mediterranean Sea (Bethoux et al. 1986; Pasqualini et al. 1998). The surface area of meadows that has been effectively mapped is 12,247 km², although substantial portions of the coastlines in the Mediterranean Sea have not been actually mapped (Telesca et al. 2015). The *P. oceanica* meadows border nearly all of the coastlines of the Mediterranean Sea, and are present from depths between ~ 1 m and ~ 40 m. *P. oceanica* can survive within a wide range of salinity (21.5–48.0) and water temperature (10–30°C) (Meinesz et al. 2009; Tomasello et al. 2009), but require clear water with a low turbidity, so are absent close to the delta of large rivers (Nile, Rhône, …) (Gobert et al. 2006). The extent of the meadows of *P. oceanica* is decreasing (Boudouresque et al. 2009; Marbà et al. 2014; Telesca et al. 2015), as most other seagrasses worldwide (Waycott et al. 2009).

*P. oceanica* meadows have an important ecological but also economic value (Costanza et al. 1997) estimated to 172 € m⁻² yr⁻¹ by Vassallo et al. (2013), as they provide numerous ecosystem goods and services (Boudouresque et al. 2006; Campagne et al. 2015). *P. oceanica* meadows are ecosystem engineers that transform and stabilize the coastal environment (Boudouresque et al. 2006). The leaves of *P. oceanica* slowdown water currents, trapping suspended particles (Dauby et al. 1995; Garcia and Duarte 2001), and the resulting lower turbidity allows a better light penetration (Carr et al. 2010). The sediment accumulation combined to the root and rhizome growth leads to the formation of the “matte” (Boudouresque and Meinesz 1982). The detached leaves in autumn will in part accumulate in the shore forming “banquettes” that can be more than 1 m high, several meters large, and several hundred meters long (Mateo et al. 2003). These structures protect beaches from erosion by the winter-time storms (Guala et al. 2006). The matte and banquettes stabilize the shoreline and in certain cases the *P. oceanica* meadows make structures equivalent to coral reef barriers (Boudouresque et al. 2006). *P. oceanica* meadows are
habitat, breeding and spawning ground, and nursery for numerous species, and host a large biodiversity; ~ 400 species of flora, several thousand species of fauna, totaling ~ 20% of the species inventoried in the Mediterranean Sea (Boudouresque et al. 2006). Furthermore, \textit{P. oceanica} meadows also contribute to sustain production and biodiversity of adjacent ecosystems, with economic consequences, in particular with regards to fisheries (Boudouresque et al. 2006).

\textit{P. oceanica} meadows are also carbon sinks (Romero et al. 1994; Mateo et al. 1997; Pergent et al. 1997). The matte is mainly composed of dead roots, rhizomes and leaves, and to a lesser extent of sedimented particles from the water column, overall corresponding to organic carbon that is relatively refractory to biological degradation, that, in addition, is compacted by a cement of calcium carbonate (Boudouresque and Meinesz 1982). Despite microbial degradation mainly in the first millimeters of the matte where \textit{O$_2$} is present (Holmer et al. 2003), a large fraction of the organic carbon in the matte will be sequestered for millennia, acting as a sink for carbon, nitrogen, and phosphorus (Romero et al. 1994; Mateo et al. 1997, 2006; Pergent et al. 1997). About 30\% of organic carbon from net primary production of \textit{P. oceanica} meadows is stored on the long-term in the matte (Mateo et al. 1997, 2006; Pergent et al. 1997; Duarte et al. 2005). This storage only lasts as long as the \textit{P. oceanica} meadow is healthy; in case of loss of the seagrass shoots, currents and waves will desegregate the matte and the released organic matter might be remineralized by bacteria (Kennedy et al. 2010; Fourqueiran et al. 2012).

Seagrass meadows are threatened by several human stressors, and these ecosystems are decreasing globally (Duarte 2002; Duarte et al. 2003; Waycott et al. 2009), including \textit{P. oceanica} (Marbà et al. 2014), with a decrease in surface coverage estimated to 34\% during the last 50 yr (Telesca et al. 2015). \textit{P. oceanica} meadows are threatened by eutrophication (waste water and aquaculture), physical destruction from shoreline construction, anchoring and trawling, and climate change (sea-level rise and warming). During the last decades, the human population as well as tourism have increased in the regions bordering the Mediterranean Sea, with an increase of urbanization on shorelines. This has led to a direct destruction of \textit{P. oceanica} meadows, as well as an increase of nutrient inputs to the coastal zone from wastewater (Boudouresque et al. 2009). Eutrophication will have a double negative impact on \textit{P. oceanica}: development of phytoplankton leading to a decrease of water transparency; proliferation of epiphytes growing on \textit{P. oceanica} leaves (Boudouresque et al. 2006). The epiphytes have a much faster growth than the \textit{P. oceanica} leaves and will compete with \textit{P. oceanica} for light and nutrients (Boudouresque et al. 2006). Organic matter and nutrients released from aquaculture and wastewater will also strongly affect \textit{P. oceanica} meadows leading a decrease of the density of shoots, and changes of the sediment biogeochemistry, as well as in benthic fauna assemblages and bacterial communities (Holmer and Kristensen 1992; La Rosa et al. 2001; Holmer and Frederiksen 2007; Papageorgiou et al. 2009; Mirto et al. 2014). Anchoring and trawling also cause damage of \textit{P. oceanica} meadows by the physical removal of shoots, and it takes up to 100 yr depending on extent of damage for the meadow to recover from such damage (Gonzales-Correa et al. 2005; Abadie et al. 2015). The slow recovery is due to the slow growth of \textit{P. oceanica} but also to the changes in the sediment physico-chemistry related to the destruction of roots and rhizomes that will be unfavorable to the recolonization (Abadie et al. 2016). Some invasive plant species such as \textit{Caulerpa} sp. and \textit{Lophocladia} \textit{latelmannii} can compete with \textit{P. oceanica} (Boudouresque et al. 2009), although they thrive in already degraded meadows with a low shoot density (Williams 2007). Finally, global and climate changes might affect the survival of \textit{P. oceanica}. The lower depth limit of the meadows corresponds to the light compensation depth (Olesen et al. 2002), that will shift with sea-level rise. \textit{P. oceanica} is also sensitive to high water temperature, and shoot mortality increases during extreme warm events (> 28.0°C) during heat waves at the end of summer (Diaz-Almela et al. 2007; Marbà and Duarte 2010), that might increase with global warming (Jordà et al. 2012).

Primary production of \textit{P. oceanica} is notoriously variable with depth and also across temporal scales: sub-daily, seasonal (Bay 1984; Pergent-Martini et al. 1994; Alcoverro et al. 1995; Gobert et al. 2006), and year-to-year (Champenois and Borges 2012). The variability of gross primary production (GPP) in \textit{P. oceanica} can be due to natural causes such as variations of incident solar radiation (SR), that varies day-to-day due to cloudiness (Gazeau et al. 2005) and seasonally (Alcoverro et al. 1995; Champenois and Borges 2012), or as a result from human stressors such as eutrophication (Apostolaki et al. 2010). Consequently, we hypothesize that high frequency monitoring of GPP could be used to diagnose the health status of \textit{P. oceanica} meadows, and its long-term evolution. Further, inter-annual variations of GPP in response to extreme weather events (heat wave, cold spell, extreme storm, abnormal mild weather, ...) can provide natural tests to check how ecosystems could respond in future to global and climate change (Jentsch et al. 2007).

The aim of the present paper is to investigate if long-term changes (decline or increase) of GPP occurred in a \textit{P. oceanica} meadow (at 10 m depth) based on a large dataset spanning a decade (2006–2016), as contribution to long-term observations of the meadow in the Bay of Revel-lata (Corsica) under the STARE-CAPMED initiative. We also quantify the inter-annual variability of GPP which has been seldom investigated in marine ecosystems, and to our best knowledge never before in seagrass meadows. We investigate the possible causes of these inter-annual variations of GPP with the analysis of additional environmental data such as water temperature, wind speed, precipitation, SR, and phytoplankton biomass. Such analysis can provide insights into the response of GPP in \textit{P. oceanica} meadows.
to future human induced changes in environmental conditions, and we particularly discuss the response to warming.

**Material and methods**

A mooring was deployed from August 2006 until October 2016 at 10 m depth over a *P. oceanica* meadow (8.725°E 42.580°N) in front of the Stareso research station (Corsica, France). The mooring was equipped with three Aanderaa optodes (3835) mounted on Alec Instrument data-loggers, located at 4.5 m, 7.0 m, and 9.5 m depth, that recorded O$_2$ saturation and water temperature on an hourly basis. Data retrieval, maintenance, and stability check of optodes was done every 3 months. The computation of GPP, community respiration (CR), and net community production (NCP) is based on the Odum (1956) method that relies on the changes of vertically integrated O$_2$ content (Q$_{O2}$ in mmol m$^{-2}$) derived from the vertical integration of volumetric concentration measurements at the 3 depths (4.5 m, 7.0 m, and 9.5 m).

Daily integrated CR (mmol O$_2$ m$^{-2}$ d$^{-1}$) is computed according to:

$$ CR = \left( \sum \left( \left[ (Q_{O2n})_{t+1} - (Q_{O2n})_t \right] + \sum F_O2n \right) / H_n \times 24 \right) $$

(1)

where $(Q_{O2n})_{t+1} - (Q_{O2n})_t$ is the change in $Q_{O2}$ during night-time $(Q_{O2n})$ between two hourly intervals $(t)$, $F_O2n$ is the air-sea O$_2$ exchange at each $t$ during night-time computed using the Ho et al. (2006) gas transfer parameterization as function of wind speed, and $H_n$ is the night-time duration in hours.

Daily integrated GPP (mmol O$_2$ m$^{-2}$ d$^{-1}$) is computed according to:

$$ GPP = \sum \left( \left[ (Q_{O2d})_{t+1} - (Q_{O2d})_t \right] + \sum F_O2d - CR \right) $$

(2)

where $(Q_{O2d})_{t+1} - (Q_{O2d})_t$ is the change in $Q_{O2}$ during day-time $(Q_{O2d})$ between two $t$, $F_O2d$ is the air-sea O$_2$ exchange at each $t$ during day-time.

Daily integrated NCP is computed as the sum of daily integrated GPP and daily integrated CR.

The computed GPP value integrates all the components of the meadow, planktonic and benthic, although Champenois and Borges (2012) showed it is largely dominated by the benthic compartment (*P. oceanica*, epiphytic and benthic macro-algae). We obtained 2821 GPP measurements from 08 August 2006 to 27 October 2016 (Supporting Information Fig. S1). Ancillary data for the analysis of inter-annual GPP variations were: sea surface temperature (SST), chlorophyll $a$ (Chl $a$), wind speed, SR, and precipitation. SST was derived from temperature measurements over the top of the canopy (optode located at 9.5 m depth). Water temperature was measured at the three depths, and the water column was always isothermal, so we chose to use the data acquired just above the *P. oceanica* canopy. Monthly Chl $a$ values were derived from moderate-resolution imaging spectroradiometer (MODIS) and processed level-3 data were retrieved from the Giovanni data portal (https://giovanni.gsfc.nasa.gov/giovanni/) for a quadrant delimited by 42.579;42.591°N and 8.723;8.728°E; for a quality assessment and calibration of the Chl $a$ MODIS products refer to Kwikatkowska et al. (2008) and Meister et al. (2012). Wind speed was measured with a Thies Clima anemometer on top of one of Stareso buildings and data were converted from the measurements height (11.8 m) to a reference height (10 m) based on Johnson (1999). SR (duration in h with SR > 120 W m$^{-2}$) and precipitation data were measured at the Calvi airport (8.793°E 42.524°N) and retrieved from the Météo France data portal (http://www.meteofrance.com/climat/france/calvi/20050001/releves). Analysis of inter-annual variations was based on monthly averages for GPP, SST, Chl $a$, wind speed, and monthly cumulated values for SR and precipitation. The annual cycle was determined from the seasonal cycle of *P. oceanica* biomass and defined from 1$^{st}$ November to 31$^{st}$ October, since leaf biomass is typically lowest in November after the autumn leaf shedding. Shoot density was measured by counts and leaf biomass on 10 shoots collected by SCUBA divers as described by Champenois and Borges (2012).

Statistical analysis was done with Graphpad Prism 6 software, using either Student $t$-test or ANOVA at the 0.05 level. A principal component analysis (PCA) was performed using the procmp function in R software (https://www.r-project.org/); data were scaled to zero mean and unit variance, prior to analysis.

The hourly dissolved oxygen and water temperature time-series are available as Supporting Information material.

**Results and discussion**

**Seasonal and inter-annual variations of GPP in the *P. oceanica* meadow in the Bay of Revellata**

Individual GPP values ($n = 2821$) varied over four orders of magnitude, ranging between 0.4 mmol O$_2$ m$^{-2}$ d$^{-1}$ and 1818 mmol O$_2$ m$^{-2}$ d$^{-1}$ (Supporting Information Fig. S1). CR and NCP were strongly correlated to GPP (Supporting Information Fig. S2), in agreement with previous investigations of marine community metabolism (Duarte and Agustí 1998). CR and NCP represented for the whole data-set 27% and 73% of GPP, and NCP averaged $23 \pm 23$ molO$_2$ m$^{-2}$ yr$^{-1}$, showing that the *P. oceanica* meadow was net autotrophic at annual scale, in agreement with previous investigations of community metabolism in *P. oceanica* meadows (e.g., Frankignoule and Bouqueigneau 1987; Barrón et al. 2006; Duarte et al. 2010). Net autotrophy was also confirmed by an overall O$_2$ oversaturation that averaged 104% (range 66–287%) during the study period (Supporting Information Fig. S1). As previously described by Champenois and Borges (2012), whatever the season, a daily variation of O$_2$ concentration was observed,
following the pattern expected from day-night cycle which was more marked during summer than during winter, and at 9.5 m than at the other two depths (Supporting Information Fig. S1). Since NCP and CR were tightly correlated to GPP (Supporting Information Fig. S2) and that GPP is the driver of NCP and CR in this type of marine environments (Duarte and Agustí 1998), hereafter, we will only investigate inter-annual variations of GPP.

Figure 1 shows the monthly means of GPP over a 10 yr period from 2007 to 2016. There are marked seasonal variations of GPP with a maximum in June–July (~ 400 mmol O₂ m⁻² d⁻¹) and a minimum in November–December (~ 100 mmol O₂ m⁻² d⁻¹). These GPP patterns coincided with an oversaturation of O₂ (107.0% averaged for the whole data-set) in June–July and close to O₂ saturation (100.8% averaged for the whole data-set) in November–December (Supporting Information Fig. S1). The seasonal patterns and range of GPP values are consistent with those we derived at the same site and with the same method based on a shorter time-series (2006–2009) (Champenois and Borges 2012), as well as the data over a P. oceanica meadow in Magalluf Bay (Mallorca Island, Spain) based on O₂ changes in benthic chambers (Barrón et al. 2006). Strong inter-annual variations were also observed with annual integrated GPP ranging from a minimum of 61.3 molO₂ m⁻² yr⁻¹ in 2007 to a maximum of 107.6 molO₂ m⁻² yr⁻¹ in 2012 (Table 1). Such inter-annual variations of GPP are consistent with the strong inter-annual variations of biometric variables over P. oceanica meadows, such as number of leaves, leaf biomass, leaf length reported at our and other studies sites in the Mediterranean Sea (Bay 1984; Pergent-Martini et al. 1994; Soullard et al. 1994; Gobert 2002; Guillén et al. 2013). The overall average of GPP over the 10 yr period was 87.7 ± 18.4 molO₂ m⁻² yr⁻¹ (coefficient of variation [CV] of 21%), close to average of measurements (n = 29) compiled by Duarte et al. (2010) over P. oceanica meadows (mainly in Spain and Greece) of 67.1 ± 11.1 molO₂ m⁻² yr⁻¹ (based on an average of 0.25 ± 0.04 mmol O₂ g dry weight (dw)⁻¹ d⁻¹ and an average biomass of 735 g dry weight (dw)⁻¹). The values compiled by Duarte et al. (2010) were derived from several different sites and from different depths, and based on incubations with benthic chambers that can under-estimate GPP measurements due to photorespiration (Champenois and Borges 2012).

Differences from year-to-year were also apparent when comparing specific periods of the seasonal cycle of monthly GPP with the 10 yr climatology average (Fig. 1). The GPP averages for the period from September to January were repeatable from year-to-year, with the exception of 2007 and 2015. Shedding of older (and longer) P. oceanica leaves occurs in late summer and early fall that will be exported by fall–winter storms (Gobert et al. 2006). The leaves will start growing again in late winter (February). This has two consequences: first, GPP from P. oceanica collapses due to loss of biomass; second, light availability increases at the sediment surface and base of the

### Table 1. Annual gross primary production (GPP in molO₂ m⁻² yr⁻¹) from 2007 to 2016 at 10 m depth over a P. oceanica meadow in the Bay of Revellata (Corsica), excluding year 2014 for which no measurements were available in July precluding annual integration.

<table>
<thead>
<tr>
<th>Year</th>
<th>GPP (molO₂ m⁻² yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2007</td>
<td>61.3±0.6</td>
</tr>
<tr>
<td>2008</td>
<td>88.8±0.9</td>
</tr>
<tr>
<td>2009</td>
<td>96.0±1.0</td>
</tr>
<tr>
<td>2010</td>
<td>92.6±0.9</td>
</tr>
<tr>
<td>2011</td>
<td>89.9±0.9</td>
</tr>
<tr>
<td>2012</td>
<td>107.6±1.1</td>
</tr>
<tr>
<td>2013</td>
<td>61.9±0.6</td>
</tr>
<tr>
<td>2015</td>
<td>97.3±1.0</td>
</tr>
<tr>
<td>2016</td>
<td>80.0±0.8</td>
</tr>
<tr>
<td>Average</td>
<td>87.7±2.6</td>
</tr>
</tbody>
</table>
Champenois and Borges showed that the lack of fall storms during
2006–2007 (Luterbacher et al. 2007) did not allow the export of dead
P. oceanica leaves, blocking the development of benthic macro-algae, leading to
a low GPP during this period. Similarly, in 2015, the first
storms and export of dead leaves only occurred in early
December, based on de visu observations during SCUBA dives.
If we exclude years 2007 and 2015, then for the period of
2007–2016, the integrated GPP from September to January is
25.9 ± 3.8 molO2 m−2 (CV = 7.4%), corresponding to 29.7% of
the annual GPP. This significant portion of annual GPP occurs when P. oceanica leaf biomass has been reported to be at
its lowest (Gobert et al. 1995), and we hypothesize GPP is mainly
sustained by sciaphile benthic red macro-algae, although this
needs to be checked in future by direct measurements.
Inter-annual variations of annual GPP (Table 1) were due to
variability during the other periods of the year, since the GPP
values for the period from September to January were repeat-
able from year-to-year. In order to understand the source of
variability we tested correlations of GPP with five other vari-
ables: SST, Chl a, SR, precipitation, and wind speed. These var-
iables were chosen because high temperature (> 28°C) can
lead to mortality of P. oceanica (Diaz-Almela et al. 2007; Marbà
and Duarte 2012), but is also an important factor controlling
metabolism (López-Urrutia et al. 2006); Chl a and SR control
light availability for photosynthesis of P. oceanica; Chl a might
also indicate a contribution of the planktonic compartment to
community GPP; precipitation can lead to inorganic nutrient
inputs in near-shore marine areas that could be significant in
the Mediterranean Sea (Koçak et al. 2010), and wind speed can
provide information on vertical mixing and nutrient inputs as
well as export of litter from the P. oceanica meadows. None of
these variables correlated significantly with GPP for the period
from September to January.
Maximum monthly SST were observed systematically in
August, on average 24.2 ± 0.8°C for the whole period, ranging
between 23.2°C in 2007 and 25.5°C in 2012 (Fig. 2A). Min-
imum monthly SST were observed in February, on average
13.4 ± 0.6°C for the whole period, ranging between 12.8°C in
2013 and 14.3°C in 2007. The yearly maximum and mini-
um of monthly GPP were decoupled in time (May/June and
November, respectively) from the maximum and minimum of
SST (August and February, respectively). The warmest year
with an annual average of 18.6°C in 2007 was also the year
with the lowest GPP (61.3 molO2 m−2 yr−1), followed by 2012
(18.5°C) that was the year with the highest GPP (107.6 molO2
m−2 yr−1). The coolest year with an annual average of 17.7°C
in 2013 had a low GPP (61.9 molO2 m−2 yr−1), followed by
2010 (17.8°C) with a GPP (92.6 molO2 m−2 yr−1) close to the
overall average (87.7 molO2 m−2 yr−1). We conclude that year-
to-year variability of annual SST was not the major factor con-
trolling inter-annual variations of annual GPP.
In general, autumn and winter were the seasons with the
highest precipitations (Fig. 2B). The cumulated annual precipi-
tation was 649 ± 138 L m−2 (CV = 23.8%) on average over the
2006–2016 period. The cumulated precipitation from
September to March was 532 ± 177 L m−2 on average over the
2006–2016 period, corresponding to 82.0% of the annual total.
The driest period was from June to August, with a cumulated
precipitation of 41 ± 22 L m−2 on average over the 2006–2016
period, corresponding to 6.3% of the annual total. The rainiest
year was 2010 (annual cumulated precipitation of 914 L m−2)
with an annual GPP (92.6 molO2 m−2 yr−1) below the overall
average. The driest year was 2007 (annual cumulated precipita-
tion of 444 L m−2) with the lowest annual GPP (61.3 molO2
m−2 yr−1). During 2013, the cumulated annual precipitation was
very close to the average over the 2006–2016 period (685 L m−2),
although the annual GPP was among the lowest of the whole
period (61.9 molO2 m−2 yr−1). No significant correlation was
found between cumulated precipitation and the intensity of the
spring phytoplankton bloom indicated by Chl a concentration.
The Mediterranean Sea is very oligotrophic, so that nutrient
inputs from wet atmospheric deposition can be significant
(Koçak et al. 2010), and phytoplankton growth can respond at
very short time-scales (~ days) to nutrient pulses due to precipita-
tion or wind (Thyssen et al. 2014). Nevertheless, over longer time
scales (seasonal to inter-annual) precipitation did not seem to be a
driver of GPP variability over P. oceanica meadows. This was also
the case for wind speed that showed low seasonal and inter-
annual variability. Average wind speed over the 2006–2016
period was 1.8 ± 0.2 m s−1 (CV = 13.7%) (Fig. 2C). Wind speed
was higher from September to March (1.9 ± 0.2 m−1) than dur-
ing the rest of the year (1.6 ± 0.1 m s−1).
Cumulated annual SR averaged 2777 ± 90 h (CV = 3.2%),
over the 2006–2016 period. 2012 was the year with the high-
est SR (2881 h) and 2010 was the year with the lowest SR
(2606 h). The period from May to September had a low varia-
tion in SR (CV = 3.0%), while the period from January to April
had a higher variation in SR (CV = 16.9%). Year 2010 had the
highest GPP (107.6 molO2 m−2 yr−1) but a low SR (2606 h),
while year 2012 had a GPP close to the overall average (92.6
molO2 m−2 yr−1) although with the highest SR (2881 h). The
yearly maximum of SR (July) did not coincide with the one
of GPP (May–June), except for year 2010. The yearly mini-
um of SR (mostly in December) did not coincide with the one
of GPP (mostly in November). Nevertheless, a significant
positive linear relationship was found for the whole
2006–2016 period between monthly GPP and cumulated
monthly SR (r² = 0.38; p < 0.0001; n = 119) (Supporting
Information Fig. S3), in agreement with previous findings on
the role of light in regulating growth of P. oceanica meadows
across time-scales from day-to-day (Gazeau et al. 2005) to seasonal
(Alcoverro et al. 1995). Taken for each yearly cycle individually,
the r² value of the linear correlation between GPP and SR ranged
from 0.23 to 0.74 (Supporting Information Fig. S4), showing that additional processes also controlled seasonal and inter-annual variations of GPP, as discussed hereafter.

Chl a values were low, in general below 1 μg L⁻¹ (Fig. 2E). The timing and amplitude of the seasonal variations of the remote sensed Chl a data were in agreement with in situ measurements in the same area (Garrido et al. 2014). The average Chl a concentration was 0.3 ± 0.2 μg L⁻¹ (CV = 72.0%) for the period 2006–2016. The seasonal maximum Chl a concentration was observed in February–March corresponding to the spring diatom bloom (Garrido et al. 2014). During the spring bloom, the maximum monthly value was in March 2015 (1.4 μg L⁻¹) and the minimum in March 2016 (0.4 μg L⁻¹). In some years, an autumn Chl a peak was also observed but lower than the corresponding spring peak. The lowest Chl a concentrations were observed during the period from May to September, with an average of 0.14 ± 0.01 μg L⁻¹ (CV = 8.9%), typical in the study area due to nutrient depletion (Garrido et al. 2014). The yearly maximum of community GPP did not coincide with the spring phytoplankton blooms.

A PCA of the above mentioned variables allowed to summarize the variance across the whole data-set (Fig. 3). The first two principal components of variance (PC1 and PC2) described 69.6% of total variance. As GPP, SST, and SR all peaked in summer (Fig. 2A,D,E) they were positively related. Since Chl a peaked in early spring during periods of low GPP and was very low during summer (period of high GPP) both variables were negatively related. Finally, GPP showed no relation to wind speed and a poor relation to precipitation.

In order to further explore inter-annual variations of GPP, SST, SR, Chl a, precipitation and wind speed, we computed the monthly anomalies (noted by ′) as the difference between each monthly value and the average value for that given month for the whole period (2006–2016), normalized by the average and expressed in % (Fig. 4). The correlation analysis of the anomalies of variables did not show any significant relations across the entire data-set. In order to further examine...
inter-annual variations, three different periods of the yearly cycle from February to August were investigated (the period from September to January was not examined since, as mentioned above, it was nearly repeatable from year to year). The first period corresponded to February and March, the second period was the month of April, and the third period was from May to August. These periods were chosen by separating the period from May to August, when Chl $a$ is systematically low, making this a coherent period. The month of April stands out as the month of the transition of winter-mixed conditions to spring/summer-thermally stratified conditions, when seasonally SST start to increase (Bay 1984). For any of these periods, there was no significant correlation between monthly anomalies of GPP ($GPP'$) and those of cumulated precipitation and wind speed (not shown), so we will only examine hereafter the correlations with anomalies of SR (SR'), SST (SST'), and Chl $a$ (Chl $a'$).

For the first period (February and March), GPP was on average $13.9 \pm 4.1$ molO$_2$ m$^{-2}$ for the whole 2006–2016 period, corresponding to 16.1% of the annual total. We calculated a multiple linear regression (MLR) between the sum of GPP' for March and February as a function of the sum of cumulated SR (SR') and average Chl $a'$ (data from year 2007 was excluded from the MLR as the lack of export of dead leaves led to abnormal GPP values):

$$GPP' = -6 + 0.0553 \times SR' + 3.08 \times Chl\ a'$$
$$t = 0.87 > t_{crit (0.95, n=9)} = 1.82$$

For the second period (month of April), GPP was on average $9.6 \pm 3.4$ molO$_2$ m$^{-2}$ for the whole 2006–2016 period, corresponding to 11.1% of the annual total. This period is characterized by a very strong inter-annual variability in SR (CV = 17.6%), SST (CV = 4.1%), and Chl $a$ (CV = 74.4%) (Fig. 4A–C). Since this is the period of the year when SST starts to increase, we included SST' in addition to SR', Chl $a'$ to compute the MLR for $GPP'$ (excluding year 2013 for which remote sensed Chl $a$ were unavailable):

$$GPP' = 29 - 0.061 \times SR' + 4.33 \times Chl\ a' - 0.31 \times SST'$$
$$t = 0.90 > t_{crit (0.95, n=9)} = 1.82$$

As for the first period (Eq. 3) a positive relation with Chl $a'$ was observed although the relationship was negative with SR' unlike the first period.

For the third period (May–August), GPP was on average $38.7 \pm 8.2$ molO$_2$ m$^{-2}$ for the whole 2006–2016 period, corresponding to 41.1% of the annual total. This period was characterized by low Chl $a$ concentrations (Fig. 2E) and no clear relation was apparent between GPP' and Chl $a'$ (Fig. 4C). However, there was a general positive variation of GPP' and SST' and SR' (Fig. 4A,B), so that a MLR was built with those variables (excluding year 2014 because GPP values were unavailable in July of that year due to malfunctioning of an oxygen meter on the mooring):

$$GPP' = -287 + 0.052 \times SR' + 11.93 \times SST'$$
$$t = 0.93 > t_{crit (0.95, n=9)} = 1.82$$

During the first (February and March) and second (month of April) periods, $GPP'$ was positively related to Chl $a'$. We previously showed that at seasonal time scales phytoplankton growth decreased community GPP by shading effect and reduced light availability for $P.$ oceanica meadow rather than actually accounting for the planktonic contribution to community GPP (Champenois and Borges 2012). Indeed, we computed based on the GPP-Chl $a$ relation developed in the $P.$ oceanica meadow of the Bay of Palma (Gazeau et al. 2005), that phytoplankton GPP was on average in February–April of 2.7 molO$_2$ m$^{-2}$ corresponding to 11% of the measured community GPP of 25.1 molO$_2$ m$^{-2}$ during the same period. From year-to-year, computed phytoplankton GPP in February–April ranged between 1.6 molO$_2$ m$^{-2}$ in 2007 and 6.2 molO$_2$ m$^{-2}$ in 2015 (CV = 46%) and cannot account for the inter-annual variability of measured community GPP during the same period that ranged between 13.9 molO$_2$ m$^{-2}$ in 2007 and 30.6 molO$_2$ m$^{-2}$ in 2009 (CV = 21%). Alternatively, a common process could enhance both benthic and planktonic GPP leading to an indirect positive relation between $GPP'$ and Chl $a'$. In the Bay of Revellata, inter-annual variations of phytoplankton growth are driven by inter-annual changes in dissolved inorganic nutrients, mainly due to weather conditions driving vertical mixing (Goffart et al. 2015). Enhanced dissolved inorganic nutrients inputs should lead to an increase of both planktonic and benthic GPP, and we hypothesize it could explain the $GPP'$ and Chl $a'$ relation. We also hypothesize
that an indirect relation to nutrient inputs might also explain the negative relation between GPP' and SST' and GPP' and SR' in April (second period, Eq. 4), as warm and sunny conditions during this month might indicate early stratification and less stormy weather leading to less nutrient inputs by mixing (Goffart et al. 2015). This might also explain why the month of April stood out in the analysis as a specific period, as this corresponds to transition period from a well-mixed winter regime to a more stratified spring regime (Bay 1984).

The positive relation between GPP' and SST' during the third period (May–August) might reflect the enhancement of metabolic activity (Arrhenius temperature dependence relation, for example López-Urrutia et al. 2006). Alternatively it could indirectly reflect sunnier weather. Indeed, a positive relationship was found between GPP' and SR' during the first (February and March, Eq. 1) and third (May–August, Eq. 5) periods, in agreement with previous studies that have shown that light availability is the major process controlling growth and

**Fig. 4.** Anomalies of monthly gross primary production (GPP' in mmol O$_2$ m$^{-2}$ d$^{-1}$, open dots), cumulated solar radiation (SR' in h month$^{-1}$, stars, A), chlorophyll a concentration (Chl a' in μg L$^{-1}$, stars, B), and sea surface temperature (SST' in °C, stars, C) from August 2006 to October 2016 at 10 m depth over a *P. oceanica* meadow in the Bay of Revellata (Corsica).
GPP of *P. oceanica* both in time (seasonally) (Alcoverro et al. 1995) and in space (with depth) (Pergent-Martini et al. 1994).

We modeled GPP combining Eqs. 3–5 for the respective periods and using a constant GPP for the period from September to January (25.9 molO$_2$ m$^{-2}$, corresponding to cumulated value averaged for the whole 2006–2016 period), excluding the 2 yr when fall storms did not export litter leading to abnormal GPP values (2007 and 2015) and excluding years 2013 (no Chl $a$ data in April) and 2014 (no GPP data in July). The modeled and observed annual GPP (Fig. 5) were significantly linearly correlated ($r^2 = 0.74 > r_{crit}(0.95, n - 6) = 0.71$), with a slope (0.797) not significantly different from 1 ($t = 0.870 < t_{crit}(0.95, n - 6) = 2.78$, $p = 0.43$), and a y-intercept (18.95) not significantly different from 0 ($t = 0.860 < t_{crit}(0.95, n - 6) = 2.78$, $p = 0.44$). The statistical model allowed to explain 74% of the inter-annual variability of GPP of *P. oceanica* meadow in our study site.

Possible future evolution of GPP in *P. oceanica* meadows in response to warming and changes in occurrence of winter storms

GPP from September to January was 17.5 molO$_2$ m$^{-2}$ and 15.2 molO$_2$ m$^{-2}$ in 2007 and 2015, respectively, due to the absence autumn storms and export of fallen leaf litter (observed de visu during the scuba dives) that we hypothesize did not allow development of benthic sciaphile flora by occultation of light. GPP during the other years averaged 25.9 molO$_2$ m$^{-2}$ for the same period. By difference, the putative GPP of benthic sciaphile flora can be estimated to 9–10 molO$_2$ m$^{-2}$ (or ~ 67 mmol O$_2$ m$^{-2}$ d$^{-1}$), corresponding to 10% of the annual GPP of the meadow. The GPP of benthic sciaphile flora was estimated indirectly and is probably over-estimated as accumulation of litter might have also decreased by occultation GPP of *P. oceanica*, and requires to be confirmed in future by direct measurements. Climatic models predict a decrease of autumn-winter storms in the Mediterranean Sea region, possibly related to an increase of the North Atlantic Oscillation (NAO) index (for example Giorgi and Lionello 2008). This is related to a stronger dominance of anti-cyclonic conditions over the Mediterranean Sea region in future, so that depressions coming from the Atlantic Ocean would be deviated further north. This might lead in future to changes of GPP seasonality and of annual NCP, due to a more systematic accumulation of leaf litter within the meadow during winter instead of export as presently observed (Champenois and Borges 2012).

A warming of surface waters is predicted for the North-West Mediterranean Sea of ~ 2°C in winter and ~ 3°C in summer for 2071/2110 compared to 1961/1990 (Giorgi and Lionello 2008; Mariotti et al. 2010; Adloff et al. 2015). This prediction is in line with the observed increase of annual SST at a rate of 0.033 ± 0.003°C yr$^{-1}$ from 1985 to 2007 reported by Garcia and Belmonte (2011). *P. oceanica* survives within a temperature range between 9°C and 29°C, but the
warming there would be a loss of 15% of incoming SR for the months of the year within the optimum temperature growth conditions for *P. oceanica*. The loss of incoming SR could to some extent be compensated by a decrease of projected cloudiness (Navarra and Tubiana 2013), although modeling of cloudiness is notoriously difficult and uncertain.

During the decade of measurements of daily SST (*n* = 3317), we recorded 272 events with daily average temperatures above 24°C (8.2% of the time), with an overall maximum value of 27.9°C. Over that period, annual GPP did not show any significant temporal trend (increase or decrease), although a very marked warming trend of 0.066°C yr⁻¹ was recorded at our study site during that time period (Fig. 6). This value is almost five times higher than the global average warming over the last 50 yr of 0.013°C yr⁻¹ (IPCC 2013). Such abnormally strong warming is probably transient and coincided with a period of sustained positive winter-time NAO index (Fig. 6). Note that the 2 yr with negative winter-time NAO index values were the coolest of the whole period and deviated from the general trend (Fig. 6). Despite this warming, the fact that the shoot density and leaf biomass in this meadow remain stable (Fig. 7) is consistent with the fact that we did not record events of daily temperature above the threshold temperature (28°C) at which *P. oceanica* shoot mortality starts occurring (Díaz-Almela et al. 2007), and that the meadow is less than 10% of the time above the limit of the temperature comfort zone for *P. oceanica*. With a projected increase of 3°C in the Mediterranean Sea at the end of the century, the average temperatures for July–September would be 26–27°C, meaning that the meadow would experience 3 months per year with temperatures above the *P. oceanica* comfort range, and the occurrence of events with SST > 28°C would also be expected to increase. Furthermore, very warm events in the Mediterranean are favorable for the development of filamentous algae (*Ceramium* sp., *Antithamnion* sp.), as observed in 2003 and 2007 in the Parc National de Port-Cros (France) (Perez 2008). A relatively large fraction of GPP in July and August are due to epiphytic filamentous macroalgae (Champenois and Borges 2012) dominated by the Ceramiales group (Jacquemart and Demoulin 2008) that compete with the host plant (*P. oceanica*) for nutrients and light. The projected warming would possibly lead to an earlier development of filamentous epiphytic algae during the year, and increase competition with *P. oceanica* for resources. Altogether, these effects are expected to lead to a future decrease of GPP in *P. oceanica* meadows even in those that are near-pristine as the one we studied.

Here, we describe for the first-time the inter-annual variations of GPP in a seagrass ecosystem based on a continuous record spanning 10 yr. We found that annual GPP in a *P. oceanica* meadow in Corsica was surprisingly variable from year to year, with extreme maximum (107.6 molO₂ m⁻² yr⁻¹) and minimum (61.3 molO₂ m⁻² yr⁻¹) values differing by a factor of 1.76. We explored the drivers of this strong inter-annual variation with a combination of favorable light and temperature conditions for *P. oceanica* would shift by 1 month from May–June to April–May that had a cumulated SR of 539 h during the period 2006–2016. This would then mean that with future projected

![Fig. 7. Shoot density (shoots m⁻²) and leaf biomass (g dry weight [dw] m⁻²) of *P. oceanica* at 10 m depth in the Bay of Revellata. Data from 1975 to 1976 are from Bay (1984) and data from 1991 to 1992 are from Gobert et al. (1995). Shoot density was not statistically different between years at 0.05 level (one-way ANOVA: *f* = 0.294, *p* = 0.938). Leaf biomass was statistically different between years (one-way ANOVA: *f* = 8.191, *p* < 0.001, respectively), but no there was no clear trend in time (decrease or increase).](image-url)
variability in \textit{P. oceanica} GPP. It is well established from previous studies that seasonal and spatial variations of productivity of \textit{P. oceanica} depend on light, and this could indeed explain part of the observed inter-annual variations. No significant long-term change (decline or increase) of GPP could be observed in our data-set, despite the fact that a sustained warming was observed in the study area at a rate that was five times higher than the global average warming over the last 50 yr, probably related to a period of prolonged positive NAO anomaly. Long-term changes in shoot density and leaf biomass of \textit{P. oceanica} were not detected in comparison to 1970s and 1990s. Overall, this indicates that the studied meadow is still within the temperature comfort zone of \textit{P. oceanica}, although this is based on the study of Boudouresque and Meinzes (1982) that should be updated by new investigations of temperature tolerance, as it might have changed over the last decades by adaptation to warming conditions, and is variable among different ecotypes (Marín-Guirao et al. 2016). Consequently, the studied meadow is expected to respond in future to further warming, that should warrant continued monitoring of GPP that can be achieved relatively easily with moored oxygen sensors, as shown here. While \textit{P. oceanica} productivity does not seem to respond significantly to expected changes in pH conditions (ocean acidification) (Cox et al. 2016), strong future changes are expected from changes in light availability notably as a consequence of eutrophication. Indeed, even in a pristine site such as the Bay of Revellata, GPP strongly responded to inter-annual variations of light availability, so that sustained periods of decreasing light conditions as expected in more eutrophied sites are expected to strongly impact \textit{P. oceanica} productivity.

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Primary production of \textit{P. oceanica}

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Author Contribution

AVB designed the experiment; WC collected and processed the data; WC interpreted the data and drafted the manuscript with substantial inputs from AVB.

Conflict of Interest

None declared.

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