Journal of *Marine Science and Engineering*

MDPI

Article

Bacterial Carbon Demand and Primary Production in a *Posidonia oceanica* System: A Re-Evaluation of Carbon Fluxes

Branko Velimirov [1,2,*] and Markus Weinbauer [3]

[1] Section for Microbiology and Molecular Biology, Medical Faculty of the Sigmund Freud Private University, Freudplatz 3, 1020 Vienna, Austria
[2] Center for Pathobiochemistry and Genetics, Medical University of Vienna, Währinger Str. 10, 1090 Vienna, Austria
[3] Laboratoire d'Oceanographie de Villefranche (LOV), Sorbonne Universités, UPMC, Université Paris 06, CNRS, BP28, 06230 Villefranche, France; markus.weinbauer@imev-mer.fr
* Correspondence: branko.velimirov@med.sfu.ac.at

Abstract: An earlier ecosystemic study on carbon balance calculations of a *Posidonia oceanica* system in the Bay of Calvi [Corsica, France], indicated that the bacterial carbon demand [BCD] between May and October [Temp > 18 °C] in the seagrass meadow could not be sustained by net leaf production of *P. oceanica* and its epiphytes [NPP]. Hence, the system was clearly heterotrophic as only one autotrophic region was recorded, namely the depth range from 0–10 m. Already published data on the production of algal macrophytes and *Cymodocea nodosa* meadows and their mapping in the Bay of Calvi allowed a re-evaluation of the carbon budgets for each specific depth range. It was shown that *C. nodosa* could contribute significantly to covering the bacterial carbon demand of the *P. oceanica* system and that a positive carbon balance could be obtained for the seagrass meadow due to this carbon input when the temperature was higher than 18 °C, even though the depth ranges between 21–30 m and 31–38 m were negative. The overall trend indicates that the system cannot rely on the phytoplanktonic production of the water column, as BCD is higher than phytoplanktonic carbon production. When integrating BCD and net primary production [NPP] of the water column in summer we noticed a lack of some 97.6 to 104.3 tons of carbon which is not covered by the seagrasses leaf production and the algal macrophytes. The obtained data indicate clearly that other carbon carbon-producing compartments like the microphytobenthos, the NPP of rhizome epiphytes, and the detrital carbon import into the Bay of Calvi need to be investigated.

Keywords: bacterial carbon demand; carbon fluxes; primary production; *Posidonia oceanica* system; *Cymodocea nodosa*; macroalgae

check for updates

Academic Editor: Aurélie Blanfuné

Received: 20 December 2024
Revised: 20 January 2025
Accepted: 22 January 2025
Published: 8 February 2025

Citation: Velimirov, B.; Weinbauer, M. Bacterial Carbon Demand and Primary Production in a *Posidonia oceanica* System: A Re-Evaluation of Carbon Fluxes. *J. Mar. Sci. Eng.* **2025**, *13*, 314. https://doi.org/10.3390/jmse13020314

Copyright: © 2025 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https://creativecommons.org/licenses/by/4.0/).

1. Introduction

Heterotrophic metabolism depends on carbohydrates that are generally provided by organisms that possess an autotrophic metabolism. This is also true for aerobic respiration which depends on oxygen derived from photosynthesis. In the marine environment many ecosystems are characterized by the presence of dense populations of autotrophic organisms such as seagrass beds [1–3], yet the overall carbon balance of the system including the water column is negative, implying that an import of carbohydrates is necessary to cover the needs of the heterotrophic compartment within the system. In this case, the system is classified as heterotrophic despite the presence of the characterizing foundation seagrass [4].

In an earlier study [5] we investigated through a mass balance ecosystemic approach the sustainability of the bacterial community of a *Posidonia oceanica* (L.) Delile system of a

Corsican bay based on available data recorded between the years 1978–2016 on the main primary producers [*P. oceanica*, its epiphytes, and the adjacent macroalgae], the phytoplankton communities as well as bacterial productivity and the biomass of bacterioplankton and benthic bacteria of the oxygenated sediment layer [5]. Against expectations, our data showed that the produced benthic macrophyte leaf tissues of both *P. oceanica* shoots including epiphytes and the macroalgae adjacent to the *P. oceanica* meadow as well as the water column dynamics could not provide the carbon needed by the aerobic sediment bacteria as based on bacterial carbon production estimates. Our data from the ecosystemic approach [5] were thus in striking contrast to those obtained from benthic chambers and O_2 optode methods from earlier investigations and various sites in the Mediterranean Sea [6–9] which suggest autotrophy in *P. oceanica* systems. Unfortunately, most of these experiments were restricted to the shallow depth range from 0–10 m while depth ranges below 10 m were mostly neglected. It is worth mentioning that at the time of the presented carbon balance calculations we had no information on the production potential of the *Cymodocea nodosa* [Ucria] Ascherson seagrass meadows of the studied bay which occur in discrete meadows within and around the *P. oceanica* system [10,11]. Henceforth, considering the deviation from the paradigm of seagrass meadow autotrophy and the available data on *C. nodosa* and macroalgal production potential, it seemed necessary to re-evaluate our ecosystemic approach. The objective of the study is to inquire to which extent the *C. nodosa* production complements the NPP of *P. oceanica* and whether the system remains heterotrophic or not. This re-evaluation addresses the following issues which may help to understand the carbon flow dynamics in the *P. oceanica* systems and the obtained negative carbon balance.

Can we define depth ranges within the seagrass meadow where the carbon balance is positive and thus indicating autotrophy, especially for periods of high [>18 °C] temperatures? It should be emphasized that the high-temperature period is of major interest to the system as its overall carbon balance, in contrast to the low-temperature period, is negative [5].

Seen that the Bay of Calvi harbours also several *C. nodosa* meadows, one can raise the question of whether an import of *C. nodosa* leaf production [10,11] into the *P. oceanica* system could contribute to equilibrating the overall summer carbon budget.

The obtained data from this study combined with data from earlier studies and a thorough bias analysis of our methods are expected to lead to a higher degree of precision in detecting autotrophic situations as we treat four depth ranges separately.

Furthermore, the above investigation shall provide a first basis for the planned development of a descriptive carbon flow model for the *P. oceanica* system which may help to evaluate the ecological state of this marine habitat for conservation purposes. It is emphasized that we used mean values from the foregoing investigations where details on data acquisition are available.

Finally, the presented study should not only help to maintain and protect ecological structures but also to understand how ecosystem services from which we derive societal benefits are maintained, such as seaweed farming [11] or blue carbon in contributing to climate mitigation [12–15].

2. Materials and Methods

2.1. Study Site

The bay of Calvi on the West coast of Corsica [42°33′74″ N, 8°45′25″ E] is characterized by an extensive *P. oceanica* bed covering some 5 km^2 over a depth range from 0 m to 38.1 m. Although this coverage corresponds to only approximately one-fourth of the total bay surface [22 km^2], the *P. oceanica* meadow covers 37.2% of the total benthic surface between 0 and 40 m depth, being thus the most abundant primary producer in the bay [Figure 1].

The dominant habitat in the bay is the sandy bottom system with a surface of 6.3 km^2, the remaining surface is covered by rocks with macroalgae, *Cymodocea nodosa* meadows, coralligene, and dead matte of *P. oceanica* [16].

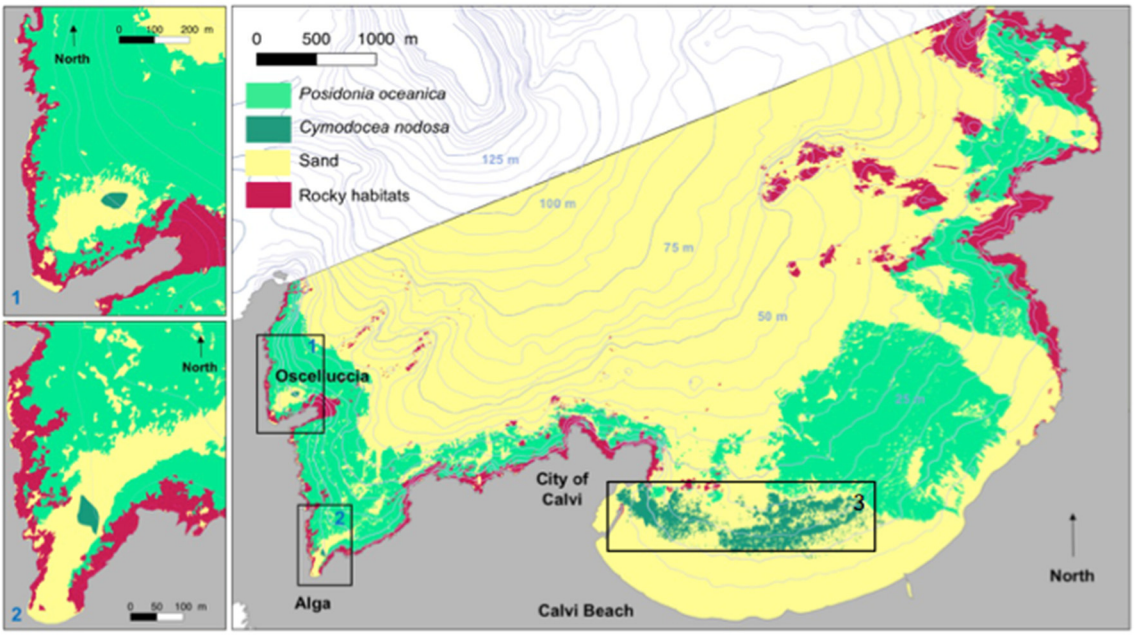


Figure 1. Locations 1, 2, and 3 of *C. nodosa* seagrass beds within and around the *P. oceanica* bed in the bay of Calvi, Corsica (France).

2.2. Data Acquisition

Detailed information on material and methods is available in Velimirov and Walenta-Simon [17,18], Velimirov et al. [5], and related. In brief,

[i] Bacterial production of sediment bacteria, using ^{3}H-thymidine and ^{14}C-leucine incorporation assays according to Kirschner and Velimirov [19] in July 1997, June 1998, June 1999 and March 2000 on triplicate samples from 10, 15, 20, 25 and 38 m depth and biomass data of sediment bacteria are from Velimirov et al. [5] while corresponding data for the water column were adopted from Velimirov and Walenta-Simon [17,18].

[ii] Production and biomass values for *P. oceanica* were obtained from Bay [20,21], Mesureur [22], and Gobert et al. [23]. and Gobert [24].

[iii] Epiphyte biomass was determined by monthly or seasonal sampling of 10 orthotropic shoots and scrapping epiphytes which were treated and weighted according to Dauby and Poulicek [25]. Epiphytic biomass production was assessed using $NaH^{14}CO_3$ incorporation in situ assays via watertight transparent Plexiglass incubators developed by Lepoint et al. [26]. Epiphyte parameters were monitored from 3 stations in 10, 20, and 30 m depth [5] and Dauby, unpubl. data]. All data on infralittoral macroalgae were derived from Jansens [27].

[iv] The bathymetry, the water column volume, and habitat surface estimation, including *C. nodosa* beds, were calculated using data derived from Abadie [11]. The final map has a resolution of 1 m.

2.3. Cymodocea nodosa Leaf Production Potential

The allocation strategy applied by Velimirov et al. [5] was also adapted for the depth range allocation of biomass [9,10] and leaf production values of *C. nodosa* which occurs in discrete meadows down to a depth of 23 m [Figure 1]. To collect data on different types of *C. nodosa* meadows at different depths, three sites were monitored in March and July

2015: Sampling site 1, Oscelluccia Bay [one station at 11 m depth], sampling site 2, Alga Bay [one station at 5 m depth], and sampling site 3, Calvi Beach [four stations at 11, 15, 20 and 23 m depths]. Shoot density was determined 10 times by station using a 0.1 m^2 quadrat. Shoots within each quadrat were collected via a non-destructive sampling technique by cutting leaves just above the meristem [10]. Collected shoots were measured according to the method proposed for *P. oceanica* by Giraud [28]. Epiphytes were scraped from leaves using a ceramic scalpel blade [25]. Leaves and epiphytes, pooled by quadrat [n = 10], were then dried at 60 °C until constant weight. Carbon and nitrogen contents were measured in ground *C. nodosa* leaves with an Elemental Analyser-Isotope Ratio Mass Spectrometry [EA-IRMS]. Net primary production of *C. nodosa* leaves was calculated as the increase of biomass variations between the different sampling periods.

2.4. Data Averaged by Depth Range and Temperature Regime

Data on biomass and production of sediment bacteria from the 15 m and 20 m depth station [5] were pooled to obtain a representative value for the 11–20 m zone, while the other data could be allocated to the remaining depth ranges.

The data for *P. oceanica* and the macroalgae were grouped into two seasonality periods characterized by temperature regimes: November to April with temperatures below 18 °C and May to October with temperatures above 18 °C and the appearance of marked thermoclines. This grouping could not be applied to the *C. nodosa* data which were derived from March and July samples and had to be allocated to the season with a temperature regime above 18 °C even though in March temperatures below 18 °C were occasionally recorded.

2.5. Bacterial Carbon Demand and Options for Balance Calculations

Bacterial carbon demand [BCD] of sediment bacteria was derived from bacterial carbon production values assuming a conservative carbon conversion efficiency of 30% [5]. The corresponding BCD values were balanced against the primary production of *P. oceanica*, its epiphytes, the macroalgae, and *C. nodosa* plus epiphytes for each depth range whereby we chose two approaches for the carbon balance calculations. As sediment surfaces represent 6.3 km^2 the largest surface cover between 0 and 38 m depth in the Bay of Calvi, a first balance calculation named hereafter option 1 including all the sediment surface between and within the *P. oceanica* system was calculated. The second balance calculation, or option 2, considered only the sediment surface within the *P. oceanica* system whereby we subtracted the surface occupied by the *P. oceanica* shoots.

3. Results and Discussion

3.1. Carbon Contribution of C. nodosa to the P. oceanica System

The peculiarity of the *C. nodosa* beds in the Bay of Calvi is that they occur in three discrete areas with one dominant meadow colonizing a depth range between 0 and 23 m depth and two smaller patches at 5 m and 11 m depth, respectively Thus leaf production estimates calculated as difference of biomass variations between sampling periods could be obtained for depth ranges [Table 1].

Even though the total surface of *C. nodosa* beds corresponds only to 10.06% of the total surface occupied by *P. oceanica*, *C. nodosa* plus epiphytes contribute 1.12 tons of $C.day^{-1}$ in the 0–10 m depth range and 1.96 tons $C.day^{-1}$ in the 11–20 m depth range indicating that the potential input of *C. nodosa* tissue into the surrounding *P. oceanica* system cannot be neglected especially for the depth ranges 0 to 10 and 11 to 20 m [Table 2].

Table 1. Shoot density, leaf and epiphyte production of *C. nodosa* from 3 depth ranges obtained via differences of leaf and epiphyte biomasses for the summer period (T > 18 °C) in the Bay of Calvi, Corsica [9,10] BM: Biomass. Numbers in parenthesis: standard deviations.

Depth Range	**0–10 m**	**11–20 m**	**21–30 m**
Surface (m^2)	**57,210**	**427,774**	**13,459**
***C. nodosa*: Leaf production parameters (summer season T > 18 °C)**			
Number of shoots per m^2 in March	346 (75)	199 (96)	0.00
Number of shoots per m^2 in July	438 (163)	183 (68)	142 (41)
Leaf BM (g C per m^2) March	0.70	0.49	0.19
Leaf BM (g C per m^2) July	16.95	3.97	3.23
Leaf BM (tons C per tot. surface) March	0.04	0.21	0.002
Leaf BM (tons C per tot. surface) July	0.96	1.70	0.04
Total leaf production (tons C per tot. surface per day)	0.93	1.48	0.04
Epiphytes: Production parameters (summer season T > 18 °C)			
BM (g C per m^2) in March	0.09	0.72	0.00
BM (g C per m^2) in July	3.44	1.82	2.25
BM (tons C per tot. surface) March	0.005	0.30	0.00
BM (tons C per tot. surface) July	0.19	0.78	0.03
Epiphyte production (g C per m^2 per .day)	0.03	0.01	0.0002
Total epiphyte production (tons C per surface per day, T > 18 °C)	0.19	0.47	0.03
Total for *C. nodosa* + epiphytes			
(tons C per tot. surface per day)	1.12	1.96	0.07

Table 2. Production rates of leaves and epiphytes of *C. nodosa* (Calculation based on data from Table 1) and *P. oceanica* plus macroalgal production in the Bay of Calvi Calculations based on data from [20–23] as well as% increase of *C. nodosa* leaf tissue in relation to *P. oceanica* and sum (=Total) of the rates for the summer period (T > 18 °C). epi: epiphytes, macroal: macroalgae, n.d. = not determined as *C. nodosa* does not occur below 30 m depth.

Depth Range (m)	**Tons C per Surface per Day *C. nodosa* + epi**	**Tons C per Surface per Day *P. oceanica* + epi + Macroal**	***C. nodosa* Biomass Increase %**	**Total**
0–10	1.12	1.81	61.0	2.93
11–20	1.96	1.04	140.0	2.99
21–30	0.07	0.35	20.0	0.42
31–38.1	n.d.	0.07	n.d.	0.07

Despite the much smaller surface extension of *C. nodosa* beds the production of this seagrass plus epiphytes for March and July represents a 61% biomass increase as compared to *P. oceanica* for the shallowest depth range but 140% for the 11–20 m depth range. Only in the 21–30 m depth range, the *C. nodosa* leaf production is far below that of *P. oceanica* corresponding to 20%. Nonetheless, it is remarkable that the sum of the NPP for *P. oceanica*

leaves, its epiphytes and the macroalgae [Table 2] within the 11–20 m depth range was much lower than the tissue production of *C. nodosa* leaves and its epiphytes by a factor of 1.88. The total above-ground production of *C. nodosa* plus epiphytes over the three depth ranges amounts to 3.15 tons C.surface^{-2}.day^{-1} when considering a production period of 153 days.

3.2. Benthic Primary Production and Bacterial Carbon Demand

C. nodosa beds are known to have their lowest above-ground biomasses between January and April and productivity that increases abruptly between May and June, with peak values in July. Thereafter, no increase in the above-ground biomass was recorded [29,30] For this reason, the obtained production values from Tables 1 and 2 were assigned to the May to October data set in order to re-evaluate the carbon fluxes for this time period where the overall carbon budget was negative. When integrating the obtained data from *C. nodosa* and its epiphytes into the carbon balance calculations we notice that in the case of option 1 the input of *C. nodosa* resulted in a new positive carbon balance for the 11–20 m depth range for May and October for both the ^{14}C-leucine and ^{3}H-thymidine approach with 1.53 and 1.2 tons of carbon per day, (Figure 2) but which was not high enough to enable a positive total system C-balance. For option 2 the *C. nodosa* contribution resulted in an increase of available carbon for the depth ranges from 0–10 m and 11–20 m, again between May and October, leading to a carbon bonus of 1.46 or 2.86 tons of carbon for the ^{14}C-leucine and ^{3}H-thymidine approach respectively. Therefore, the overall trend is a carbon balance increase for the first two depth ranges indicating autotrophy while the deeper regions of the *P. oceanica* bed remain heterotrophic despite inputs from adjacent macroalgae and *C. nodosa* beds [Figure 2]. Nonetheless, the inputs of the *C. nodosa* beds and the adjacent algal systems are high enough to balance the bacterial carbon demands in summer in the case of option 2 and lead to a total system carbon balance with an excess carbon bonus to be used in the Bay of Calvi [Figure 2].

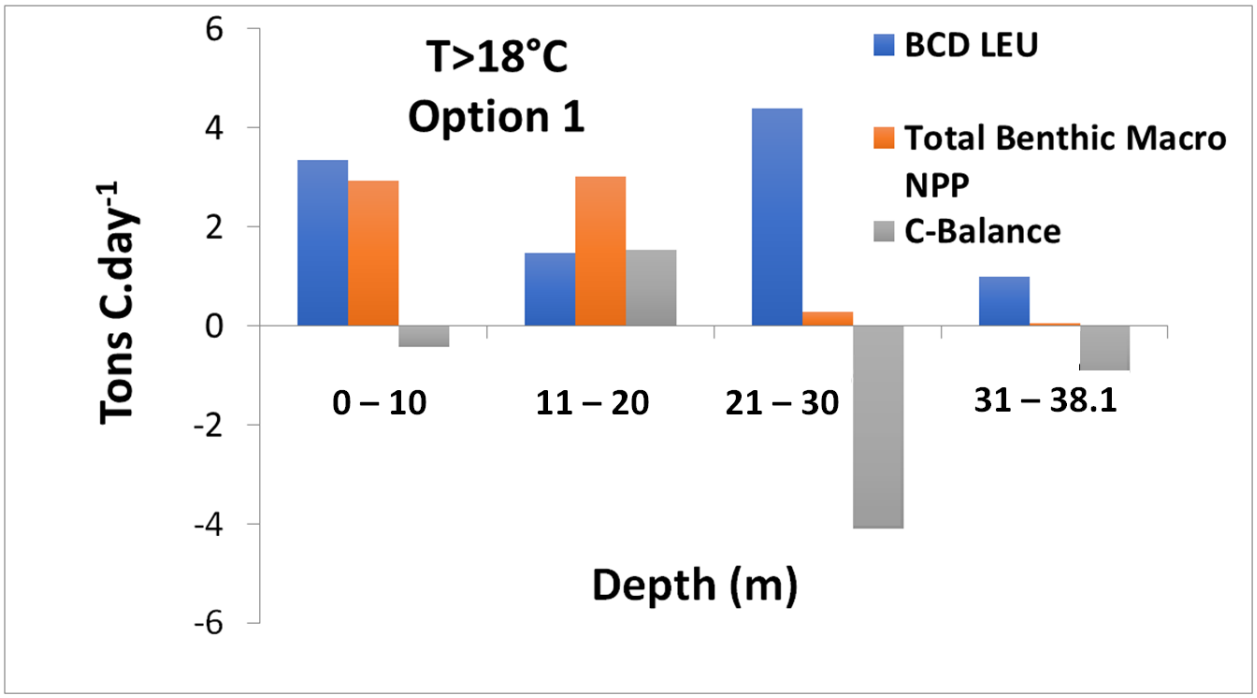
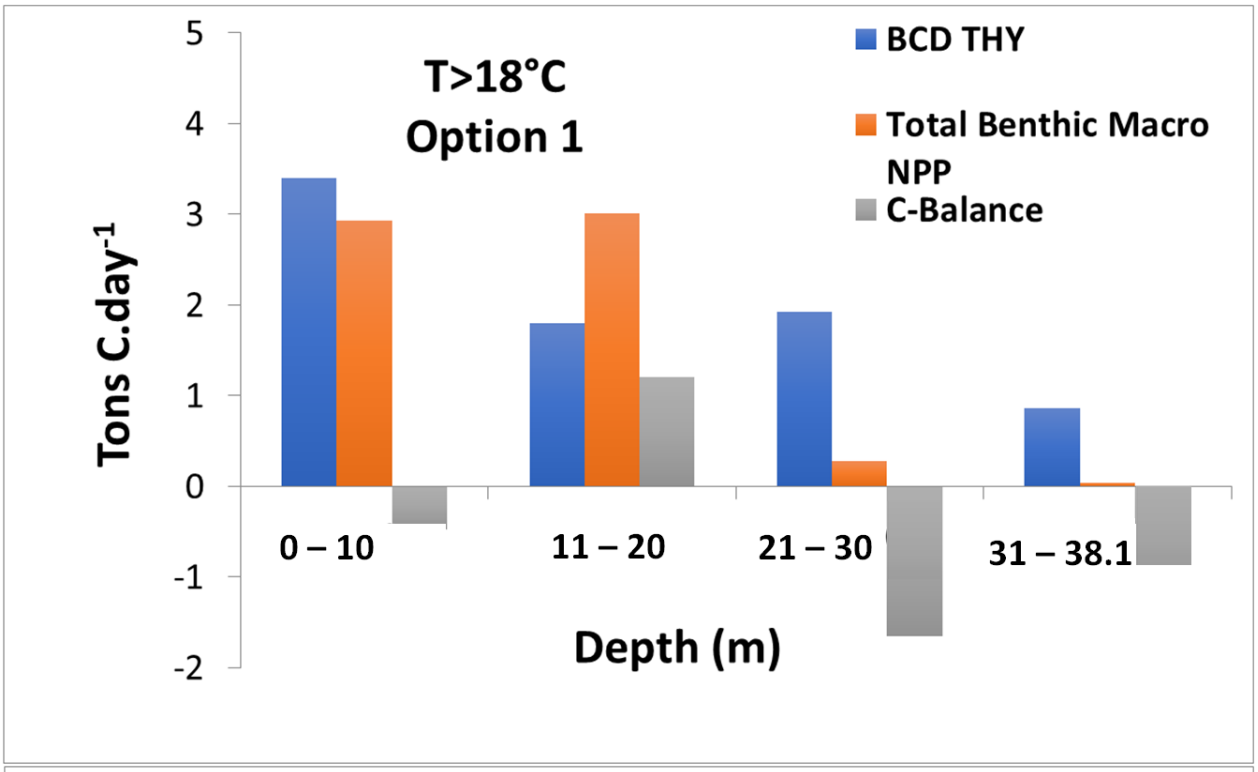


Figure 2. *Cont.*



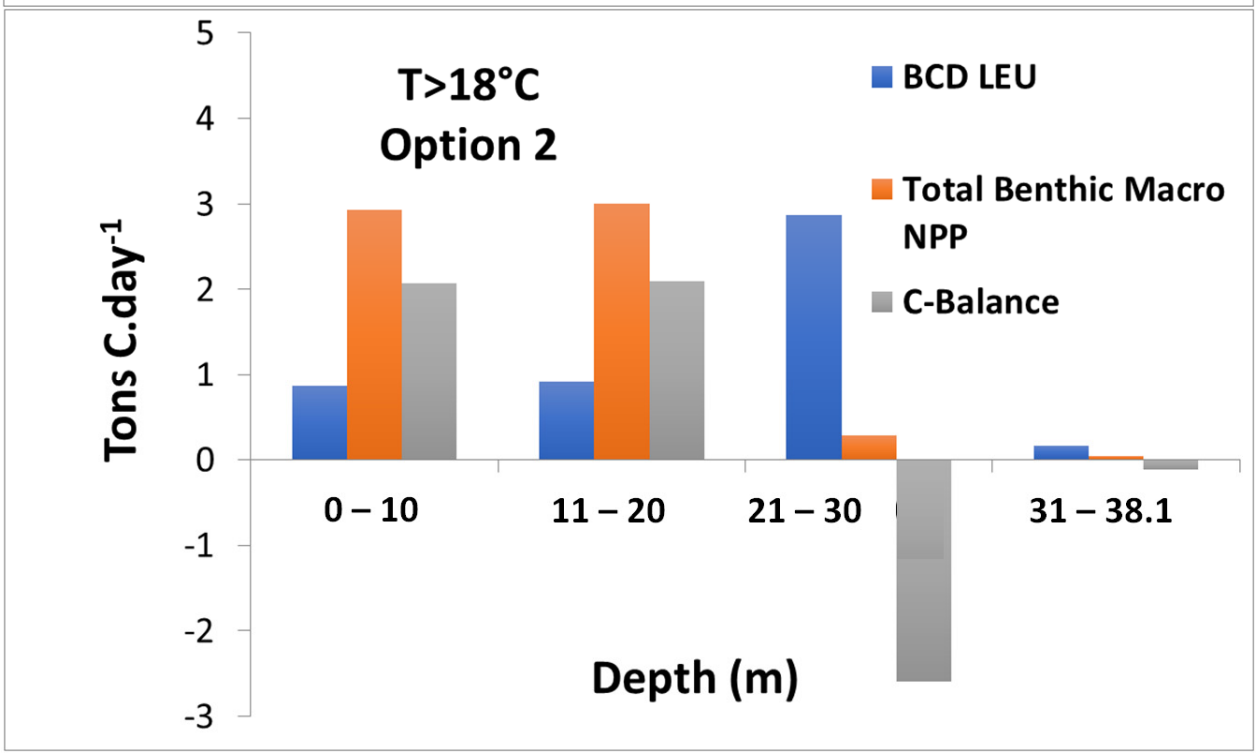


Figure 2. *Cont.*

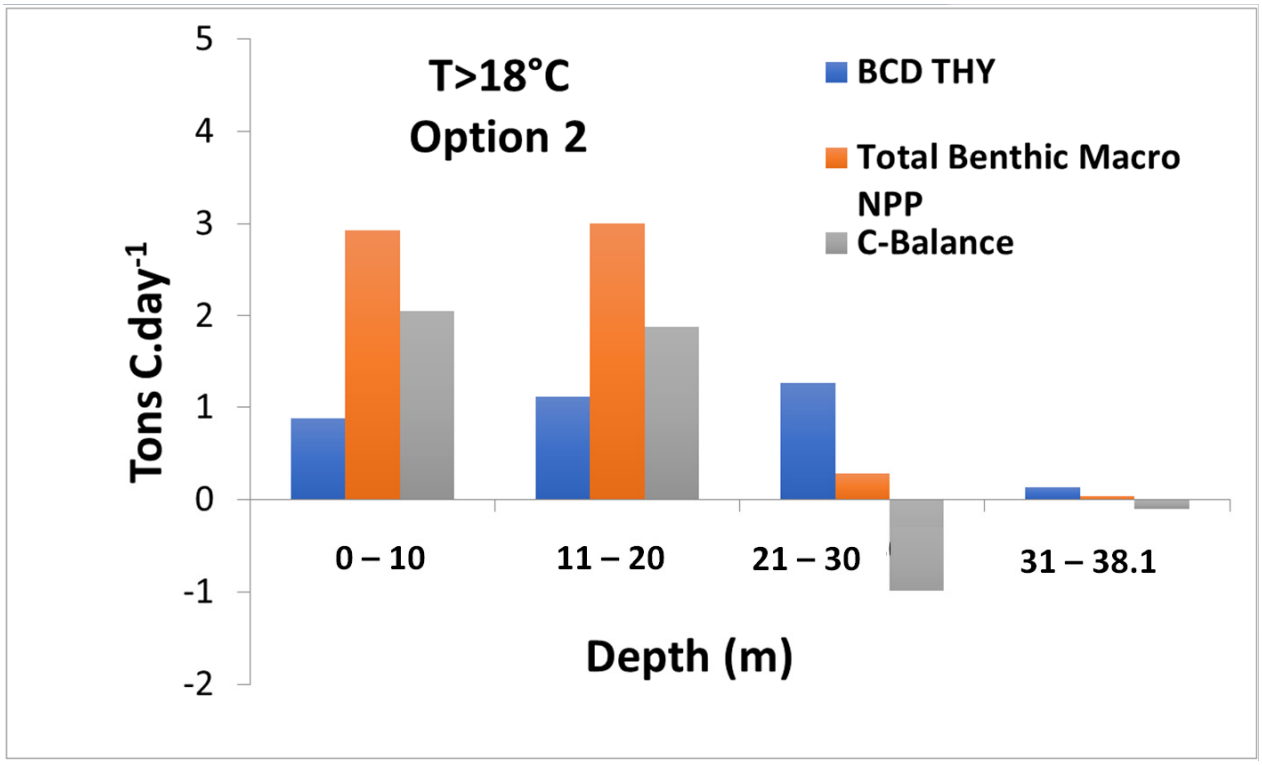


Figure 2. Carbon demand of sediment bacteria [BCD] determined by ^{14}C-Leucine [LEU] and ^{3}H-thymidine [THY] incorporation, net total primary production of *P. oceanica* plus epiphytes, macroalgae and *C. nodosa* plus epiphytes [=Total Benthic Macro NPP] and carbon balance calculations for the period with temperatures > 18 °C for options 1 and 2.

3.3. Re-Evaluation of the Carbon Balance Considering the Bacteriplanctonic Compartment

From data published in our earlier study which were averaged by depth ranges, we provide evidence that in none of the four depth ranges between 0 and 38.1 m the net primary production of *P. oceanica* leaves and their epiphytes suffices to cover the bacterial carbon demand when considering the total sediment system [i.e., option 1], irrespective of the temperature regime. In the case of option 2, when relating the production values to the bacterial carbon demand in the oxygenated sediment layer within the seagrass bed only, we noticed again that during temperature regimes above 18 °C, all four depth ranges had a negative carbon balance. In this context it should be mentioned that BCD from sediment bacteria obtained from isotope incorporation experiments, gave no significant difference for incorporation means between leucine [LEU] and thymidine [THY] assay, using the Mann-Whitney-U Test, [$p > 0.05$] [31].

The only case where we could calculate a positive balance was the depth range between 0–10 m at a temperature regime below 18 °C, indicating that leaf primary production could equate to the bacterial carbon demand of the sediment bacteria, albeit with a very small carbon bonus ranging from 0.03 to 0.34 tons of carbon [5]. It was therefore obvious that the *P. oceanica* system needs a carbon subsidy which was expected to be provided by the adjacent macroalgal community.

The impact of *C. nodosa* leaf tissue which main impact is observed in June/July has clearly strengthened the carbon budget both for specific depth ranges, namely 0–10 m and 11–20 m. Therefore, the integration of *C. nodosa* leaf production into the budget calculations leads to a positive total system carbon budget for the benthic compartment during the warmer temperature regime. Thus, it could be ascertained that the inputs of the adjacent primary producer systems are possibly major drivers permitting the recorded bacterial sediment production and the remineralization within the *P. oceanica* system. However, the

overall positive carbon budget at the >18 °C temperature regime experiences a shift in the negative direction when integrating the water columns' carbon budget [Table 3] of the pelagic compartment above the seagrass system.

Table 3. Carbon budget calculations for options 1 and 2 for April to October [>18 °C] including the water column values for the volumes above each depth range, the overall carbon balance values of the *P. oceanica* meadow for both isotope assays as shown in Figure 2 and the respective differences between the carbon budgets [i.e., meadow minus water column]. Total Phyto: Total phytoplankton. BM: Biomass, NPPphyto: Phytoplankton net primary production. Data from Velimirov and Walenta [18,19], and Velimirov et al. [5] and this study. Carbon conversion Chl a: C according to Fuhrmann et al. [32].

Depth Range	0–10 m	11–20 m	21–30 m	31–38.1 m
Water column production parameters				
Phytoplankton: summer season T > 18 °C				
Total Phyto. BM (tons C per volume)	1.15	0.75	0.46	0.09
Total NPPphyto (tons C per volume per day)	19.95	7.11	4.07	2.58
Bacteriopankton carbon demand (BCD)	63.40	35.07	−17.50	−11.55
Carbon balance water column (NPPphyto minus BCD)	−43.45	−27.96	−17.50	−11.55
Option 1: summer season T > 18 °C				
C-balance meadow (LEU) tons C per surface per surface per day	−0.42	1.53	−4.10	−0.94
C-balance meadow (THY) tons C per surface per day	−0.47	1.21	−4.10	−0.94
C-balance (meadow LEU minus water column)	−43.81	−26.42	−21.60	−12.49
C-balance (meadow THY ninus water column)	−43.92	−26.75	−19.14	−12.36
Option 2: summer season T > 18 °C				
C-balance meadow (LEU) tons C per surface per day	2.06	2.09	−2.58	−0.11
C-balance meadow (THY) tons C per surface per day	2.05	1.88	−0.98	−0.09
C-Balance (meadow LEU minus water column)	−41.39	−25.87	−20.08	−11.66
C-Balance (meadow THYminzus water column)	−41.4	−26.08	−18.48	−11.64

A lack of 102.1 to 104.3 tons of carbon for option 1 was noticed and 97.6 to 99.0 tons of carbon are missing in the case of option 2 which can not be covered by both seagrasses [*P. oceanica* and *C. nodosa*] and the algal macrophytes [Table 4].

Table 4. Total Carbon balance calculations for the whole system, i.e., *P. oceanica* meadow and the overlying water column for the summer period [>18 °C], indicating a negative carbon budget for both isotope assays and both options 1 and 2. All calculations based on data from Table 3.

Total Production Values for the Summer Period (T > 18 °C)	Option 1	Option 2
NPP *P. oceanica* and *C. nodosa* leaves + epiphytes and macroalgae minus BCD LEU and C-balance water column (=NPPphyto-BCD Bacterioplankton) Values in Tons Carbon per day	−104.3	−99.0
NPP *P. oceanica* and *C. nodosa* leaves + epiphytes and macroalgae minus BCD THY and C-balance water column (=NPPphyto-BCD Bacterioplankton). Values in Tons Carbon per day	−102.1	−97.6

3.4. Potential Carbon Sources and Bias Analysis

Among the remaining potential carbon sources to be discussed, we noticed on the one hand a total lack of information on the production potential of the microbenthic algae colonizing the sandy substrate within the seagrass meadow. In the case of option 1 where the totality of the sediment surfaces around and within the seagrass beds is considered a carbon contribution from the microphytobenthos could be expected. This applies also to the epiphytic community on the rhizome system of *P. oceanica* for which no data on primary production are so far available. On the other hand, we also noticed a lack of data on the detrital input [33,34] transported via storms and currents into the bay, rain-driven terrigenic carbon input, and the organic import from the two rivers Fiume Seccu and Fiume Figarelle. An additional point to be mentioned is the missing information concerning the importance of organic and inorganic nutrients from upwelled water masses originating from the deep water canyons adjacent to the Bay of Calvi. So far, we have no data on the amount of detrital carbon in the deep water canyons off Calvi Bay, and therefore estimation of the potential contribution from these sites via upwelled water is not possible.

Bias considerations concerning our methodological approach, however, supported the obtained trends of our findings that the *P. oceanica* system tends towards heterotrophy. (1) the oxygenated sediment layer is up to 25 cm deep while we assumed an average depth extension of only 10 cm for our calculations implying that the BCD of sediment bacteria may be underestimated. This implies that the BCD of this compartment is even higher than expected. (2) we have no estimations on the BCD of the sediment bacteria in the anoxic sediment layer, which could lead to an additional increase in the BCD. (3) grazing impact on macroalgae, *C. nodosa* and *P. oceanica* leaves was not included in the carbon balance budgets, thus implying that less carbon is available to cover the BCD (4) it is justified to assume that less detrital carbon from *P. oceanica* leaf production is available for bacterial degradation as the values for the deepest depth range are overestimations, as we had to assume that the measured leaf production rates were representative of the 31–38.1 m zone [5], (5) for the purpose of balance calculations we assumed that all the produced macroalgal and seagrass leaf detritus is available for bacterial degradation within their specific depth ranges instead of considering export out of the various depth ranges [35–37] or even out of the bay of Calvi to the adjacent canyons at a depth of over 200 m. The mentioned 5 points support the hypothesis that the overall BCD may be higher than estimated while less carbon than calculated is available, indicating that the whole *P. oceanica* system is heterotrophic and one has to expect a negative net community production [NCP < 0] and a P:R < 1 if no carbon subsidy is provided.

4. Conclusions

The above results and the bias analysis indicate that the *P. oceanica* system relies for a major part of its extension on the import of carbon detritus to cover the carbon demand of the sediment bacteria of the oxygenated sediment layer and thereby warrant nutrient regeneration. During the warmer season with temperatures above 18 °C a carbon subsidy is requested for all depth ranges of the meadow. Most of this requested carbon is assumed to be imported from the adjacent macroalgal system between 0–20 m and by the *C. nodosa* meadow as well as by the above-mentioned detrital sources, underlining the heterotrophic status of the *P. oceanica* system.

An additional carbon input could be provided by the phytoplanktonic compartment, but this input is limited to the season between November and April being negative for the season > 18 °C [Table 3]. Therefore, the overall trend of our data indicates that the *P. oceanica* system may obtain enough detrital carbon import during the winter and early spring seasons requested by the bacterial compartment. Yet, if we integrate the bacterioplanktonic

carbon demand between late spring and autumn we notice a situation where the water column would need all the excess carbon from the meadow and the adjacent macrophytes without being able to balance the bacterial carbon demand [Table 4]. The question of whether the water column above the seagrass bed, irrespective of its depth extension, should be considered as part of the seagrass ecosystem remains a matter of debate. In the present study, however, we confined ourselves to show (1) how carbon fluxes between the water column, benthic primary producers, and the respective bacterial compartments may lead to an overall carbon budget for a defined area in the bay of Calvi, (2) help to detect pitfalls in our reasoning and (3) allow to detect determining parameters for the functioning of the system which were ignored or insufficiently monitored.

A consequence of the trends obtained via carbon balance calculations is to emphasize the focus of our investigations on the above-mentioned parameters which may cause bias in the calculations, determine production rates for the microphytobenthos and epiphytes on the *P. oceanica* rhizomes, and concentrate on import/export processes of organic and inorganic nutrients in the bay of Calvi.

Author Contributions: Conceptualization: B.V., writing-original draft preparation: B.V. and M.W.; writing—review an editing: B.V. and M.W.; visualization: B.V.; supervision: B.V. and M.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was partly funded by the Territorial Collectivity of Corsica and by The French Water Agency (PACA-Corsica).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data available on request.

Acknowledgments: We thank S. Gobert, P. Lejeune, and J. Richir for their valuable comments and positive criticism as well as R. Pieraccini and A. Abadie for both comments and field work, supported by the staff of the STARESO research station in Calvi. Furthermore, B.V. appreciated the stimulating discussions with A.V. Borges on the pathways of carbon flows within seagrass beds. This study is part of the STARE-CAPMED (STAtion of Reference and rEsearch on Change of local and global Anthropogenic Pressures on Mediterranean Ecosystems Drifts) program.

Conflicts of Interest: The authors declare no conflicts of interest.

References

1. Anton, A.; Baldry, K.; Coker, D.J.; Duarte, C.M. Drivers of the low metabolic rates of seagrass meadows in the Red Sea. *Front. Mar. Sci.* **2020**, *7*, 69. [CrossRef]
2. Burkholz, C.; Duarte, C.M.; Garcias-Bonet, N. Thermal dependence of seagrass ecosystem metabolism in the Red Sea. *Mar. Ecol. Prog. Ser.* **2019**, *614*, 79–90. [CrossRef]
3. Gazeau, F.; Duarte, C.M.; Gattuso, J.-P.; Barron, C.; Navarro, N.; Ruiz, S.; Prairie, Y.T.; Calleja, M.; Delille, B.; Frankignoulle, M.; et al. Whole-system metabolism and CO_2 fluxes in a Mediterranean bay dominated by seagrass beds (Palma Bay, NW Mediteranean). *Biogeosciences* **2005**, *2*, 43–60. [CrossRef]
4. Barsanti, M.; Delbono, I.; Ferretti, O.; Peirano, A.; Bianchi, C.N.; Morri, C. Measuring change of Mediterranean coastal biodiversity: Diachronic mapping of the meadow of the seagrass *Cymodocea nodosa* (Ucria) Ascherson in the Gulf of Tigullio (Ligurian Sea, NW Mediterranean). *Hydrobiologia* **2007**, *580*, 35–41. [CrossRef]
5. Velimirov, B.; Lejeune, P.; Kirschner, A.; Jousseaume, M.; Abadie, A.; Pete, D.; Dauby, P.; Richir, J.; Gobert, S. Estimating carbon fluxes in a *Posidonia oceanica* system: Paradox of the bacterial carbon demand. *Estuar. Coast. Shelf Sci.* **2016**, *171*, 23–34. [CrossRef]
6. Ott, J. Growth and production in *Posidonia oceanica* (L.) Delile. *Mar. Ecol.* **1980**, *1*, 47–64. [CrossRef]
7. Velimirov, B. DOC-dynamics in a mediterranean seagrass system. *Mar. Ecol. Prog. Ser.* **1986**, *28*, 21–41. [CrossRef]
8. Frankignoulle, M.; Bouquegneau, J.-M. Seasonal variations of the diel carbon budget of a marine macrophytes ecosystem. *Mar. Ecol. Prog. Ser.* **1987**, *38*, 197–199. [CrossRef]

9. Champenois, W.; Borges, A.V. Seasonal and interannual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnol. Oceanogr.* **2012**, *57*, 347–361. [CrossRef]
10. Pieraccini, R. Temporal and Spatial Variation of *Cymodocea nodosa* in the Calvi Bay; First Approach. Master's Thesis, Undergraduate Program of Environmental Science, Msc University of Genova, Genova, Italy, 2015; p. 30.
11. Abadie, A.; Richir, J.; Pieraccini, R.; Velimirov, B.; Leduc, M.; Lepoint, G.; Gobert, S. Investigating the potential of *Cymodocea nodosa* (Ucria) Ascherson as a coastal carbon sink coupling marine habitats cartographies and in situ non-destructive sampling. In Proceedings of the Poster Presentation, International Seagrass Biology Workshop, Wales, UK, 16–21 October 2016.
12. Duarte, C.M.; Wu, J.; Xiao, X.; Bruhn, A.; Krause-Jaensen, D. Can seaweed farming play a role in climate change mitigation and adaptation? *Front. Mar. Sci.* **2017**, *4*, 100. [CrossRef]
13. Romero, J.; Pergent, G.; Pergent- Martini, C.; Matéo, M.A.; Regnier, C. The detritic compartment in a *Posidonia oceanica* meadow: Litter features, decomposition rates and mineral stocks. *Mar. Ecol.* **1992**, *13*, 69–83. [CrossRef]
14. Romero, J.; Perez, L.; Matéo, M.A.; Sala, E. The belowground organs of the Mediterranean seagrass *Posidonia oceanica* as a biogeochemical sink. *Aquat. Bot.* **1994**, *47*, 13–19. [CrossRef]
15. Macreadie, P.I.; Costa, M.D.P.; Atwood, T.B.; Friess, D.A.; Kelleway, J.J.; Kennedy, H.; Lovelock, C.E.; Serrano, O.; Duarte, C.M. Blue carbon as natural climate solution. *Nat. Rev. Earth Environ.* **2021**, *2*, 826–839. [CrossRef]
16. Abadie, A. Evolution des Herbiers à *Posidonia oceanica* (L.) Delile dans la Baie de Calvi (Corse, France) et Influence de L'ancrage dans la Baie de l'Alga. Master's Thesis, Aix-Marseille University, Marseille, France, 2012.
17. Velimirov, B.; Walenta-Simon, M. Seasonal changes in specific growth rates, production and biomass of a bacterial community in the water column above a mediterranean seagrass system. *Mar. Ecol. Prog. Ser.* **1992**, *80*, 237–248. [CrossRef]
18. Velimirov, B.; Walenta-Simon, M. Bacterial growth rates and productivity within a seagrass system: Seasonal variations in a *Posidonia oceanica* bed. *Mar. Ecol. Prog. Ser.* **1993**, *96*, 101–107. [CrossRef]
19. Kirschner, A.K.T.; Velimirov, B. Benthic bacterial secondary production measured via simultaneous ^{3}H-thymidine and ^{14}C-leucine incorporation, and its implication for the carbon cycle of a shallow macrophyte-dominated backwater system. *Limnol. Oceanogr.* **1999**, *44*, 1871–1881. [CrossRef]
20. Bay, D. Etude In Situ de la Production Primaire d'un Herbier de Posidonies (*Posidonia oceanica* (L.) Delile) de la baie de Calvi, Corse. Ph.D. Thesis, University in Liège, Liège, Belgium, 1978; 251p.
21. Bay, D. A field study of the growth dynamics and productivity of *Posidonia oceanica* in Calvi bay, Corsica. *Aquat. Bot.* **1984**, *20*, 43–64. [CrossRef]
22. Mesureur, B. Un Aspect Écologique de l'herbier de Posidonies dans la Baie de Calvi: Production Primaire et Secondaire de la Couverture Épiphytique. Master's Thesis, University in Liège, Liège, Belgium, 1981; 55p.
23. Gobert, S.; Belkhiria, S.; Dauby, P.; Havelange, S.; Soullard, M.; Bouquegneau, J.-M. Variations temporelles de la phénologie et de la composition biochimique de la phanérogame marine *Posidonia oceanica* en baie de Calvi. *Bull. Société R. Sci. Liège* **1995**, *64*, 263–284.
24. Gobert, S.; Kyramarios, M.; Lepoint, G.; Pergent-Martini, C.; Bouquegneau, J.M. Variations à différentes échelles spatiales de l'herbier à *Posidonia oceanica* (L.) Delile; effets sur les paramètres physico-chimiques du sédiment. *Oceanol. Acta* **2003**, *26*, 199–207. [CrossRef]
25. Dauby, P.; Poulicek, M. Methods for removing epiphytes from seagrasses: SEM observations on treated leaves. *Aquat. Bot.* **1995**, *52*, 217–228. [CrossRef]
26. Lepoint, G.; Millet, S.; Dauby, P.; Gobert, S.; Bouquegneau, J.-M. Annual nitrogen budget of the seagrass *Posidonia oceanica* as determined by in situ uptake experiments. *Mar. Ecol. Prog. Ser.* **2002**, *237*, 87–96. [CrossRef]
27. Jansens, M. Etude In Situ de la Production Primaire des Macroalgues d'une Baie Mediterraneenne et Influence dans le cycle du Carbone. Ph.D. Thesis, University in Liège, Liège, Belgium, 2001; p. 270.
28. Giraud, G. Sur une méthode de mesure et de comptage des structures foliaires de *Posidonia oceanica* (Linnaeus) Delile. *Bull. Mus. D'histoire Nat. Marseille* **1979**, *39*, 33–39.
29. Cancemi, G.; Buia, M.C.; Mazella, L. Structure and growth dynamics of *Cymodocea nodosa* meadows. *Sci. Mar.* **2002**, *66*, 365–373.
30. Rico-Raimondino, V. Contribution à l'étude des Stocks et flux d'Éléments dans les Herbiers à *Posidonia oceanica*. Ph.D. Thesis, University of the Mediterranean—Aix-Marseille II, Marseille, France, 1995; 248p.
31. Zar, J.H. *Biostatistical Analysis*; Prentice-Hall, Inc.: Englewood Cliffs, NJ, USA, 1974; 620p.
32. Fuhrmann, J.A.; Sleeter, T.D.; Carlson, C.A.; Proctor, L.M. Dominance of bacterial biomass in the Sargasso Sea and its ecological implications. *Mar. Ecol. Prog. Ser.* **1989**, *57*, 207–217. [CrossRef]
33. Mateo, M.A.; Romero, J.; Pérez, M.; Littler, M.M.; Littler, D.S. Dynamics of millenary organic deposits resulting from growth of the mediterranean seagrass *Posidonia oceanica*. *Estuar Coast Shelf Sci.* **1997**, *44*, 103–110. [CrossRef]
34. Velimirov, B. Organic matter derived from a seagrass meadow: Origin, properties and quality of particles. *Mar. Ecol.* **1987**, *20*, 43–73. [CrossRef]

35. Cebrian, J.; Duarte, C.M. Detrital stocks and dynamics of the seagrass *Posidonia oceanica* (L.) Delile in the Spanish Mediterranean. *Aquat. Bot.* **2001**, *70*, 295–309. [CrossRef]
36. Duarte, C.M.; Cebrian, I. The fate of marine autotrophic production. *Limnol. Oceanogr.* **1996**, *41*, 1758–1766. [CrossRef]
37. Duarte, C.M.; Agusti, S.; Regaudie-de-Gioux, A. The role of marine biota in the biogeochemical and geological cycles of carbon. In *The Role of Marine Biota in the Functioning of the Biosphere*; Duarte, C.M., Ed.; Fundacion BBVA: Madrid, Spain, 2011; pp. 39–54.

Disclaimer/Publisher's Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.