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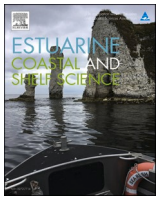

Community gross primary production and respiration in epilithic macroalgae and *Posidonia oceanica* macrophytodetritus accumulation in the Bay of Revellata (Corsica)

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ABSTRACT

We report estimates of community gross primary production (GPP), community respiration (CR), and net community production (NCP) based on the change of dissolved O_2 during incubations over epilithic turf-forming macroalgae (*Halopteris scoparia*, *Padina pavonica*, and *Dictyota dichotoma*) on 7 occasions and in accumulations of *Posidonia oceanica* macrophytodetritus (*i.e.* litter) on 8 occasions in the Bay of Revellata (Corsica) from March 2009 to May 2011. In the epilithic macroalgae community, GPP ranged between 7.8 and 82.2 mmol O_2 m^{-2} d^{-1}, CR ranged between −108.5 and −13.6 mmol O_2 m^{-2} d^{-1}, and NCP ranged between −53.2 and −5.7 mmol O_2 m^{-2} d^{-1}. In the *P. oceanica* macrophytodetritus accumulation, GPP ranged between 5.7 and 91.6 mmol O_2 m^{-2} d^{-1}, CR ranged between −112.8 and −27.2 mmol O_2 m^{-2} d^{-1}, and NCP ranged between −46.8 and −9.9 mmol O_2 m^{-2} d^{-1}. GPP in both the epilithic macroalgae community and the *P. oceanica* macrophytodetritus accumulation peaked in summer and was lowest in fall, following the seasonal variation of incoming light. GPP correlated to macroalgal biomass but was unrelated to the biomass of living macroscopic plant material in the *P. oceanica* macrophytodetritus accumulation. The annual average of GPP was equivalent in the epilithic macroalgae and *P. oceanica* macrophytodetritus accumulation communities (17.6 and 19.4mol O_2 m^{-2} yr^{-1}). Both the epilithic macroalgae community and the *P. oceanica* macrophytodetritus accumulation were net heterotrophic with an annual average NCP of −6.1 and −8.8mol O_2 m^{-2} yr^{-1}, respectively. The NCP of the adjacent *P. oceanica* meadow at 10 m depth based on simultaneous measurements based on the open water O_2 mass balance from moored O_2 probes (optodes) was 28.9mol O_2 m^{-2} yr^{-1}. The potential export of dissolved organic carbon from the *P. oceanica* meadow could quantitatively meet the carbon demand to sustain the net heterotrophy of the adjacent epilithic macroalgae community in the Bay of Revellata. We also show the limitation and possibly over-estimation of extrapolating decay rates based on litter bag experiments with small quantities of material to "real" macrophytodetritus biomass densities.

1. Introduction

Net ecosystem production (NEP) is the balance of the inputs and outputs of organic matter within an ecosystem (e.g. Chapin III et al., 2006) and reflects whether an ecosystem is a net exporter of organic matter (net autotrophic) or is a net consumer of organic matter requiring an external subsidy of organic matter (net heterotrophic). Incubations allow to measure gross primary production (GPP) and community respiration (CR) at the scale of a community, allowing to compute net community production (NCP = GPP + CR). The determination of NCP of all the communities of an ecosystem allows deriving NEP of the entire ecosystem.

Vegetated coastal habitats (marshes, mangroves, seagrasses, macroalgae) are characterized by high primary production rates (Smith, 1981; Mcleod et al., 2011). There is a high efficiency in the carbon (C) preservation underneath seagrass meadows (Cebrián, 1999). Consequently, seagrass meadows are characterized by extremely high organic C burial rates compared to land vegetation (Mcleod et al., 2011). In addition, seagrass meadows export to adjacent communities part of the primary production and are net autotrophic ecosystems (Duarte et al., 2010). Marine macroalgae are also highly productive, yet, there is little C burial, so that a large fraction of annual primary production is

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exported to adjacent systems (Krause-Jensen and Duarte, 2016; Ortega et al., 2019; Duarte et al., 2022; Pessarrodona et al., 2022; Filbee-Dexter et al., 2024). Yet, it is debated whether macroalgal ecosystems are net autotrophic or net heterotrophic (Gallagher et al., 2022; Stafford, 2022; Gallagher and Shelamoff, 2022; Filbee-Dexter et al., 2023; Gallagher, 2023), which might seem surprising given the high GPP rates reported in these systems. Macroalgae harbor epiphytic heterotrophic microbial and invertebrate communities (Haywood et al., 1995; Bulleri et al., 2002; Beleneva and Zhukova, 2006; Wiese et al., 2009; Bengtsson et al., 2012) that could sustain high heterotrophic respiration (HR) rates, driving the whole community to net heterotrophy despite high GPP rates, if there is an external subsidy of organic carbon to support HR.

Posidonia oceanica is a seagrass (Magnoliopsida) endemic of the Mediterranean Sea that forms extensive meadows that are among the most productive ecosystems on Earth (Duarte et al., 2010). Primary production has been extensively measured in *P. oceanica* meadows based on biomass changes at the scale of leaves (Zieman, 1974), of shoots (Pergent and Pergent-Martini, 1991), or of meadow patches (Bay, 1984), *ex-situ* incubations with radioactive (^{14}C) or stable (^{13}C) C isotope tracers (Mateo et al., 2001), O_2 change during incubations in chambers (Barrón et al., 2006), open water O_2 mass balance (Champenois and Borges, 2012), and O_2 eddy covariance (Long et al., 2015; Koopmans et al., 2020). The fate of primary production (herbivory/decomposition, burial, export) is less well quantified (Pergent et al., 1997; Cebrian and Duarte, 2001).

The leaf detritus from *P. oceanica* shoots accumulate as litter within the meadows (between shoots) and in sandy patches within or adjacent to meadows referred hereafter as macrophytodetritus accumulations (Boudouresque et al., 2016; Lepoint and Hyndes, 2022). Macrophytodetritus accumulations are composed of dead material as well as photosynthetically active plant remains from the meadow (detached or attached epiphytic macroalgae and detached living seagrass shoots), drift macroalgae from adjacent rocky environments, and benthic microalgae (Fig. S1). Macrophytodetritus accumulation occurs throughout the year but is maximal during fall when leaf fall increases (Romero et al., 1992). The patches of macrophytodetritus accumulation are heterogeneous in composition, surface cover, thickness, and persistence, from ephemeral to year-long presence (Boudouresque et al., 2016). The *P. oceanica* macrophytodetritus accumulation shelters abundant micro-organisms (bacteria, fungi, protozoa, microalgae) and vagile meio- and macro-fauna dominated by a few groups of crustaceans (Mascart et al., 2015; Costa et al., 2019). These detritivores have a mixed diet composed of seagrass detritus, epiphytes growing on the detritus, and drift macroalgae (Lepoint et al., 2006; Remy et al., 2018). The fauna contributes to the decomposition of the macrophytodetritus accumulation (Costa et al., 2019) that has been quantified from decay experiments in litter bags (Romero et al., 1992; Mateo and Romero, 1996, 1997; Cebrián et al., 1997; Pergent et al., 1997; Apostolaki et al., 2009; Costa et al., 2019; Lee et al., 2022). In the Bay of Revellata, meiofauna invertebrates present in macrophytodetritus accumulations can reach a maximum density of ~78,000 individuals m^{-2} consisting mainly of copepods and nematodes in equivalent abundance (Mascart et al., 2015). Among copepods, 41 species belong to the order of the Harpacticoida, and 3 species belong to the orders Calanoida, Cyclopoida and Syphonostomatoida (Mascart et al., 2015). The most diverse harpacticoid families are Miraciidae and Tisbidae (Mascart et al., 2015).

Near-shore marine habitats such as macroalgal communities and seagrass meadows are usually non-overlapping but can be adjacent or even entangled. There should be long-distance interactions, such as trophic subsidies (Hyndes et al., 2014; Säwström et al., 2016) as shown in salt marshes exporting significant quantities of plant detritus to nearby oyster reefs (van de Koppel et al., 2015) or in kelp forests to benthic communities in a deep fjord (Filbee-Dexter et al., 2018). Velimirov et al. (2016) concluded that the *P. oceanica* meadow in the Bay of Revellata was net heterotrophic, and that the demand in organic C was supplied as dissolved organic C (DOC) from adjacent epilithic macroalgal communities. Such a hypothetical transfer of DOC would then require the epilithic macroalgal community in the Bay of Revellata to be itself net autotrophic, although the metabolic trophic status of this community was not directly assessed by Velimirov et al. (2016). Independent studies of community metabolism concluded that the *P. oceanica* meadow in the Bay of Revellata was net autotrophic (Frankignoulle and Bouquegneau, 1987; Champenois and Borges, 2012, 2018, 2021).

The present study is in continuity of three previous analysis of community metabolism based on the O_2 mass balance (Odum, 1956) using a mooring equipped by 3 optodes at 10 m depth in a *P. oceanica* seagrass meadow in the Bay of Revellata in Corsica (Champenois and Borges, 2012, 2018, 2021). We report measurements of community metabolic rates (GPP, CR, and NCP) based on change of O_2 measured during incubations with chambers epilithic macroalgae communities on 7 occasions and in *P. oceanica* macrophytodetritus accumulations on 8 occasions in the Bay of Revellata (Corsica) from March 2009 to May 2011. The first objective of this study is to determine the net metabolic status (autotrophic or heterotrophic) of benthic communities immediately adjacent to the *P. oceanica* seagrass meadows (epilithic turf-forming macroalgae and *P. oceanica* macrophytodetritus accumulations), and to compare to the NCP of the seagrass meadow itself at the scale of the Bay of Revellata. The second objective of this work is to compare the respiration rates measured with benthic chambers on *P. oceanica* macrophytodetritus accumulations with degradation rates derived from litter bag experiments compiled from literature, that to date were the only available estimates of decay of *P. oceanica* macrophytodetritus.

2. Material and methods

2.1. Chamber incubations

The chamber incubations ($n = 3$ maximum) over the *P. oceanica* macrophytodetritus accumulation were done in a sand patch (20 m^{-2}) at 8m depth close to harbor of the STARESO station (42°34′48′′N, 8°43′29′′E) on 8 occasions from March 2009 to November 2010 (March 4, 2009, June 2, 2009, August 19, 2009, November 11, 2009, February 19, 2010, June 4, 2010, August 20, 2010, November 5, 2010). This sand patch traps macrophytodetritus (dead *P. oceanica* leaves, uprooted seagrass shoots, and drift macroalgae, Fig. S1) most of the year, with accumulations covering between 25% and 100% of the surface of the sand patch. The incubation set-up consisted in a transparent polypropylene chamber, a 12V water pump powered by batteries, and a polyvinyl chloride (PVC) water tank, connected by PVC transparent tubing (Fig. S2). The total water volume of the incubation setup was 60L with the PVC water tank contributing to 8L. The chamber covered a surface (S) of 0.13 m^2 of benthic substrate. The inner surface area of the whole chamber set-up (inner walls of the chamber, PVC water tank, and tubing) was 1.2 m^2 with the PVC water tank contributing to 0.16 m^2. The change in O_2 concentration was measured and logged every 5 min with an Aanderaa O_2 optode (3835) mounted on Alec Instruments loggers placed inside the PVC water tank. The optode was placed inside the PVC water tank to avoid interference by shading should it had been placed suspended in the chamber itself. The extra water volume from the PVC water tank also avoids the occurrence within the chamber of extremely high O_2 levels during day time that can lead to photorespiration (Champenois and Borges, 2012). Light intensity was measured with a HOBO light sensor placed 2m away from the chamber. The chambers were deployed at dawn for 24h. Water was sampled with a 60 ml polypropylene syringe at the start of the incubation at dawn (T0), at dusk (T1), and at dawn the following day (T2). The water was sampled at T0, 10 min after installing the chamber to allow the homogenization of the water within the incubation setup. The water was transferred to 60 ml biological oxygen demand bottles, and fixed with Winkler reagents. Oxygen was measured by Winkler titration with a potentiometric

end-point determination using the protocol, reagents, and calibrations given by IOC (1994). The concentration of O_2 measured by the optodes and by Winkler titration converged at ±2.0 μmol kg^{-1}. At the end of the incubations the material underlying the chamber was collected, washed with freshwater to remove seawater, sorted into three categories (living macroalgae, living *P. oceanica* leaves on detached shoots, and dead material), dried in the oven at 60 °C during 48h, and weighted. The C and nitrogen (N) elemental composition was determined using an elemental analyser (vario MICRO cube™, Elementar), using glycine standard (31.98%C, 18.72%N), and data reported as the ratio of % of the dry mass.

The chamber incubations (n = 1) over epilithic turf-forming macroalgae were made on rocks close to the STARESO station at 8 m depth (42°34′43′′N, 8°43′30′′E) on 7 occasions from June 2009 to May 2011 (June 10, 2009, August 15, 2009, February 23, 2010, June 01, 2010, August 24, 2010, February 20, 2011 et May 31, 2011). The incubation set-up and procedure was identical to the one used over the macrophytodetritus accumulation (see above), except the total volume was 19.5 L and the chamber was made of polycarbonate and covered a S of 0.04 m^2 of benthic substrate (Fig. S3). The inner surface area of the whole chamber set-up was 0.5 m^2. The chamber was fixed over the substrate with elastic straps attached to webbed straps fixed on the rocks. Polyethylene foam ensured water-tightness of the chamber that was checked during initial tests with injections of fluorescein. Discrete samples for the determination of O_2 concentration by titration by the Winkler method were also collected at T0, T1, and T2. At the end of the incubation the total biomass of macroalgae beneath the chamber was collected, washed with freshwater to remove seawater, dried at 60 °C for 48h in an oven, and weighted. The composition of the turf-forming macroalgal assemblage was dominated by *Halopteris scoparia*, *Padina pavonica*, and *Dictyota dichotoma*, as commonly observed in the area (Katz et al., 2021).

After each incubation, the benthic chambers deployed over either the macrophytodetritus accumulations or the epilithic macroalgae were thoroughly cleaned with fresh-water, dried, and stored in a clean environment. Before each deployment, the chambers were rinsed with seawater.

2.2. Open water O_2 measurements over a macro-algae community

On a single occasion (June 02, 2010), an optode was deployed in the water column in a setting to attribute the changes of dissolved O_2 concentration to macroalgae cover and minimize the signal from other communities such as the adjacent *P. oceanica* meadow. The optode was deployed at a depth of 6.5m, 0.5m above the bottom of rock cuvette located at 7m depth with a surface area of about 20 m^2 and bordered by rocks with a height of 2–3m height. All the rock surface of this cuvette was covered by macroalgae.

2.3. Metabolic computations

Rates of GPP, NCP, and CR from the chamber incubations over the macrophytodetritus accumulation and the epilithic macroalgae community were computed from the change of O_2 concentration, the total incubated volume of water, S, and night-time (H_n) and day-time (H_d) duration.

CR (mmol O_2 m^{-2} d^{-1}) is given by:

$$CR = (Q_{O2C(T2)} - Q_{O2C(T1)})/H_n \times 24/S$$

where $Q_{O2C(T1)}$ and $Q_{O2C(T2)}$ are the content of O_2 (mmol O_2) in the incubated volume (based on O_2 concentration and total incubated volume) at T_1 and T_2, respectively.

GPP (mmol O_2 m^{-2} d^{-1}) is given by:

$$GPP = ((Q_{O2C(T1)} - Q_{O2C}(T0))/H_d - (Q_{O2C(T2)} - Q_{O2C(T1)})/H_n) \times H_d/S$$

where $Q_{O2C(T0)}$ is the content of O_2 (mmol O_2) in the incubated volume at T_0.

HR was computed from CR by removing the autotrophic respiration estimated as a constant fraction of GPP of 51% for macroalgae and 57% for seagrasses (Duarte and Cebrián, 1996). For the macrophytodetritus accumulation, we used an average value of 54%.

Rates of GPP, NCP, and CR over the *P. oceanica* seagrass meadow were previously published and derived from the open water mass balance of O_2 (Odum, 1956) as explained in detail by Champenois and Borges (2012).

Degradation rates in macrophytodetritus accumulation were computed based on decay rates (k in d^{-1}) from litter bag experiments from the loss of dry mass computed with an exponential decay function divided by time, according to:

$$W_0(1\text{-}e^{-kt})/t$$

where W_0 is the initial mass density of macrophytodetritus accumulation (dead material fraction) in dry weight (dw) (g_{dw} m^{-2}) and t is the time interval (d).

This equation allows deriving a flux per unit of time for a consistent comparison with HR and is based on the change of biomass:

$$(W_0\text{-}W_t)/t$$

where W_t is the dry mass (g) remaining at time t given by the equation describing the decomposition rate based on the loss of dry mass during time fitted to an exponential curve (Petersen and Cummins 1974)

$$W_t = W_0 e^{-kt}$$

The resulting daily degradation rate in g_{dw} m^{-2} d^{-1} was converted into mol C m^{-2} d^{-1} using a C content of 33.6% of total mass as g_{dw} (Duarte, 1990). For the comparison with HR, we assumed equivalence of respiration in mol C and mol O_2.

The k values from a given experiment (k_{bag}) and respective deployment time (t_{bag}) were normalized to a given time (t_{norm}) (91, 182, 274d) according to Mateo and Romero (1996):

$$k_{norm} = k_{bag} \text{ x } e^{-k' \Delta t}$$

where k_{norm} is the k normalized to t_{norm}, Δt is the difference between t_{bag} and t_{norm}, and k' is a conversion constant. The value of k' was not specified by Mateo and Romero (1996), so we derived a value −0.00486 d^{-1} from data reported by Romero et al. (1992) of paired experiments lasting 1 and 6 months.

2.4. Data availability

Daily metabolic rates (GPP, CR, NCP) over epilithic macroalgae and corresponding macroalgal biomass are given in Table S1. Daily metabolic rates (GPP, CR, NCP) over *P. oceanica* macrophytodetritus accumulation and corresponding total biomass are given in Table S2, and the relative abundance of fractions in macrophytodetritus accumulation are given in Table S3.

3. Results

3.1. Epilithic turf-forming macroalgae metabolism

Fig. 1 shows an example of daily variation of $\%O_2$ during an incubation with a chamber over epilithic turf-forming macroalgae carried out on June 01, 2010 at 8m depth. At the start of the incubation at dawn (03:30 universal time (UT)) $\%O_2$ was close to 100%, increased to 130% during the course of the day due to primary production, and decreased during the night down to 80% at the end of the incubation. There was a net decrease of O_2 during the 24h incubation, implying that the epilithic macroalgae community was net heterotrophic. In order to test the hypothesis that the net decrease of O_2 was due to an effect of the chamber,

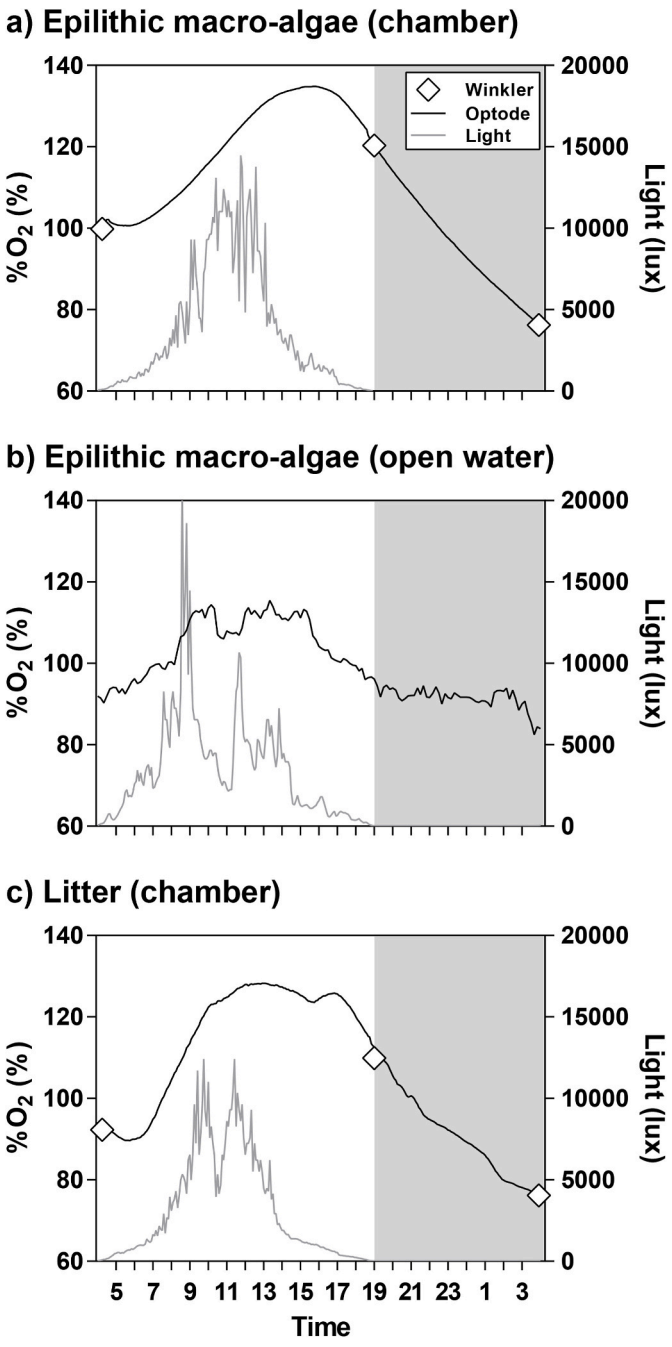

Fig. 1. Examples of temporal evolution of O_2 saturation level (%O_2 in %) during 24h (dawn to dawn next day) measured with optodes (black line) and by discrete samples measured by the Winkler method (diamond) over epilithic macroalgae in an incubation chamber (June 01, 2010) and in open water within a cuvette (June 02, 2010), and over *Posidonia oceanica* macrophytodetritus accumulation in an incubation chamber (18/082010), and light (grey line in lux), at ~8 m depth at proximity of *P. oceanica* meadow in the Bay of Revellata (Corsica). Night-time is indicated in grey, time is in universal time.

we measured %O_2 variations at daily scale in open-water on a single occasion (June 02, 2010) in a rock cuvette covered by macroalgae (Fig. 1). The daily light intensity during the open-water incubation on June 02, 2010 and during the chamber incubation on June 01, 2010 were similar, 275 and 257 kJ m^{-2}, respectively. In the open-water, the amplitude of %O_2 daily variations was lower (max-min = 32.9%) than in the chamber (max-min = 59.0%) due a propagation of O_2 by mixing in the un-confined water column. The %O_2 decreased from 92 to 84% during 24h (dawn to dawn) also indicating net heterotrophy. This suggests that the net heterotrophy recorded during the chamber incubations did not artificially result from the confinement within the chamber.

Fig. 2 summarizes metabolic fluxes (GPP, CR, and NCP) measured during seven incubations with chambers over epilithic turf-forming macroalgae from June 2009 to May 2011 (Table S1). GPP ranged between 7.8 and 82.2 mmol O_2 m^{-2} d^{-1}, CR ranged between −108.5 and −13.6 mmol O_2 m^{-2} d^{-1}, and NCP ranged between −53.2 and −5.7 mmol O_2 m^{-2} d^{-1}. Seasonal variations of GPP and CR followed those of algal biomass (Figs. 2 and 3). NCP was negative during all incubations, with an average of −23.8 mmol O_2 m^{-2} d^{-1}. The GPP: CR ratio (commonly called P:R ratio in topical literature) was positively correlated to the algal biomass, excluding the data-point from the incubation on August 24, 2010 (Fig. 3). The incubation on August 24, 2010 was characterized by a particularly low NCP value (−53.2 mmol O_2 m^{-2} d^{-1}) due to low CR values (−101.9 mmol m^{-2} d^{-1}) possibly related to the presence of one or several large invertebrates trapped in the chamber. This was consistent with computed HR on August 24, 2010 being the lowest recorded and distinctly lower than the other data points at equivalent macroalgal biomass and GPP (Fig. S4). The low NCP on August 24, 2010 could additionally be related to relatively lower GPP (48.7 mmol m^{-2} d^{-1}) than the other data points at equivalent biomass, possibly related to lower incoming light. Yet, GPP and GPP normalized by macroalgal biomass showed scatter as a function of integrated daily light intensity, and the data-point of August 24, 2010 did not stand out from the other data (Fig. S5). So, the particularly low NCP value on August 24, 2010 seems to primarily reflect particularly intense HR possibly related to large or numerous trapped invertebrates in the chamber. The negative correlation between NCP and macroalgae biomass (excluding the data-point from the incubation on August 24, 2010) was not statistically significant ($r^2 = 0.61$, $p = 0.067$, Table S4) but this was the case of the positive correlation of the GPP: CR ratio with algal biomass (Table S4).

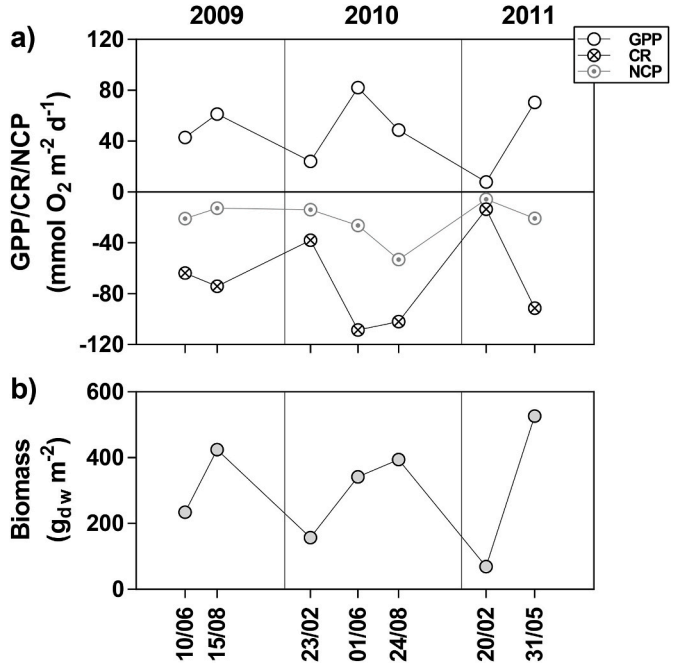

Fig. 2. Gross primary production (GPP in mmol m^{-2} d^{-1}), community respiration (CR in mmol m^{-2} d^{-1}), and net community production (NCP in mmol m^{-2} d^{-1}) measured by O_2 change in an incubation chamber over epilithic macroalgae at ~8 m depth (a) and corresponding macroalgal biomass in dry weight (g_{dw} m^{-2}) (b) at proximity of a *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) on 7 occasions from June 2009 to May 2011 (June 10, 2009, August 15, 2009, February 23, 2010, June 01, 2010, August 24, 2010, February 20, 2011 et May 31, 2011).

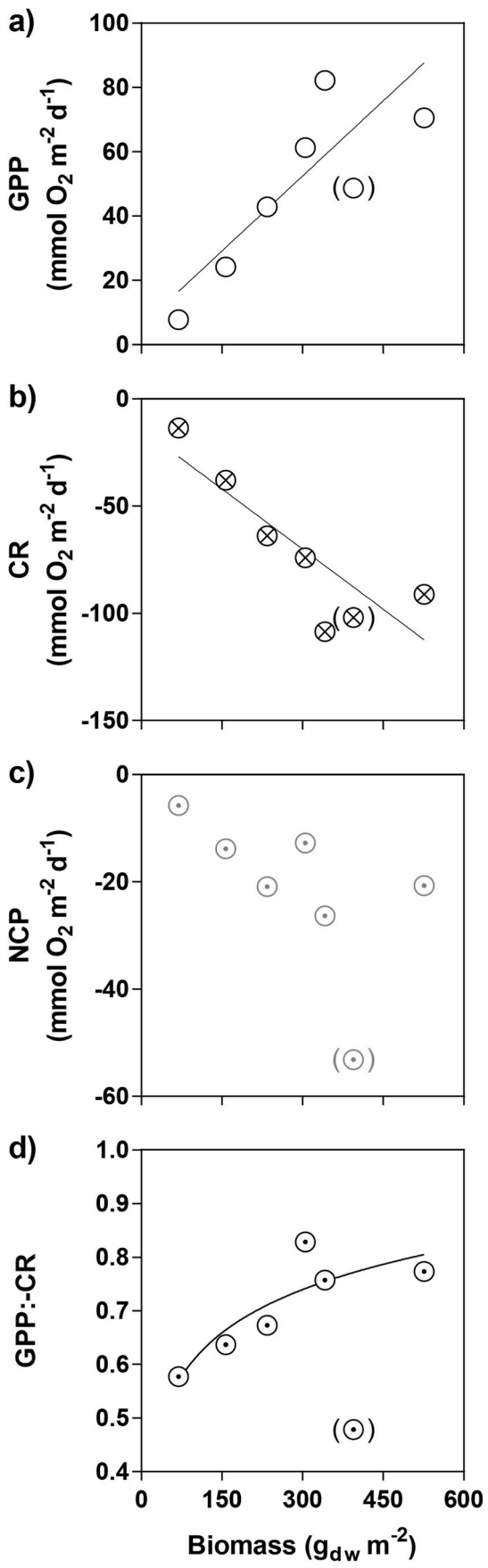

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Fig. 3. Gross primary production (GPP in mmol m^{-2} d^{-1}) (a), community respiration (CR in mmol m^{-2} d^{-1}) (b), and net community production (NCP in mmol m^{-2} d^{-1}) (c), and GPP: CR ratio (unitless) (d) measured by O_2 change in an incubation chamber over epilithic macroalgae at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) 7 occasions from June 2009 to May 2011 (June 10, 2009, August 15, 2009, February 23, 2010, June 01, 2010, August 24, 2010, February 20, 2011 et May 31, 2011). The data point on August 24, 2010 (in brackets) was excluded from the linear regressions given in Table S4.

3.2. *P. oceanica* macrophytodetritus accumulation metabolism

Fig. 1 shows an example of daily variation of $\%O_2$ during an incubation with a chamber over *P. oceanica* macrophytodetritus accumulation carried out on August 19, 2009 at 8m depth. $\%O_2$ increased from 92% at dawn to 125% at 13:00 and decreased to 76% at dawn next day. Such a temporal variation showed photosynthetic activity in the *P. oceanica* macrophytodetritus accumulation related to drift macroalgae and living uprooted *P. oceanica* shoots and their epiphytes.

Metabolic rates (GPP, CR, and NCP) were measured with benthic chambers on 8 occasions from March 2009 to November 2010 over *P. oceanica* macrophytodetritus accumulation in the Bay of Revellata (Fig. 4). GPP ranged between 5.7 and 91.6 mmol O_2 m^{-2} d^{-1}, CR ranged between −112.8 and −27.2 mmol O_2 m^{-2} d^{-1}, and NCP ranged between −46.8 and −9.9 mmol O_2 m^{-2} d^{-1}. CR was strongly correlated GPP (r^2 = 0.86, p = 0.001) but did not correlate with macrophytodetritus accumulation biomass (total, living, or detrital fraction) (Table S3). No relation was found between GPP and the fraction of living plants in macrophytodetritus accumulation.

Variations of metabolic rates (GPP, CR, and NCP) could have been driven by temperature seasonal variations. The negative correlation between NCP in the macrophytodetritus accumulation and water temperature (Fig. 5), indicates a stronger net heterotrophy in warmer conditions. However, there was no correlation between CR and water temperature.

We compiled k data from published litter bag experiments measured on fresh senescent *P. oceanica* leaves present on living shoots (n = 29), on detached dead leaves (n = 11), and on randomly selected leaves from living shoots, presumably a mix of living and senescent leaves (n = 1) (Table S5). The k values determined on detached dead leaves were lower (0.0052 ± 0.0033 d^{-1}) than those determined on fresh senescent leaves (0.0087 ± 0.0051 d^{-1}) (Mann-Whitney (M-W) test p = 0.0141). The same difference was found when normalizing the k values to 91d (k_{91}) (0.0058 ± 0.0036 *versus* 0.0090 ± 0.0051 d^{-1}, M-W test p = 0.0429), to 182d (k_{182}) (0.0037 ± 0.0023 *versus* 0.0058 ± 0.0033 d^{-1}, M-W test p = 0.0429), and to 274d (k_{274}) (0.0024 ± 0.0015 *versus* 0.0037 ± 0.0021 d^{-1}, M-W test p = 0.0429).

We computed the daily litter decay rates based on averaged normalized k data from experiments on detached dead leaves for three time intervals (90, 182, 274d) using the biomass of dead macrophytodetritus accumulation corresponding to the chamber incubations (Table S3). The resulting daily litter decay rates were compared with HR computed from CR measured with O_2 change in chambers over macrophytodetritus accumulation (Fig. 6). We chose 3 different time intervals (91, 182, 274 d) to compute the daily decay rates from k data from published litter bag experiments because it is not possible to know for how long the macrophytodetritus were present within the accumulation patch. The macrophytodetritus accumulation patch was present year-round in our study site although shrinking or expanding seasonally in extent (Mascart et al., 2015) as well as in thickness as indicated by the total biomass density (Fig. 4).

The daily decay rates computed from k were on average 2.8, 1.7, and 1.1 times higher than the HR estimates, for 90, 182, 274d time intervals, respectively.

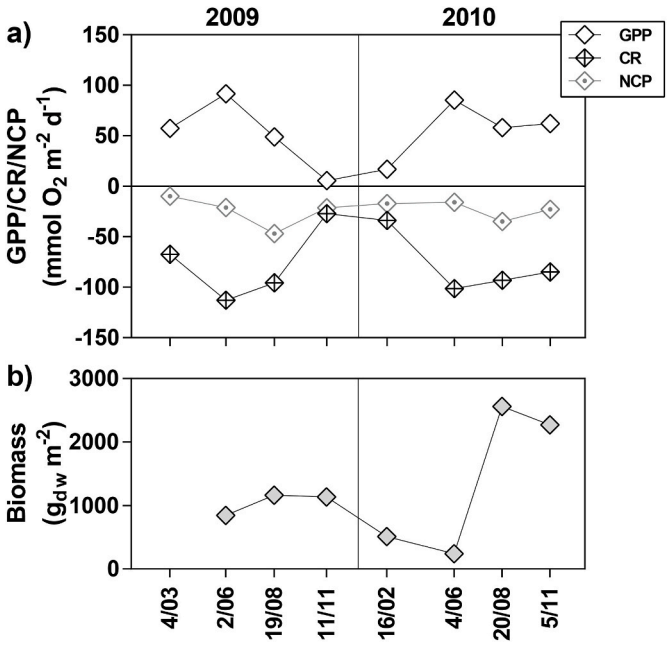


Fig. 4. Gross primary production (GPP in mmol m^{-2} d^{-1}), community respiration (CR in mmol m^{-2} d^{-1}), and net community production (NCP in mmol m^{-2} d^{-1}) measured by O_2 change in an incubation chamber over *Posidonia oceanica* macrophytodetritus accumulation (a) and corresponding biomass in dry weight (g_{dw} m^{-2}) (b) at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) on 8 occasions from March 2009 to November 2010 (March 4, 2009, June 2, 2009, August 19, 2009, November 11, 2009, February 19, 2010, June 4, 2010, August 20, 2010, November 5, 2010). The relative contribution of different fractions of the litter biomass is given in Table S4.

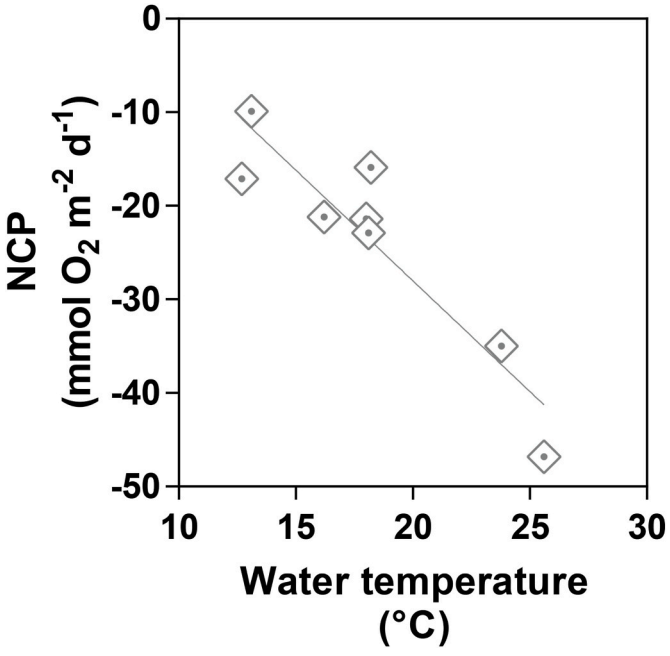


Fig. 5. Net community production (NCP in mmol m^{-2} d^{-1}) measured by O_2 change in an incubation chamber over *Posidonia oceanica* macrophytodetritus accumulation versus water temperature (°C) at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) on 8 occasions from March 2009 to November 2010 (March 4, 2009, June 2, 2009, August 19, 2009, November 11, 2009, February 19, 2010, June 4, 2010, August 20, 2010, November 5, 2010). Solid line corresponds to the linear regression Table S4.

3.3. Comparison with the seagrass meadow metabolism

Metabolic rates (GPP, CR, and NCP) obtained in 2010 of epilithic macroalgae and of the *P. oceanica* macrophytodetritus accumulation were compared to those of the meadow at 10m depth based on the open-water mass balance with O_2 continuous measurements (Champenois and Borges, 2012) (Fig. 7). The seasonal variations of GPP of epilithic macroalgae and of the *P. oceanica* macrophytodetritus accumulation follow those of the meadow peaking in summer and being lowest in late fall, following the seasonal variations of incoming daily light intensity. GPP of the meadow was between 3.5 and 7.3 times higher than of one of *P. oceanica* macrophytodetritus accumulation and between 3.7 and 16.9 higher than the one of epilithic macroalgae.

The seasonal variations of CR of the three communities followed the one of GPP. In February, June, and August, CR of the meadow was between 1.7 and 3.7 times higher than of one of *P. oceanica* macrophytodetritus accumulation and between 2.1 and 7.2 higher than the one of epilithic macroalgae. In November, CR of the meadow was close to the one of epilithic macroalgae (only 1.1 times higher). The meadow was net autotrophic with a NCP ranging between 40.9 and 90.8 mmol O_2 m^{-2} d^{-1} with higher values in spring and summer than in fall and early winter. The epilithic macroalgae and of the *P. oceanica* macrophytodetritus accumulation communities were net heterotrophic and there was no clear seasonal variations of NCP. The NCP of the meadow was between 1.3 and 6.4 times higher (in absolute values) than of one of *P. oceanica* macrophytodetritus accumulation and between 4.0 and 8.8 higher than the one of epilithic macroalgae.

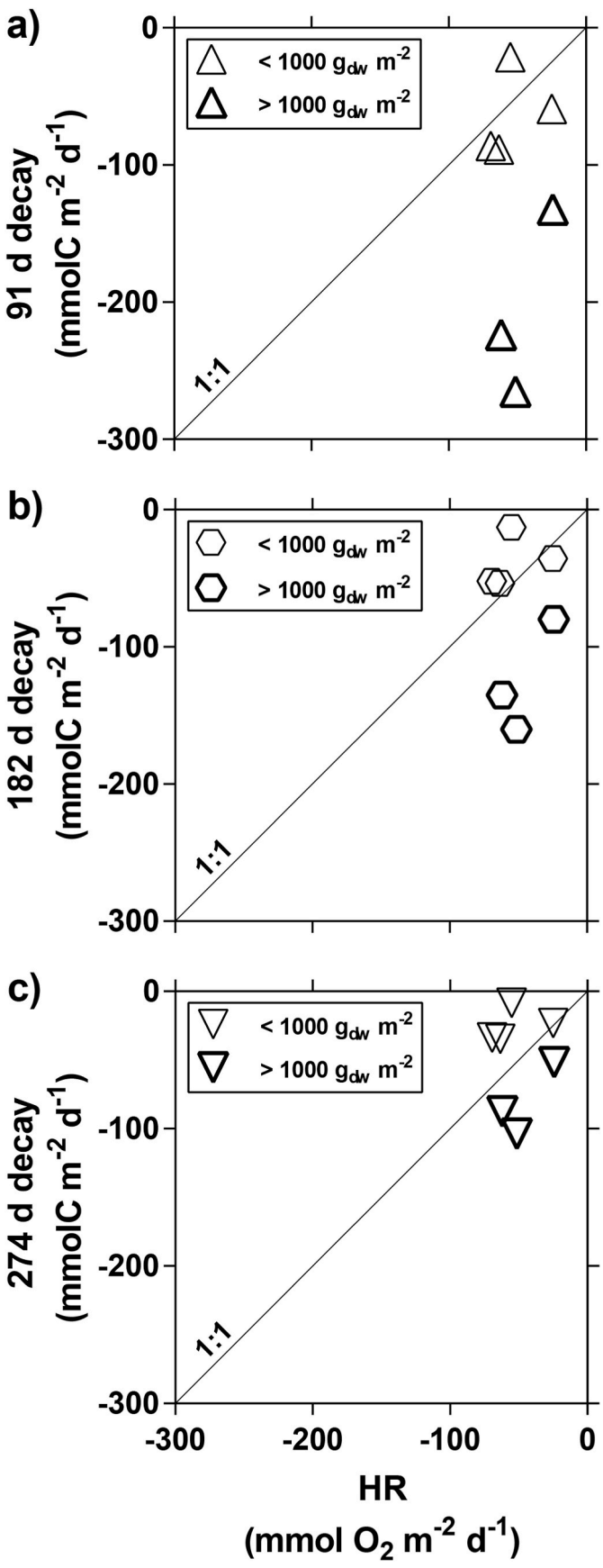
On an annual scale, GPP, CR, and NCP of the meadow was 5.4, 2.7, and 4.7 times higher (in absolute term) than of one of epilithic macroalgae, respectively (Table 1).

4. Discussion

4.1. Epilithic turf-forming macroalgae metabolism

A net decrease of O_2 over 24h was systematically observed over epilithic turf-forming macroalgae during 7 chamber incubations over 2 years (June 2009 to May 2011) indicating that the sampled communities were net heterotrophic. There is the possibility that the net decrease of O_2 content was due to a chamber effect due to either the confinement and/or reduction of hydrodynamism (e.g. Berg et al., 2022) or the growth of heterotrophic micro-organisms on the inner walls of the chamber apparatus. Our chamber design included an additional tank to house the optode increasing the inner surface area by 32% compared to other chamber designs devoid of an additional tank (Mallon et al., 2022). Yet, the microbial development on the inner walls of the chamber was expected to be very low as the growth rate of marine heterotrophic bacteria is slow (Kirchman, 2016). In addition to the slow growth rate, the actual growth also depends on the initial biomass of micro-organisms that was expected to be very low because, after incubations, the benthic chambers were thoroughly cleaned with fresh-water, dried, and stored in a clean environment. Sommer et al. (2008, 2010) showed that deployments of benthic chambers during several days did not show an acceleration of O_2 uptake over time indicating an undetectable effect on O_2 change of eventual growth of micro-organisms, although, admittedly, in different benthic environments than those studied here. A net decrease of O_2 over 24h was also observed in open-water on a single occasion (June 02, 2010) in a rock cuvette covered by macroalgae, suggesting that the net daily decrease of O_2 observed in incubations over epilithic macroalgae was independent of effects of the chamber.

Macroalgae host numerous invertebrate species by providing nurseries and protective environments (Haywood et al., 1995; Bulleri et al., 2002). The surfaces of marine macroalgae also provide a habitat for microbial communities (Beleneva and Zhukova, 2006; Wiese et al., 2009; Bengtsson et al., 2012). The respiration from invertebrate and



(caption on next column)

Fig. 6. Daily litter decay rates (mmol C m^{-2} d^{-1}) computed from dead macrophytodetritus biomass density and average decay rates derived from litter bag experiments (Table S5) integrated over 91 (a), 182 (b), and 274 (c) days *versus* heterotrophic respiration (HR in mmol O_2 m^{-2} d^{-1}) derived from O_2 change in chamber incubations. Data were differentiated according to low and high dead macrophytodetritus biomass (< or >1000 g_{DW} m^{-2} d^{-1}). The solid line indicates the 1:1 line.

microbial communities contribute to CR driving the community towards net heterotrophy despite macroalgal GPP (Duarte et al., 2022). GPP is several times higher in foliose macroalgae assemblages due to a higher biomass than in turf-forming macroalgae assemblages (Miller et al., 2009). Turfs support greater abundance of invertebrate macrofauna than foliose assemblages because turfs are structurally better habitats for macrofauna (e.g. Hacker and Steneck, 1990). In a study in Naples Reef off southern California, turfs were found to be net heterotrophic due to the combination of low GPP and a high abundance of invertebrate macrofauna (Miller et al., 2009). In the Mediterranean Sea, turf-forming macroalgae assemblages dominate in the rocky environments of the infralittoral zone (Piazzi et al., 2002), while foliose macroalgae assemblages are more abundant in the circalittoral zone (Joher et al., 2012). Only three other studies reported metabolic rates in macroalgae communities adjacent to *P. oceanica* meadows in the Mediterranean Sea (Ruiz-Halpern et al., 2014; Egea et al., 2019a; Marx et al., 2021). In *Caulerpa prolifera* and *Halimeda incrassata* communities in the vicinity of *P. oceanica* meadows, community metabolism was found to be close to equilibrium (NCP = 0, e.g. GPP=CR) (Ruiz-Halpern et al., 2014; Egea et al., 2019a; Marx et al., 2021). There are only a surprisingly small number of additional studies reporting NCP in macroalgal communities for further comparison. Gallagher et al. (2022) compiled NCP estimates in macroalgal communities globally that were in the majority net heterotrophic (10 out of 19 sites), although the NCP values were low and close to metabolic balance (NCP = 0).

We hypothesize that the net heterotrophy of the macroalgal community was sustained by external organic C inputs as suggested by the tendencies of NCP and GPP: CR ratio with algal biomass indicating that the relative heterotrophy increased at lower macroalgal biomass. The organic C required to sustain the community net heterotrophy is most likely provided by the adjacent *P. oceanica* meadow either as particulate organic C (POC) or DOC, as discussed hereafter. The transfer of material from one coastal ecosystem to another is mediated by dissolved (DOM) and particulate organic matter (Hyndes et al., 2014; Säwström et al., 2016). There are some reports of DOM uptake by macroalgae (Van Engeland et al., 2011; Volkmann et al., 2016) and abundant evidence of DOC export from seagrass meadows from living plants (Cawley et al., 2012; Wang et al., 2014; Egea et al. 2018, 2019a, 2019b, 2020, 2023; Jiang et al., 2022; Jiménez-Ramos et al., 2022) and wrack (Lavery et al., 2013; Liu et al., 2018).

4.2. *P. oceanica* macrophytodetritus accumulation metabolism

The correlation of CR with GPP and the lack of correlation with macrophytodetritus accumulation biomass (total, living, or detrital fraction) suggest that a part of CR could be related to autotrophic respiration and not the HR that would be expected to increase with the detrital fraction of the macrophytodetritus accumulation biomass. However, within the mass of macrophytodetritus accumulation, low O_2 conditions or even anoxia are encountered (Mascart et al., 2015). This is expected to limit heterotrophic respiration which might explain the lack of relationship between CR and macrophytodetritus accumulation biomass (total, living, or detrital fraction).

The lack of correlation between GPP and the fraction of living plants in macrophytodetritus accumulation might be explained by the fact that only the surface of macrophytodetritus accumulation is illuminated so that only the exposed living macroscopic plants present in the macrophytodetritus accumulation can photosynthesize. Alternatively, part of

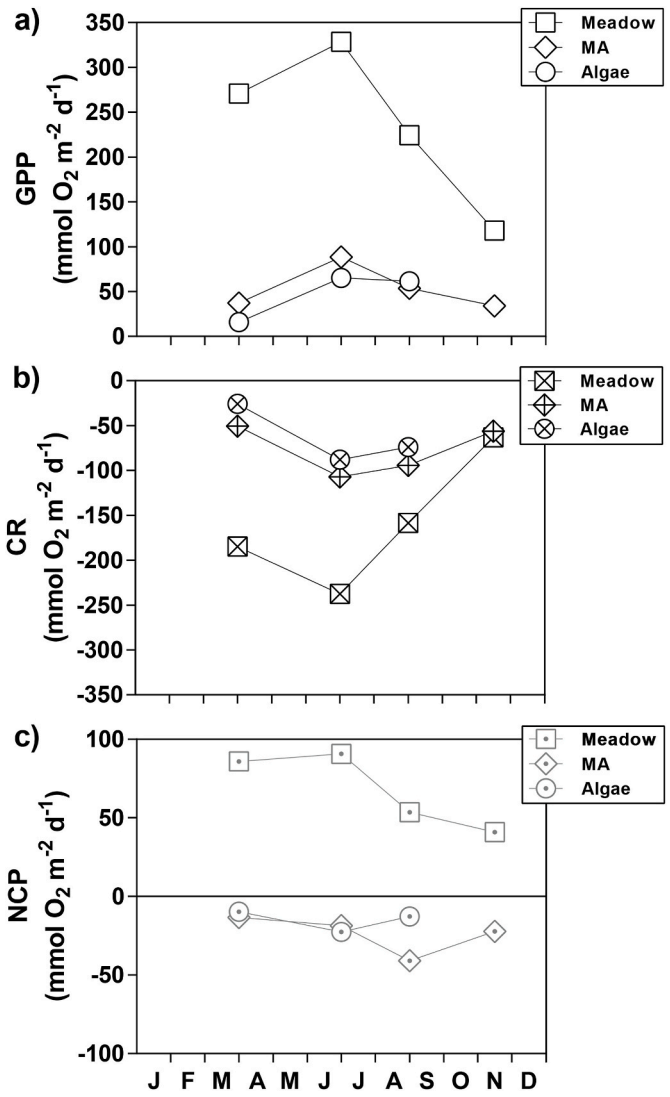


Fig. 7. Gross primary production (GPP in mmol m^{-2} d^{-1}), community respiration (CR in mmol m^{-2} d^{-1}), and net community production (NCP in mmol m^{-2} d^{-1}) in a *Posidonia oceanica* seagrass meadow (10 m depth), *P. oceanica* macrophytodetritus accumulation (MA) (8 m depth), and epilithic macroalgae (8 m depth) in the Bay of Revellata (Corsica), based on chamber measurements for litter (n = 4) and macroalgae (n = 3), and open-water O_2 mass balance for the meadow (n = 4) (Champenois and Borges, 2012) in 2010.

Table 1
Annual averaged gross primary production (GPP in mol m^{-2} yr^{-1}), community respiration (CR in mol m^{-2} yr^{-1}), and net community production (NCP in mol m^{-2} yr^{-1}) in a *Posidonia oceanica* seagrass meadow (10 m depth), *P. oceanica* macrophytodetritus accumulation (MA) (8 m depth), and epilithic macroalgae (8 m depth) in the Bay of Revellata (Corsica), based on chamber measurements for litter (n = 4) and macroalgae (n = 3), and open-water O_2 mass balance for the meadow (n = 4) (Champenois and Borges, 2012) in 2010. The individual measurements given in Fig. 7 were averaged to provide an annual value.

	GPP (mol O_2 m^{-2} yr^{-1})	CR (mol O_2 m^{-2} yr^{-1})	NCP (mol O_2 m^{-2} yr^{-1})
Meadow	94.2 ± 14.9	−63.9 ± 9.2	28.9 ± 8.1
Macrophytodetritus accumulation	19.4 ± 10.8	−28.1 ± 11.5	−8.8 ± 4.3
Epilithic macroalgae	17.6 ± 10.4	−23.7 ± 12.7	−6.1 ± 2.7

GPP could be related to diatoms growing of the surfaces of the macrophytodetritus accumulation sustained by nutriments diffusing from below (Lepoint et al., 2002). Microalgae were not quantified in the macrophytodetritus accumulation during this study. All substrates including dead leaves are known to be abundantly covered by diatoms (Lepoint et al., 2006). Nutrient concentrations, in particular NH_4^+, are higher in the macrophytodetritus accumulation than in the water column (Mascart et al., 2015) or in the *seagrass* meadow itself (Lepoint et al., 2002) and probably boost microalgae development.

For a consistent comparison with HR, the decay rates were recomputed per unit of time from reported *k* data from litter bag experiments (Table S5) using three possible time intervals: 91d, 182d, and 274d. The C:N ratio changes with the age of *P. oceanica* material and could provide a tentative indication on the age of the incubated material and consequently on the most appropriate time interval for integrating the *k* data from litter bag experiments. The C:N ratio of the macrophytodetritus accumulations where the chamber incubations were carried out in the Bay of Revellata averaged 50.7 ± 6.5 (range 37.0–61.3). These values were above the C:N ratio values of senescent leaves from living shoots (26.9–30.2) reported in litter bag decay experiments (Romero et al., 1992; Mateo and Romero, 1996, 1997; Lee et al., 2022) (Table S5), excluding the high C:N values of Apostolaki et al. (2009) that might reflect the more oligotrophic nature of the Aegean Sea compared to the sites in the Western Mediterranean Sea (Lepoint et al., 2002). The C:N ratio values in macrophytodetritus accumulations in the Bay of Revellata were closer but still higher than the C:N ratio values of detached leaves (litter) reported in litter bag decay experiments (33.0–37.5) (Mateo and Romero, 1996; Costa et al., 2019) (Table S5). This might suggest that the macrophytodetritus over which we carried out the chamber measurements of metabolic rates was composed of material older and possibly more refractory than the material used in published litter decay experiments either with senescent leaves from living shoots or from detached leaves (Table S5). This could suggest than the daily decay rates derived from *k* data using a long time interval (274d) might be more representative and more comparable to HR than those derived from shorter time intervals given the putative refractory nature of the material in the macrophytodetritus accumulations indicated by the high C:N ratios.

The higher values of daily decay rates computed from *k* data from litter bag experiments than the HR estimates derived from chamber incubations (between 1.1 and 2.8 times higher for 274d and 90d time intervals, respectively) could be due to the fact that the disappearance of detrital material measured during litter bag experiments include several processes such as detritus decay, fragmentation by detritivores, and washing off of detrital particles smaller than the mesh size of the bag (Harrison, 1989), while HR only provides an estimate of detritus decay from the degradation by heterotrophs. The daily decay rates diverged more from HR for a higher biomass of dead macrophytodetritus (>1000g_{DW} m^{-2}) than for a lower biomass (<1000g_{DW} m^{-2}) (Fig. 6). This reflects that at high biomass of macrophytodetritus, HR might be limited by O_2 availability because of the occurrence of low O_2 conditions or even anoxia within the thick mass of macrophytodetritus accumulation (Mascart et al., 2015). The reported decay experiments in litter bags were made on small quantities of material (<30g) (Table S5) that were presumably well exposed to oxygenated conditions, as the bags were suspended in the water column. Decay experiments in litter bags do not capture the limitation of O_2 availability that might slow down organic matter degradation in thick macrophytodetritus accumulations.

4.3. Benthic metabolism in the Bay of Revellata

The metabolic rates we report for the meadow were measured at 10 m depth. Between 0 and 10 m in the Bay of Revellata, the epilithic macroalgal and meadow communities occupy a similar surface area (0.8 km^2) according to the map of benthic communities reported by Velimirov et al. (2016). Based on these surface area coverage estimates, the integrated NCP of epilithic macroalgae was 4.9 mega-mol O_2 yr^{-1} and

the integrated NCP of the *P. oceanica* meadow was 23.1mega-mol O_2 yr^{-1}. The DOC export from *P. oceanica* meadows has been estimated to correspond between 10% and 72% of NCP (Barrón and Duarte, 2009; Champenois and Borges, 2021). The DOC export from *P. oceanica* meadows between 0 and 10 m would then potentially range between 2.2 and 16.6mega-mol O_2 yr^{-1} encompassing the NCP of the epilithic macroalgae (4.9mega-mol O_2 yr^{-1}). Note that the total surface area of the meadow (0–40m) in the Bay of Revellata is ~5 km^2, so more than 5 times higher than the surface area of epilithic macroalgae (Velimirov et al., 2016). However, it would be unreasonable to extrapolate the NCP estimates at 10 m to the whole depth range of the meadow, since *P. oceanica* primary production decreases exponentially with depth (Pergent et al., 1997). The export of particulate detritus at 10m in the Bay of Revellata was estimated to ~70% of NCP corresponding to an integrated value of ~16 mega-mol O_2 yr^{-1}. This export is in excess of the NCP of the epilithic macroalgae (4.9 mega mol O_2 yr^{-1}), but is presumably mostly in the form of macrodetritus. However, the macrodetritus can be locally partly broken down into small particles that could be transported and settle over epilithic macroalgae. Dauby et al. (1995) showed that 90% of the particules settling in sediment traps over the *P. oceanica* meadow in the Bay of Revellata originated from re-suspended particles from the seagrass meadow. Macroalgae and associated suspensivore fauna efficiently trap particles from the water column (Hendriks et al., 2010).

Given that the net heterotrophy of macroalgal community needs to be also sustained by external DOC inputs most probably from the *P. oceanica* meadow, this implies that DOM exuded from the macroalgae is also consumed by the heterotrophic microbial communities associated to the macroalgae. This finding is based on measurements in a single site, but if representative of the macroalgal community at larger scale in the Bay of Revellata, it would be in direct contradiction with the hypothesis of Velimirov et al. (2016) of a net heterotrophy of the *P. oceanica* meadow in the Bay of Revellata sustained by DOC inputs from epilithic macroalgal communities. Such hypothesis would also require that DOC inputs from epilithic macroalgal communities to be transported from surface waters down to 40 m (the lower extend of the meadow) which is unlikely given the dilution in the water column and dispersion by water currents. The net heterotrophy of the *P. oceanica* meadow in the Bay of Revellata postulated by Velimirov et al. (2016) is probably due to the over-estimation of benthic bacterial C demand vertically integrated over a depth of sediment oxic layer (10 cm) that is one order of magnitude higher than the typical values in coastal sediments (≤5 mm) (Glud et al., 1994), including seagrasses sediments (Holmer et al., 2003; Trevathan-Tackett et al., 2017; Brodersen et al., 2019).

On an annual scale, GPP, CR, and NCP of the meadow was 4.9, 2.3, and 3.3 times higher (in absolute terms) than of one of *P. oceanica* macrophytodetritus accumulation, respectively (Table 1). To our best knowledge there is no estimate of the relative contribution of macrophytodetritus accumulation to the overall surface of *P.* meadows in general or in a specify site, although it is possible to map it with the photogrammetry technique (Marre et al., 2020). Based on our perception from field work, we roughly evaluate the relative cover of macrophytodetritus accumulation to ≤1% of the total surface of meadow. The NCP of macrophytodetritus accumulation would then correspond to about 0.2mega-mol O_2 yr^{-1}, a marginal off-set compared to the meadow NCP at 10m in the Bay of Revellata (23.1mega mol O_2 yr^{-1}). Although a marginal player in the overall NCP budget of the whole seagrass meadow, the macrophytodetritus accumulation habitat has a community of animals mainly composed of crustaceans which display low diversity but extremely high abundance (Mascart et al., 2015), making this habitat very attractive for fish populations (Lepoint and Hyndes, 2022).

5. Conclusions

Adjacent marine ecosystems transfer nutrients and organic matter that sustain part of the primary and secondary production in the community receiving these transfers. Metabolic rates (GPP, CR, and NCP) in adjacent marine ecosystems can, consequently, be linked, net autotrophic communities exporting organic matter potentially sustaining at least partly the net heterotrophy of adjacent communities. Conversely, net heterotrophic communities exporting inorganic nutrients potentially sustain at least partly the net autotrophy of adjacent communities. Here, we investigated GPP, CR, and NCP in epilithic turf-forming macro-algal and macrophytodetritus accumulation communities adjacent to a *P. oceanica* seagrass meadow at 8m depth. GPP in *P. oceanica* macrophytodetritus accumulation (19mol O_2 m^{-2} yr^{-1}) was surpringly high and quantitatively comparable to the GPP of epilithic macro-algae (18mol O_2 m^{-2} yr^{-1}). We attribute this relatively high GPP in the macrophytodetritus accumulation to living drift macroalgae, living detached seagrass shoots, and benthic diatoms. These primary producers were imported from adjacent communities (seagrass meadow and rocky macroalgal mats) and benefit from illuminated conditions and NH_4^+ diffusing from the mass of underlying macrophytodetritus accumulation. The investigated epilithic macro-algal and macrophytodetritus accumulation communities were net heterotrophic (−9 and -6mol O_2 m^{-2} yr^{-1}, respectively) in contrast to the neighboring seagrass meadow that was net autotrophic (29mol O_2 m^{-2} yr^{-1}). The net heterotrophy of the epilithic macro-algal community should be sustained by an external subsidy of organic C that we hypothesize was provided by the neighboring seagrass meadow as DOC or POC.

Degradation rates of macrophytodetritus accumulation adjacent to *P. oceanica* meadows have been so far estimated from litter bag experiments. The direct comparison with HR derived from O_2 change in incubation chambers was uneasy due to variability in k values (in particular with regards to the nature and age of the material on which the experiments were performed) and to the choice of time interval over which the daily decay rates can be integrated for a consistent comparison with HR. Both approaches converged at low macrophytodetritus biomass density (<1000g_{DW} m^{-2}) but diverged at higher macrophytodetritus biomass density (>1000g_{DW} m^{-2}) in particular for the computations based on shorter time intervals. We hypothesize that this discrepancy resulted from limitation of HR by O_2 availability at high biomass of macrophytodetritus, due to low O_2 conditions within the mass of macrophytodetritus accumulation. We show the limitation and possibly over-estimation of extrapolating decay rates based on litter bag experiments with small quantities of material to "real" macrophytodetritus biomass densities.

CRediT authorship contribution statement

W. Champenois: Writing – original draft, Investigation, Formal analysis, Conceptualization. **G. Lepoint:** Writing – review & editing, Project administration, Investigation, Formal analysis, Conceptualization. **A.V. Borges:** Writing – review & editing, Supervision, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.108971.

References

Apostolaki, E.T., Marbà, N., Holmer, M., Karakassis, I., 2009. Fish farming impact on decomposition of Posidonia oceanica litter. J. Exp. Mar. Biol. Ecol. 369, 58–64. https://doi.org/10.1016/j.jembe.2008.10.022.

Barrón, C., Duarte, C.M., 2009. Dissolved organic matter release in a Posidonia oceanica meadow. Mar. Ecol. Prog. Ser. 374, 75–84. https://doi.org/10.3354/meps07715.

Barrón, C., Duarte, C.M., Frankignoulle, M., Borges, A.V., 2006. Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (Posidonia oceanica) meadow. Estuar. Coast 29, 417–426. https://doi.org/10.1007/BF02784990.

Bay, D., 1984. A field study of the growth dynamics and productivity of Posidonia oceanica (L.) Delile in Calvi Bay, Corsica. Aquat. Bot. 20, 43–64. https://doi.org/10.1016/0304-3770(84)90026-3.

Beleneva, I.A., Zhukova, N.V., 2006. Bacterial communities of some brown and red algae from peter the great bay, the sea of Japan. Microbiology 75, 348–357. https://doi.org/10.1134/S0026261706030180.

Bengtsson, M., Sjøtun, K., Lanzén, A., Øvreås, L., 2012. Bacterial diversity in relation to secondary production and succession on surfaces of the kelp Laminaria hyperborea. ISME J. 6, 2188–2198. https://doi.org/10.1038/ismej.2012.67.

Berg, P., Huettel, M., Glud, R.N., Reimers, C.E., Attard, K.M., 2022. The method and its contributions to defining oxygen and carbon fluxes in marine environments. Ann. Rev. Mar. Sci 14, 431–455. https://doi.org/10.1146/annurev-marine-042121-012329.

Boudouresque, C.F., Pergent, G., Pergent-Martini, C., Ruitton, S., Thibaut, T., Verlaque, M., 2016. The necromass of the Posidonia oceanica seagrass meadow: fate, role, ecosystem services and vulnerability. Hydrobiologia 781, 25–42. https://doi.org/10.1007/s10750-015-2333-y.

Brodersen, K.E., Trevathan-Tackett, S.M., Nielsen, D.A., Connolly, R.M., Lovelock, C.E., Atwood, T.B., Macreadie, P.I., 2019. Oxygen consumption and sulfate reduction in vegetated coastal habitats: effects of physical disturbance. Front. Mar. Sci. 6, 14. https://doi.org/10.3389/fmars.2019.00014.

Bulleri, F., Benedetti-Cecchi, L., Acunto, S., Cinelli, F., Hawkins, S.J., 2002. The influence of canopy algae on vertical patterns of distribution of low-shore assemblages on rocky coasts in the northwest Mediterranean. J. Exp. Mar. Biol. Ecol. 267, 89–106. https://doi.org/10.1016/S0022-0981(01)00361-6.

Cawley, K.M., Ding, Y., Fourqurean, J., Jaffé, R., 2012. Characterising the sources and fate of dissolved organic matter in Shark Bay, Australia: a preliminary study using optical properties and stable carbon isotopes. Mar. Freshw. Res. 63, 1098–1107. https://doi.org/10.1071/MF12028.

Cebrián, J., Duarte, C.M., Marbà, N., Enríquez, S., 1997. Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. Mar. Ecol.: Prog. Ser. 155, 29–44. https://doi.org/10.3354/meps155029.

Cebrián, J., 1999. Patterns in the fate of production in plant communities. Am. Nat. 154 (4), 449–468. https://doi.org/10.1086/303244.

Cebrian, J., Duarte, C.M., 2001. Detrital stocks and dynamics of the seagrass Posidonia oceanica (L.) Delile in the Spanish Mediterranean. Aquat. Bot. 70, 295–309. https://doi.org/10.1016/S0304-3770(01)00154-1.

Chapin III, F.S., Woodwell, G.M., Randerson, J.T., Rastetter, E.B., Lovett, G.M., Baldocchi, D.D., Clark, D.A., Harmon, M.E., Schimel, D.S., Valentini, R., Wirth, C., Aber, J.D., Cole, J.J., Goulden, M.L., Harden, J.W., Heimann, M., Howarth, R.W., Matson, P.A., McGuire, A.D., Melillo, J.M., Mooney, H.A., Neff, J.C., Houghton, R.A., Pace, M.L., Ryan, M.G., Running, S.W., Sala, O.E., Schlesinger, W.H., Schulze, E.-D., 2006. Reconciling carbon-cycle concepts, terminology, and methods. Ecosystems 9, 1041–1050. https://doi.org/10.1007/s10021-005-0105-7.

Champenois, W., Borges, A.V., 2018. Inter-annual variations over a decade of primary production of the seagrass Posidonia oceanica. Limnol. Oceanogr. https://doi.org/10.1002/lno.11017.

Champenois, W., Borges, A.V., 2021. Net community metabolism of a Posidonia oceanica meadow. Limnol. Oceanogr. 66, 2126–2140. https://doi.org/10.1002/lno.11724.

Champenois, W., Borges, A.V., 2012. Seasonal and inter-annual variations of community metabolism rates of a Posidonia oceanica seagrass meadow. Limnol. Oceanogr. 57 (1), 347–361. https://doi.org/10.4319/lo.2012.57.1.0347.

Costa, V., Mazzola, A., Rossi, F., Vizzini, S., 2019. Decomposition rate and invertebrate colonization of seagrass detritus along a hydrodynamic gradient in a Mediterranean coastal basin: the Stagnone di Marsala (Italy) case study. Mar. Ecol. 40, e12570. https://doi.org/10.1111/maec.12570.

Dauby, P., Bale, A.J., Bloomer, N., Canon, C., Ling, R.D., Norro, A., Robertson, J.E., Simon, A., Théate, J.M., Watson, A.J., Frankignoulle, M., 1995. Particle fluxes over a Mediterranean seagrass bed: a one year case study. Mar. Ecol. Prog. Ser. 126, 233–246. https://doi.org/10.3354/meps126233.

Duarte, C.M., 1990. Seagrass nutrient content. Mar. Ecol. Prog. Ser. 67, 201–207. https://doi.org/10.3354/meps067201.

Duarte, C.M., Marbà, N., Gacia, E., Fourqurean, J.W., Beggins, J., Barrón, C., Apostolaki, E.T., 2010. Seagrass community metabolism: assessing the carbon sink capacity of seagrass meadows. Global Biogeochem. Cycles 24, GB4032. https://doi.org/10.1029/2010GB003793.

Duarte, C.M., Gattuso, J.-P., Hancke, K., Gundersen, H., Filbee-Dexter, K., Pedersen, M. F., Middelburg, J.J., Burrows, M.T., Krumhansl, K.A., Wernberg, T., Moore, P., Pessarrodona, A., Ørberg, S.B., Pinto, I.S., Assis, J., Queirós, A.M., Smale, D.A., Bekkby, T., Serrão, E.A., Krause-Jensen, D., 2022. Global estimates of the extent and production of macroalgal forests. Global Ecol. Biogeogr. 31, 1422–1439. https://doi.org/10.1111/geb.13515.

Duarte, C.A., Cebrián, J., 1996. The fate of marine autotrophic production. Limnol. Oceanogr. 41, 1758–1766. https://doi.org/10.4319/lo.1996.41.8.1758.

Egea, L.G., Jiménez-Ramos, R., Hernández, I., Bouma, T.J., Brun, F.G., 2018. Effects of ocean acidification and hydrodynamic conditions on carbon metabolism and dissolved organic carbon (DOC) fluxes in seagrass populations. PLoS One 13 (2), e0192402. https://doi.org/10.1371/journal.pone.0192402.

Egea, L.G., Barrón, C., Jiménez–Ramos, R., Hernández, I., Vergara, J.J., Pérez–Lloréns, J. L., Brun, F.G., 2019a. Coupling carbon metabolism and dissolved organic carbon fluxes in benthic and pelagic coastal communities. Estuar. Coast Shelf Sci. 227, 106336. https://doi.org/10.1016/j.ecss.2019.106336.

Egea, L.G., Jiménez–Ramos, R., Hernández, I., Brun, F.G., 2019b. Effect of in Situ short–term temperature increase on carbon metabolism and dissolved organic carbon (DOC) fluxes in a community dominated by the seagrass Cymodocea nodosa. PLoS One 14 (1), e0210386. https://doi.org/10.1371/journal.pone.0210386.

Egea, L.G., Jiménez-Ramos, R., Hernández, I., Brun, F.G., 2020. Differential effects of nutrient enrichment on carbon metabolism and dissolved organic carbon (DOC) fluxes in macrophytic benthic communities. Mar. Environ. Res. 162, 105179. https://doi.org/10.1016/j.marenvres.2020.105179.

Egea, L.G., Pérez-Estrada, C.J., Jiménez-Ramos, R., Hernández, I., López-López, S., Brun, F.G., 2023. Changes in carbon metabolism and dissolved organic carbon fluxes on seagrass patches (Halodule wrightii) with different ages in Southern Gulf of California. Mar. Environ. Res. 191, 106136. https://doi.org/10.1016/j.marenvres.2023.106136.

Filbee-Dexter, K., Wernberg, T., Norderhaug, K.M., Ramirez-Llodra, E., Pedersen, M.F., 2018. Movement of pulsed resource subsidies from kelp forests to deep fjords. Oecologia 187, 291–304. https://doi.org/10.1007/s00442-018-4121-7.

Filbee-Dexter, K., Pessarrodona, A., Duarte, C.M., Krause-Jensen, D., Hancke, K., Smale, D., Wernberg, T., 2023. Seaweed forests are carbon sinks that may help mitigate CO2 emissions: a comment on Gallagher et al. (2022). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 80, 1814–1819. https://doi.org/10.1093/icesjms/fsad107.

Filbee-Dexter, K., Pessarrodona, A., Pedersen, M.F., Wernberg, T., Duarte, C.M., Assis, J., Bekkby, T., Burrows, M.T., Carlson, D.F., Gattuso, J.-P., Gundersen, H., Hancke, K., Krumhansl, K.A., Kuwae, T., Middelburg, J.J., Moore, P.J., Queirós, A.M., Smale, D. A., Sousa-Pinto, I., Suzuki, N., Krause-Jensen, D., 2024. Carbon export from seaweed forests to deep ocean sinks. Nat. Geosci. https://doi.org/10.1038/s41561-024-01449-7.

Frankignoulle, M., Bouquegneau, J.-M., 1987. Seasonal variations of the diel carbon budget of a marine macrophytes ecosystem. Mar. Ecol. Prog. Ser. 38, 197–199. https://doi.org/10.3354/meps038197.

Gallagher, J.B., Shelamoff, V., 2022. Reply to Stafford's (2022) comment on "Seaweed ecosystems may not mitigate CO2 emissions" by Gallagher et al. (2022). ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79, 1703–1704. https://doi.org/10.1093/icesjms/fsac088, 2022.

Gallagher, J.B., Shelamoff, V., Layton, C., 2022. Seaweed ecosystems may not mitigate CO2 emissions. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79, 585–592. https://doi.org/10.1093/icesjms/fsac011, 2022.

Gallagher, J.B., 2023. Reply to the comment by Filbee-Dexter et al. (2023) "Seaweed forests are carbon sinks that may help mitigate CO2 emissions". ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 80, 1820–1826. https://doi.org/10.1093/icesjms/fsad119.

Glud, R.N., Gundersen, J.K., Jørgensen, B.B., Revsbech, N.P., Schulz, H.D., 1994. Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: in situ and laboratory measurements. Deep-Sea Res. Part I 41, 1767–1788. https://doi.org/10.1016/0967-0637(94)90072-8.

Hacker, S.D., Steneck, R.S., 1990. Habitat architecture and the abundance and body size-dependent habitat selection of a phytal amphipod. Ecology 71, 2269–2285. https://doi.org/10.2307/1938638.

Harrison, P.G., 1989. Detrital processing in seagrass systems: a review of factors affecting decay rates, remineralization and detritivory. Aquat. Bot. 23, 263–288. https://doi.org/10.1016/0304-3770(89)90002-8.

Haywood, M.D.E., Vance, D.J., Loneragan, N.R., 1995. Seagrass and algal beds as nursery habitats for tiger prawns (Penaeus semisulcatus and P. esculentus) in a tropical Australian estuary. Mar. Biol. 122, 213–223. https://doi.org/10.1007/BF00348934.

Hendriks, I.E., Bouma, T.J., Morris, E.P., Duarte, C.M., 2010. Effects of seagrasses and algae of the Caulerpa family on hydrodynamics and particle trapping rates. Mar. Biol. 157, 473–481. https://doi.org/10.1007/s00227-009-1333-8.

Holmer, M., Duarte, C.M., Marbá, N., 2003. Sulfur cycling and seagrass (*Posidonia oceanica*) status in carbonate sediments. Biogeochemistry 66, 223–239. https://doi.org/10.1023/B:BIOG.0000005326.35071.51.

Hyndes, G.A., Nagelkerken, I., McLeod, R.J., Connolly, R.M., Lavery, P.S., Vanderklift, M. A., 2014. Mechanisms and ecological role of carbon transfer within coastal seascapes. Biol. Rev. 89, 232–254. https://doi.org/10.1111/brv.12055.

IOC, 1994. Protocols for the Joint Global Ocean Flux Study (JGOFS) Core Measurements, JGOFS Report 19, 170pp. United Nations Educational, Scientific and Cultural

Organization-Intergovernmental Oceanographic Commission, Paris, France. https://doi.org/10.25607/OBP-1409.
Jiang, Z., Li, L., Fang, Y., Lin, J., Liu, S., Wu, Y., Huang, X., 2022. Eutrophication reduced the release of dissolved organic carbon from tropical seagrass roots through exudation and decomposition. Mar. Environ. Res. 179, 105703. https://doi.org/10.1016/j.marenvres.2022.105703.
Jiménez-Ramos, R., Tomas, F., Reynés, X., Romera-Castillo, C., Pérez-Lloréns, J.L., Egea, L.G., 2022. Carbon metabolism and bioavailability of dissolved organic carbon (DOC) fluxes in seagrass communities are altered under the presence of the tropical invasive alga Halimeda incrassata. Sci. Total Environ. 839, 156325. https://doi.org/10.1016/j.scitotenv.2022.156325.
Joher, S., Ballesteros, E., Cebrian, E., Sánchez, N., Rodríguez-Prieto, C., 2012. Deep-water macroalgaldominated coastal detritic habitats on the continental shelf off mallorca and menorca (balearic islands, western mediterranean). Bot. Mar. 55, 485–497. https://doi.org/10.1515/bot-2012-0113.
Katz, L., Sirjacobs, D., Gobert, S., Lejeune, P., Danis, B., 2021. Distribution of macroalgae in the area of calvi (Corsica). Biodivers. Data J. 9, e68249. https://doi.org/10.3897/BDJ.9.e68249.
Kirchman, D.L., 2016. Growth rates of microbes in the oceans. Ann. Rev. Mar. Sci 8, 285–309. https://doi.org/10.1146/annurev-marine-122414-033938.
Koopmans, D., Holtappels, M., Chennu, A., Weber, M., de Beer, D., 2020. High net primary production of mediterranean seagrass (Posidonia oceanica) meadows determined with aquatic eddy covariance. Front. Mar. Sci. 7 (118), 1–13. https://doi.org/10.3389/fmars.2020.00118.
Krause- Jensen, D., Duarte, C.M., 2016. Substantial role of macroalgae in marine carbon sequestration. Nat. Geosci. 9, 737–742. https://doi.org/10.1038/ngeo2790.
Lavery, P.S., McMahon, K., Weyers, J., Boyce, M.C., Oldham, C.E., 2013. Release of dissolved organic carbon from seagrass wrack and its implications for trophic connectivity. Mar. Ecol. Prog. Ser. 494, 121–133. https://doi.org/10.3354/meps10554.
Lee, J., Gambi, M.C., Kroeker, K.J., Munari, M., Peay, K., Micheli, F., 2022. Resilient consumers accelerate the plant decomposition in a naturally acidified seagrass ecosystem. Global Change Biol. 28, 4558–4576. https://doi.org/10.1111/gcb.16265.
Lepoint, G., Millet, S., Dauby, P., Gobert, S., Bouquegneau, J.-M., 2002. Annual nitrogen budget of the seagrass Posidonia oceanica as determined by in situ uptake experiments. Mar. Ecol. Prog. Ser. 237, 87–96. https://doi.org/10.3354/meps237087.
Lepoint, G., Cox, A.-S., Dauby, P., Poulicek, M., Gobert, S., 2006. Food sources of two detritivore amphipods associated with the seagrass Posidonia oceanica leaf litter. Mar. Biol. Res. 2 (5), 355–365. https://doi.org/10.1080/17451000600962797.
Lepoint, G., Hyndes, G.A., 2022. Tropicalization of seagrass macrophytodetritus accumulations and associated food webs. Front. Mar. Sci. 9. https://doi.org/10.3389/fmars.2022.943841.
Liu, S., Jiang, Z., Zhou, C., Wu, Y., Arbi, I., Zhang, J., Huang, X., Trevathan-Tackett, S.M., 2018. Leaching of dissolved organic matter from seagrass leaf litter and its biogeochemical implications. Acta Oceanol. Sin. 37, 84–90. https://doi.org/10.1007/s13131-018-1233-1.
Long, M.H., Berg, P., Falter, J.F., 2015. Seagrass metabolism across a productivity gradient using the eddy covariance, Eulerian control volume, and biomass addition techniques. J. Geophys. Res. 120, 3624–3639. https://doi.org/10.1002/2014JC010352.
Mallon, J., Banaszak, A.T., Donachie, L., Exton, D., Cyronak, T., Balke, T., Bass, A.M., 2022. A low-cost benthic incubation chamber for in-situ community metabolism measurements. PeerJ 10, e13116. https://doi.org/10.7717/peerj.13116.
Marre, G., Deter, J., Holon, F., Boissery, P., Luque, S., 2020. Fine-scale automatic mapping of living Posidonia oceanica seagrass beds with underwater photogrammetry. Mar. Ecol. Prog. Ser. 643, 63–74. https://doi.org/10.3354/meps13338.
Marx, L., Flecha, S., Wesselmann, M., Morell, C., Hendriks, I.E., 2021. Marine macrophytes as carbon sinks: comparison between seagrasses and the non-native alga Halimeda incrassata in the western mediterranean (mallorca). Front. Mar. Sci. 8, 746379. https://doi.org/10.3389/fmars.2021.746379.
Mascart, T., Lepoint, G., Deschoemaeker, S., Binard, M., Remy, F., De Troch, M., 2015. Seasonal variability of meiofauna, especially harpacticoid copepods, in *Posidonia oceanica* macrophytodetritus accumulations. J. Sea Res. 95, 149–160. https://doi.org/10.1016/j.seares.2014.07.009.
Mateo, M.A., Romero, J., 1996. Evaluating seagrass leaf litter decomposition: an experimental comparison between litter-bag and oxygen-uptake methods. J. Exp. Mar. Biol. Ecol. 202, 97–106. https://doi.org/10.1016/0022-0981(96)00019-6.
Mateo, M.A., Romero, J., 1997. Detritus dynamics in the seagrass Posidonia oceanica: elements for an ecosystem carbon and nutrient budget. Mar. Ecol.: Prog. Ser. 151, 43–53. https://doi.org/10.3354/meps151043.
Mateo, M.A., Renom, P., Hemminga, M.A., Peene, J., 2001. Measurement of seagrass production using the 13C stable isotope compared with classical O2 and 14C methods. Mar. Ecol. Prog. Ser. 223, 157–165. https://doi.org/10.3354/meps223157.
Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2. Front. Ecol. Environ. 9, 552–560. https://doi.org/10.1890/110004.
Miller, R.J., Reed, D.C., Brzezinski, M.A., 2009. Community structure and productivity of subtidal turf and foliose algal assemblages. Mar. Ecol. Prog. Ser. 388, 1–11. https://doi.org/10.3354/meps08131.
Odum, H.T., 1956. Primary production in flowing waters. Limnol. Oceanogr. 1, 102–117. https://doi.org/10.4319/lo.1956.1.2.0102.
Ortega, A., Geraldi, N.R., Alam, I., Kamau, A.A., Acinas, S.G., Logares, R., Gasol, J.M., Massana, R., Krause- Jensen, D., Duarte, C.M., 2019. Important contribution of macroalgae to oceanic carbon sequestration. Nat. Geosci. 12, 748–754. https://doi.org/10.1038/s41561-019-0421-8.
Petersen, R.C., Cummins, K.W., 1974. Leaf processing in a woodland stream. Freshw. Biol. 4, 343–368. https://doi.org/10.1111/j.1365-2427.1974.tb00103.x.
Pergent, G., Rico-Raimondino, V., Pergent-Martini, C., 1997. Fate of primary production in Posidonia oceanica meadows of the Mediterranean. Aquat. Bot. 59, 307–321. https://doi.org/10.1016/S0304-3770(97)00052-1.
Pergent, G., Pergent-Martini, C., 1991. Leaf renewal cycle and primary production of Posidonia oceanica in the bay of Lacco Ameno (Ischia, Italy) using lepidochronological analysis. Aquat. Bot. 42, 49–66. https://doi.org/10.1016/0304-3770(91)90105-E.
Pessarrodona, A., Assis, J., Filbee-Dexter, K., Burrows, M.T., Gattuso, J.-P., Duarte, C.M., Krause-Jensen, D., Moore, P.J., Smale, D.A., Wernberg, T., 2022. Global seaweed productivity. Sci. Adv. 8, eabn2465. https://doi.org/10.1126/sciadv.abn2465.
Piazzi, L., Pardi, G., Balata, D., Cecchi, E., Cinelli, F., 2002. Seasonal dynamics of a subtidal North-Western Mediterranean macroalgal community in relation to depth and substrate inclination. Bot. Mar. 45, 243–252. https://doi.org/10.1515/BOT.2002.023.
Remy, F., Mascart, T., De Troch, M., Michel, L.N., Lepoint, G., 2018. Seagrass organic matter transfer in Posidonia oceanica macrophytodetritus accumulations. Estuar. Coast Shelf Sci. 212, 73–79. https://doi.org/10.1016/j.ecss.2018.07.001.
Romero, J., Pergent, G., Pergent-Martini, C., Mateo, M.-A., Regnier, C., 1992. The detritic compartment in a Posidonia oceanica meadow: litter features, decomposition rates, and mineral stocks. Mar. Ecol. 13, 69–83. https://doi.org/10.1111/j.1439-0485.1992.tb00341.x.
Ruiz-Halpern, S., Vaquer-Sunyer, R., Duarte, C.M., 2014. Annual benthic metabolism and organic carbon fluxes in a semi-enclosed Mediterranean bay dominated by the macroalgae Caulerpa prolifera. Front. Mar. Sci. 1, 67. https://doi.org/10.3389/fmars.2014.00067.
Säwström, C., Hyndes, G.A., Eyre, B.D., Huggett, M.J., Fraser, M.W., Lavery, P.S., Thomson, P.G., Tarquinio, F., Steinberg, P.D., Laverock, B., 2016. Coastal connectivity and spatial subsidy from a microbial perspective. Ecol. Evol. 6, 6662–6671. https://doi.org/10.1002/ece3.2408.
Sommer, S., Türk, M., Kriwanek, S., Pfannkuche, O., 2008. Gas exchange system for extended in situ benthic chamber flux measurements under controlled oxygen conditions: first application - sea bed methane emission measurements at Captain Arutyunov mud volcano. Limnol Oceanogr. Methods 6. https://doi.org/10.4319/lom.2008.6.23.
Sommer, S., Linke, P., Pfannkuche, O., Niemann, H., Treude, T., 2010. Benthic respiration in a seep habitat dominated by dense beds of ampharetid polychaetes at the Hikurangi Margin (New Zealand). Mar. Geol. 272, 223–232. https://doi.org/10.1016/j.margeo.2009.06.003.
Smith, S.V., 1981. Marine macrophytes as a global carbon sink. Science 211, 838–840. https://doi.org/10.1126/science.211.4484.838.
Stafford, R., 2022. Comment on “Seaweed ecosystems may not mitigate CO2 emissions” by Gallagher et al. (2022. ICES (Int. Counc. Explor. Sea) J. Mar. Sci. 79, 1701–1702. https://doi.org/10.1093/icesjms/fsac087, 2022.
Trevathan-Tackett, S.M., Seymour, J.R., Nielsen, D.A., Macreadie, P.I., Sanderman, T.C.J. J., Baldock, J., Howes, J.M., Steven, A.D.L., Ralph, P.J., 2017. Sediment anoxia limits microbial-driven seagrass carbon remineralization under warming conditions. FEMS (Fed. Eur. Microbiol. Soc.) Microbiol. Ecol. 93. https://doi.org/10.1093/femsec/fix033.
van de Koppel, J., van der Heide, T., Altieri, A.H., Eriksson, B.K., Bouma, T.J., Olff, H., Silliman, B.R., 2015. Long-distance interactions regulate the structure and resilience of coastal ecosystems. Ann. Rev. Mar. Sci 7, 139–158. https://doi.org/10.1146/annurev-marine-010814-015805.
Van Engeland, T., Bouma, T.J., Morris, E.P., Brun, F.G., Peralta, G., Lara, M., Hendriks, I. E., Soetaert, K., Middelburg, J.J., 2011. Potential uptake of dissolved organic matter by seagrasses and macroalgae. Mar. Ecol. Prog. Ser. 427, 71–81. https://doi.org/10.3354/meps09054.
Velimirov, B., Lejeune, P., Kirschner, A., Jousseaume, M., Abadie, A., Pête, D., Dauby, P., Richir, J., Gobert, S., 2016. Estimating carbon fluxes in a Posidonia oceanica system: paradox of the bacterial carbon demand. Estuar. Coast Shelf Sci. 171, 23–34. https://doi.org/10.1016/j.ecss.2016.01.008.
Volkmann, C., Halbedel, S., Voss, M., Schubert, H., 2016. The role of dissolved organic and inorganic nitrogen for growth of macrophytes in coastal waters of the Baltic Sea. J. Exp. Mar. Biol. Ecol. 477, 23–30. https://doi.org/10.1016/j.jembe.2016.01.005.
Wang, X., Chen, R.F., Cable, J.E., Cherrier, J., 2014. Leaching and microbial degradation of dissolved organic matter from salt marsh plants and seagrasses. Aquat. Sci. 76, 595–609. https://doi.org/10.1007/s00027-014-0357-4.
Wiese, J., Thiel, V., Nagel, K., Staufenberger, T., Imhoff, J.F., 2009. Diversity of antibiotic-active bacteria associated with the brown alga Laminaria saccharina from the Baltic Sea. Mar. Biotechnol. 11, 287–300. https://doi.org/10.1007/s10126-008-9143-4.
Zieman, J.C., 1974. Methods for the study of the growth and production of turtle grass, Thalassia testudinum konig. Aquaculuture 4, 139–143. https://doi.org/10.1016/0044-8486(74)90029-5.

Supplemental Material

Community gross primary production and respiration in epilithic macroalgae and *Posidonia oceanica* macrophytodetritus accumulation in the Bay of Revellata (Corsica)

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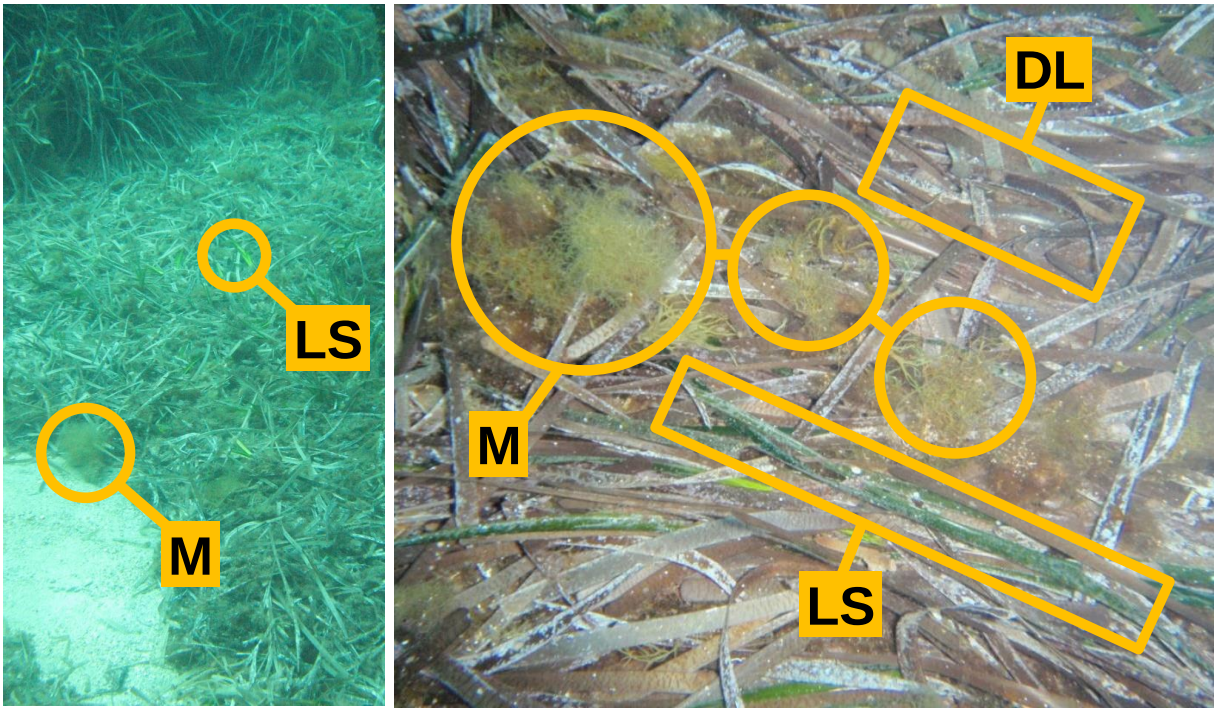

Figure S1: Photographs of *Posidonia oceanica* macrophytodetritus accumulation at ~8 m depth in the Bay of Revellata (Corsica). M = drift macroalgae; LS = Living shoot; DL = dead leaf.

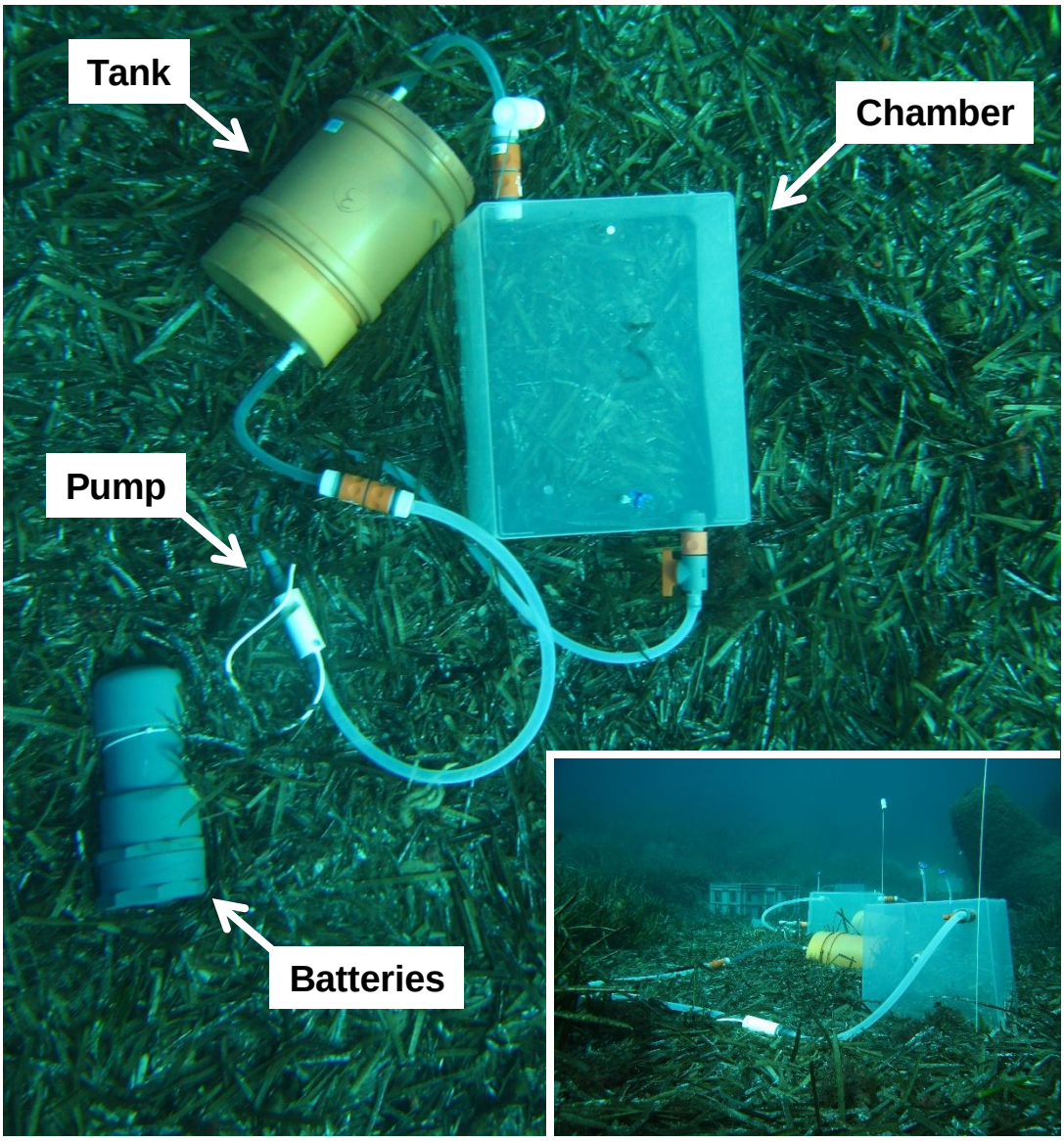

Figure S2: Incubation setup used the measure metabolic rates from temporal changes of O2 in an incubation chamber over *Posidonia oceanica* at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica).

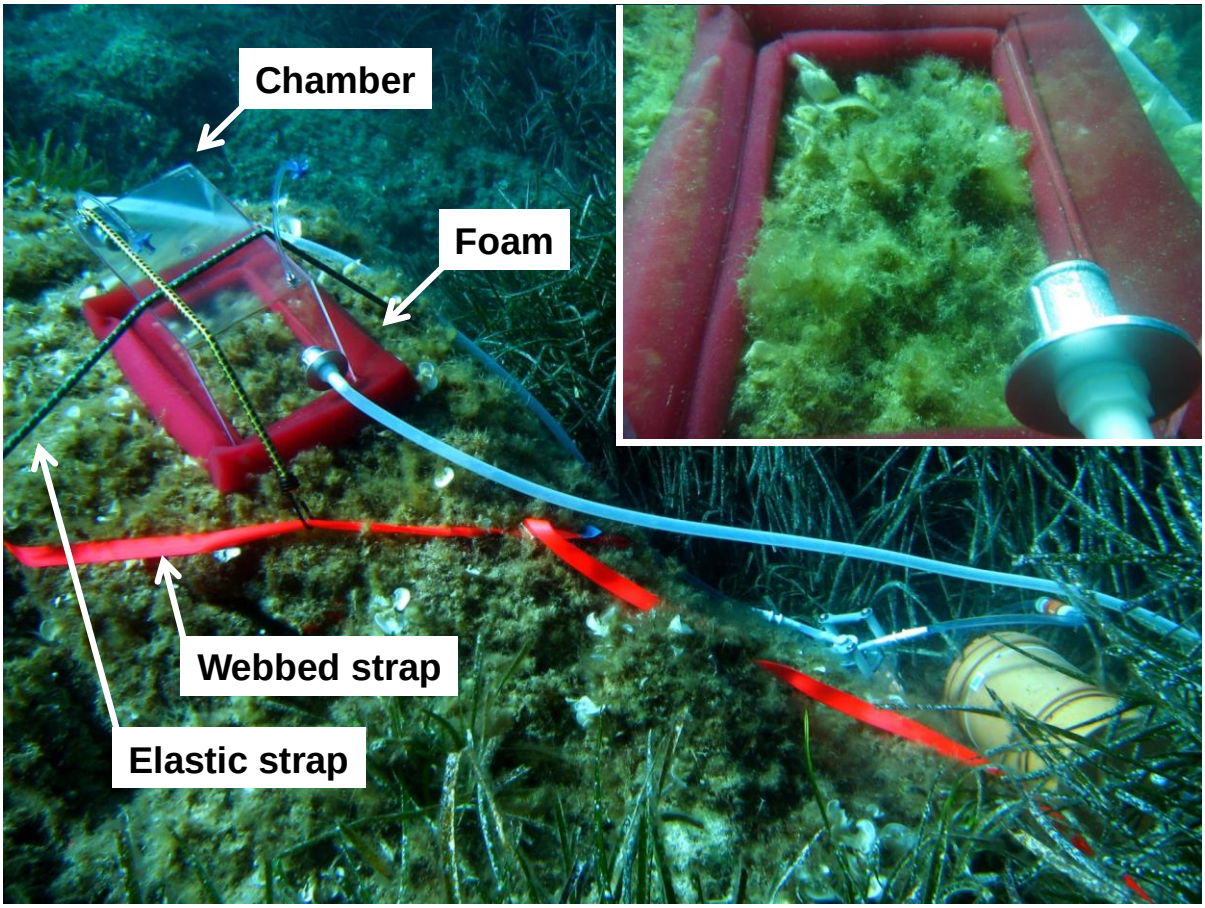

Figure S3: Incubation setup used the measure metabolic rates from temporal changes of O2 in an incubation chamber over epilithic macro-algae at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica).

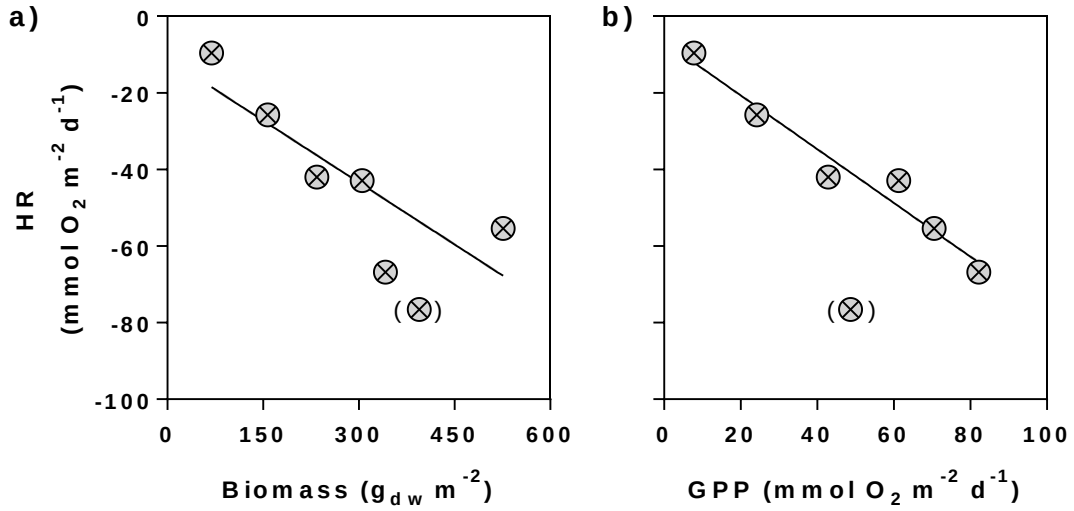

Figure S4: Heterotrophic respiration (HR in mmol O_2 m^{-2} d^{-1}) as a function of macroalgal biomass in dry weight (g_{dw} m^{-2}) (a) and of gross primary production (GPP in mmol O_2 m^{-2} d^{-1}) (b) computed from community respiration measured by O_2 change in an incubation chamber over epilithic macro-algae at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) 7 occasions from June 2009 to May 2011 (10/06/2009, 15/08/2009, 23/02/2010, 01/06/2010, 24/08/2010, 20/02/2011 et 31/05/2011). The data point on 24/08/2010 is indicated by brackets and was excluded from the linear regressions (Table S4) shown by solid lines.

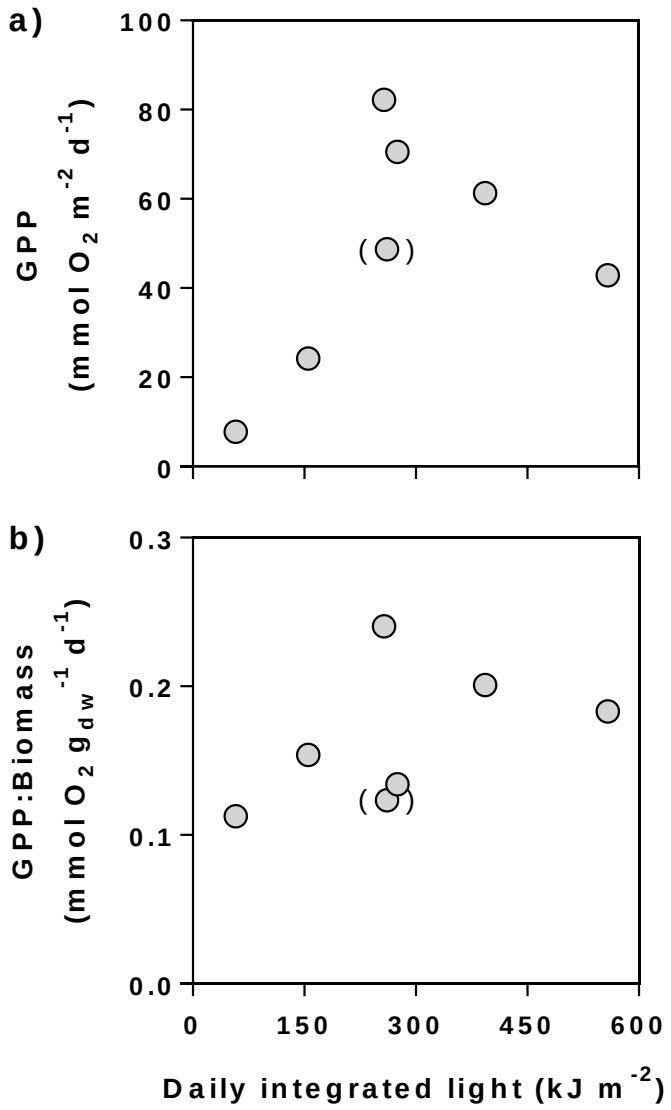

Figure S5: Gross primary production (GPP in mmol m^{-2} d^{-1}) (a), and GPP normalized by macro-algal biomass in dry weight (GPP:Biomass mmol g_{dw}^{-1} d^{-1}) measured by O_2 change in an incubation chamber over epilithic macro-algae at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) 7 occasions from June 2009 to May 2011 (10/06/2009, 15/08/2009, 23/02/2010, 01/06/2010, 24/08/2010, 20/02/2011 et 31/05/2011). The data point on 24/08/2010 is indicated by brackets.

Table S1: Average ± standard deviation of gross primary production (GPP in mmol m^{-2} d^{-1}), community respiration (CR in mmol m^{-2} d^{-1}), and net community production (NCP in mmol m^{-2} d^{-1}) measured by O_2 change in *n* incubation chambers over *Posidonia oceanica* macrophytodetritus accumulation and corresponding total biomass in dry weight (g_{dw} m^{-2}), daily water temperature (Temp in °C), and daily incoming light energy (kJ m^{-2} d^{-1}) at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) on 8 occasions from March 2009 to November 2010. The relative contribution of different fractions of the macrophytodetritus accumulation biomass is given in Table S3. *nd* = no data.

Date	*n*	GPP (mmol O_2 m^{-2} d^{-1})	CR (mmol O_2 m^{-2} d^{-1})	NCP (mmol O_2 m^{-2} d^{-1})	Biomass (g_{dw} m^{-2})	Temp (°C)	Light (kJ m^{-2} d^{-1})
04-03-09	3	57.4 ± 2.1	-67.3 ± 26.3	-9.9 ± 2.1	*nd*	13.1	31
02-06-09	2	91.6 ± 15.5	-112.8 ± 55.6	-21.2 ± 15.5	845	16.2	350
19-08-09	2	48.9 ± 12.1	-95.7 ± 54.8	-46.8 ± 12.1	1164	25.6	346
11-11-09	3	5.7 ± 9.4	-27.2 ± 15.3	-21.4 ± 9.4	1136	18.0	84
16-02-10	1	16.8	-33.9	-17.1	509	12.7	86
04-06-10	3	85.4 ± 8.2	-101.3 ± 49.6	-15.9 ± 8.2	241	18.2	205
20-08-10	3	58.2 ± 9.6	-93.2 ± 35.3	-35.0 ± 9.6	2559	23.8	351
05-11-10	2	62.0 ± 13.5	-84.9 ± 35.7	-22.9 ± 13.5	2270	18.1	98

Table S2 : Gross primary production (GPP in mmol m^{-2} d^{-1}), community respiration (CR in mmol m^{-2} d^{-1}), and net community production (NCP in mmol m^{-2} d^{-1}) measured by O_2 change in an incubation chamber (*n*=1) over epilithic macro-algae at ~8 m depth, corresponding macro-algal biomass in dry weight (g_{dw} m^{-2}), daily average water temperature (Temp in °C), and daily incoming light energy (kJ m^{-2} d^{-1}) at proximity of a *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) on 7 occasions from June 2009 to May 2011.

Date	n	GPP (mmol O_2 m^{-2} d^{-1})	CR (mmol O_2 m^{-2} d^{-1})	NCP (mmol O_2 m^{-2} d^{-1})	Biomass (g_{dw} m^{-2})	Temp (°C)	Light (kJ m^{-2} d^{-1})
10-06-09	1	42.9	-63.8	-20.9	234.2	20.3	558
15-08-09	1	61.3	-74	-12.7	305.1	25.0	393
23-02-10	1	24.2	-38	-13.8	157.2	13.2	155
01-06-10	1	82.2	-108.5	-26.3	342	19.1	257
24-08-10	1	48.7	-101.9	-53.2	394.6	23.8	261
20-02-11	1	7.8	-13.6	-5.7	69.4	13.2	57.7
31-05-11	1	70.6	-91.2	-20.7	526	20.0	275

Table S3: *Posidonia oceanica* macrophytodetritus accumulation total biomass in dry weight (g_{dw} m^{-2}) and relative contribution of living macro-algae (% algae), of living *P. oceanica* leaves (%leaves) on detached shoots, and dead material at ~8 m depth at proximity of *Posidonia oceanica* meadow in the Bay of Revellata (Corsica) on 8 occasions from March 2009 to November 2010. *nd* = no data.

Date	Total biomass (g_{dw} m^{-2})	% algae (%)	% leaves (%)	% dead material (%)
04-03-09	*nd*	*nd*	*nd*	*nd*
02-06-09	845	14.1	2.4	83.5
19-08-09	1164	33.5	7.6	58.9
11-11-09	1136	1.1	6.3	92.7
16-02-10	509	0.3	7.1	92.6
04-06-10	241	22.6	6.2	71.2
20-08-10	2559	21.5	9	69.6
05-11-10	2270	3.3	1.6	92.9

Table S4: Linear regressions and statistics at 0.05 level shown in Figures.

Figure	Variables	Y = aX + b	r^2	*p*	*n*
Fig. 3	GPP *versus* Biomass	Y = 0.1556*X + 5.785	0.75	0.0253	6
Fig. 3	CR *versus* Biomass	Y = -0.1869*X - 13.95	0.73	0.0304	6
Fig. 3	NCP *versus* log(Biomass)	Y = -18.68*X + 27.37	0.61	0.0674	6
Fig. 3	GPP:-CR *versus* log(Biomass)	Y = 0.2678*X + 0.07614	0.76	0.0241	6
Fig. 5	NCP *versus* Temperature	Y = -2.366*X + 19.31	0.85	0.0012	8
Fig. S4	HR *versus* Biomass	Y = -0.1078*X - 11.01	0.70	0.0377	6
Fig. S4	HR *versus* GPP	Y = -0.7023*X - 6.557	0.96	0.0007	6

Table S5: Compilation of decay rates (k in d^{-1}) in litter bag experiments of *Posidonia oceanica* detached dead leaves (Litter), senescent leaves sampled from living shoot (Fresh senescent), and random leaf from living shoot (Random), season (start experiment), initial weight (W_0) in g of dry (dw) or fresh (fw) weight, duration in days, carbon to nitrogen (C:N) ratio (%weight:%weight) reported in literature: (1) Costa et al. (2019) (2) Mateo and Romero (1996) (3) Romero et al. (1992) (4) Mateo and Romero (1997) (5) Apostolaki et al. (2009) (6) Pergent et al. (1997) (7) Cebrián et al. (1997) (8) Lee et al. (2022). k_{91}, k_{182}, k_{274} are the decay rates recomputed to 91, 182, and 274 days according to Mateo and Romero (1996). ? = unspecified in the publication

Location	Station	Season	W_0 (g)	Duration (d)	k (d^{-1})	k_{91} (d^{-1})	k_{182} (d^{-1})	k_{274} (d^{-1})	C:N	Material	Reference
Stagnone di Marsala (Italy)	Site 1	Summer	3 (dw)	221	0.0011	0.0021	0.0013	0.0009	37.5	Litter	(1)
Stagnone di Marsala (Italy)	Site 2	Summer	3 (dw)	221	0.0030	0.0056	0.0036	0.0023	34.7	Litter	(1)
Stagnone di Marsala (Italy)	Site 3	Summer	3 (dw)	221	0.0044	0.0082	0.0053	0.0034	33.0	Litter	(1)
Medas Islands (Spain)	5m	Winter	10 (dw)	80	0.0042	0.0040	0.0026	0.0016	35.9	Litter	(2)
Medas Islands (Spain)	13m	Winter	10 (dw)	80	0.0029	0.0027	0.0018	0.0011	35.9	Litter	(2)
Medas Islands (Spain)	5m	Summer	10 (dw)	64	0.0089	0.0078	0.0050	0.0032	35.9	Litter	(2)
Medas Islands (Spain)	13m	Summer	10 (dw)	64	0.0060	0.0052	0.0034	0.0022	35.9	Litter	(2)
Medas Islands (Spain)	5m	Fall	10 (dw)	78	0.0037	0.0035	0.0022	0.0014	35.9	Litter	(2)
Medas Islands (Spain)	13m	Fall	10 (dw)	78	0.0040	0.0037	0.0024	0.0015	35.9	Litter	(2)
Medas Islands (Spain)	5m	Summer	10 (dw)	117	0.0133	0.0150	0.0097	0.0062	35.9	Litter	(2)
Medas Islands (Spain)	13m	Summer	10 (dw)	117	0.0052	0.0059	0.0038	0.0024	35.9	Litter	(2)
Medas Islands (Spain)	5m	Winter	10 (dw)	80	0.0052	0.0049	0.0032	0.0020	29.1	Fresh senescent	(2)
Medas Islands (Spain)	13m	Winter	10 (dw)	80	0.0044	0.0042	0.0027	0.0017	29.1	Fresh senescent	(2)
Medas Islands (Spain)	5m	Summer	10 (dw)	64	0.0096	0.0084	0.0054	0.0035	29.1	Fresh senescent	(2)
Medas Islands (Spain)	13m	Summer	10 (dw)	64	0.0058	0.0051	0.0033	0.0021	29.1	Fresh senescent	(2)
Medas Islands (Spain)	5m	Fall	10 (dw)	78	0.0060	0.0056	0.0036	0.0023	29.1	Fresh senescent	(2)
Medas Islands (Spain)	13m	Fall	10 (dw)	78	0.0053	0.0050	0.0032	0.0020	29.1	Fresh senescent	(2)
Medas Islands (Spain)	5m	Summer	10 (dw)	117	0.0136	0.0154	0.0099	0.0063	29.1	Fresh senescent	(2)
Medas Islands (Spain)	13m	Summer	10 (dw)	117	0.0075	0.0085	0.0055	0.0035	29.1	Fresh senescent	(2)
Lacco Ameno (Italy)	5m	Summer	30 (fw)	30	0.0100	0.0074	0.0048	0.0031		Fresh senescent	(3)
Lacco Ameno (Italy)	20m	Summer	30 (fw)	30	0.0101	0.0075	0.0048	0.0031	29.9	Fresh senescent	(3)
Lacco Ameno (Italy)	20m	Summer	30 (fw)	182	0.0076	0.0118	0.0076	0.0049	29.9	Fresh senescent	(3)
Lacco Ameno (Italy)	5m	Fall	30 (fw)	30	0.0170	0.0126	0.0081	0.0052		Fresh senescent	(3)
Lacco Ameno (Italy)	20m	Fall	30 (fw)	30	0.0078	0.0058	0.0037	0.0024		Fresh senescent	(3)
Lacco Ameno (Italy)	5m	Fall	30 (fw)	182	0.0062	0.0096	0.0062	0.0040		Fresh senescent	(3)
Lacco Ameno (Italy)	20m	Fall	30 (fw)	182	0.0031	0.0048	0.0031	0.0020		Fresh senescent	(3)
Medas Islands (Spain)	5m	Summer & Winter	30 (fw)	85	0.0220	0.0213	0.0137	0.0088	30.2	Fresh senescent	(4)
Medas Islands (Spain)	13m	Summer & Winter	30 (fw)	85	0.0190	0.0184	0.0119	0.0076	28.6	Fresh senescent	(4)
Sounion (Greece)	Control/Cages	Summer	10 (fw)	182	0.0033	0.0051	0.0033	0.0021	47.0	Fresh senescent	(5)
Sounion (Greece)	Control/Control	Summer	10 (fw)	182	0.0061	0.0094	0.0061	0.0039	52.0	Fresh senescent	(5)
Cortiou (France)	Cortiou 10	Summer	30 (fw)	132	0.0162	0.0197	0.0127	0.0081		Fresh senescent	(6)
Riou (France)	Riou 10	Summer	30 (fw)	100	0.0126	0.0131	0.0085	0.0054		Fresh senescent	(6)
Riou (France)	Riou 10	Winter	30 (fw)	22	0.0023	0.0016	0.0011	0.0007		Fresh senescent	(6)
Riou (France)	Riou 18	Summer	30 (fw)	1498	0.0101					Fresh senescent	(6)
Riou (France)	Riou 18	Winter	30 (fw)	127	0.0036	0.0043	0.0028	0.0018		Fresh senescent	(6)
Ischia (Italy)	Ischia 10	Summer	30 (fw)	25	0.0097	0.0070	0.0045	0.0029		Fresh senescent	(6)
Ischia (Italy)	Ischia 10	Winter	30 (fw)	168	0.0062	0.0090	0.0058	0.0037		Fresh senescent	(6)
Ischia (Italy)	Ischia 20	Summer	30 (fw)	148	0.0086	0.0113	0.0073	0.0047		Fresh senescent	(6)
Ischia (Italy)	Ischia 20	Winter	30 (fw)	111	0.0033	0.0036	0.0023	0.0015		Fresh senescent	(6)
Cala Jonquet (Spain)	4m	Summer	?	150	0.0091	0.0121	0.0078	0.0050		Fresh senescent	(7)
North Castello (Italy)	Ambient pH	Summer	?	117	0.0055	0.0062	0.0040	0.0026	26.9	Random	(8)
Vullatura (Italy)	Ambient pH	Summer	?	117	0.0035	0.0040	0.0026	0.0016	26.9	Random	(8)