

Mediterranean seagrasses as carbon sinks: Methodological and regional differences

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Abstract. The increasing rates of CO₂ due to anthropogenic activities are causing important potential climate threats for the Mediterranean Sea: ocean acidification and warming. In this region, two seagrass species, *Posidonia oceanica* and *Cymodocea nodosa* can play a crucial role in climate change mitigation. Seagrasses can act as carbon sinks; buffer lowering pH values during the day and store carbon in the sediment underneath their meadows. In this study, we analysed published and unpublished data (collected for this study) on seagrass community metabolism to compare two methodologies: benthic chambers and multiparametric sensors and evaluate trends through time for these two species. Furthermore, we analysed seasonal trends of both seagrass species' metabolic rates and their variation between the Eastern and Western Mediterranean basins. Most evaluated meadows, 80.9%, were autotrophic. Calculated metabolic rates differ between methodologies, with multiparametric sensors estimating rates almost an order of magnitude higher, 143.22 ± 28.21 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for Net Community Production (NCP) compared to an average of 18.75 ± 3.80 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for measurements with benthic chambers. However, sensors are not able to differentiate between habitats and only useful to assess seagrass metabolism at a broader community level, whereas benthic chambers are capable to evaluate rates at species level and confirm that *P. oceanica* is more productive compared to *C. nodosa*. We found similar metabolic rates in the Eastern and Western Mediterranean regions for *P. oceanica* with the benthic chamber technique and higher NCP in the West based on sensor measurements.

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1 Introduction

A fifth of the global carbon sequestration in marine sediments (Duarte et al., 2004; Kennedy et al., 2010) (Duarte et al., 2004; Kennedy et al., 2010; Mcleod et al., 2011; Greiner et al., 2013) can be attributed to seagrass meadows, despite the fact that they cover only a 0.1% of the ocean surface. This "blue carbon", which is defined as organic carbon buried in sediments underneath marine vegetation, is the result of the combination of intense metabolic activity of the vegetation, high trapping capacity of allochthonous matter and an effective carbon preservation in sediments underneath meadows (Cebrian, 1999). Due to the enhanced deposition rates caused by the physical presence of the canopies in the water-column seagrass meadows capture suspended organic matter, which accumulates as organic matter in the sediment (Romero et al., 1994; Pergent et al., 1997; Mateo et al., 2006; Hendriks et al., 2008; Kennedy et al., 2010). However, also the *in situ* (Greiner et al., 2013) plant growth,

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for which productivity can be a proxy, contributes to organic matter accumulation in the sediment. Even though carbon dioxide (CO₂) uptake through metabolic activity is on much shorter timescales compared to carbon storage, seagrass productivity and growth contributes to the sequestration and storage of a considerable amount of carbon in underlying sediments (McLeod et al., 2011; Fourqurean et al., 2012). There are species specific differences in carbon (Mateo et al., 1997; Lo Iacono et al., 2008; Serrano et al., 2016) burial rates and stocks: for *Cymodocea nodosa*, the annual carbon burial from productivity at a specific site has been estimated as 4.4 g C m⁻² y⁻¹ whereas *P. oceanica* accumulated 66.4 g C m⁻² y⁻¹ at the same location (Cebrián et al., 1997). In general, seagrass communities tend to be autotrophic, although primary production varies depending on the evaluated temporal scales: daily, seasonally (Bay, 1984; Alcoverro et al., 1995; Gobert et al., 2006; Hendriks et al., 2014) and annually (Champenois et al., 2012, 2019). Furthermore, primary production and related carbon storage also depend on many other variables such (Lavery et al., 2013; Alongi et al., 2016) as structural complexity (Trevathan-Tackett et al., 2015), (Armitage et al., 2016) (Samper-Villarreal et al., 2016) (Serrano et al., 2014) size of the meadow (Ricart et al., 2017) local nutrient dynamics, hydrodynamics and water depth. A consistent methodology to estimate seagrass productivity is crucial to estimate its contribution to the global carbon sink capacity and to approximate the economic and ecological consequences of the decline of this ecosystem worldwide (Orth et al., 2006; Waycott et al., 2009). Despite their importance, little is known about the effect of increasing rates of atmospheric CO₂ on these ecosystems and predictions for the open ocean may not reflect future conditions in coastal zones (Hendriks et al., 2010; Hofmann et al., 2011; Kelly et al., 2013; Lacoue-Labarthe et al., 2016), the main habitat for seagrasses. Increasing dissolved CO₂ in the water column generates pH changes and contributes to the complex biogeochemical dynamics driving coastal ecosystems (Aufdenkampe et al., 2011), which are often also affected by human activities. Dynamics of the carbonate system in coastal regions are frequently influenced by benthic ecosystems that have the capacity to buffer physical and chemical conditions of the environment (Gutiérrez et al., 2011). By capturing CO₂ and releasing oxygen (O₂), seagrass ecosystems drive fluctuations in pH and dissolved oxygen concentrations in the adjacent water column that follow daily and seasonal patterns modulated (Duarte et al., 2013; Hendriks et al., 2014) (Duarte et al., 2013) by metabolic activity. Primary production is hence an important component in the assessment of pH variation in coastal ecosystems. Through their photosynthetic activity, pH modification of the adjacent water mass by seagrasses attenuates ocean acidification, possibly providing a temporary refuge for calcifying organisms while oxygenating the water column through O₂ production (Hendriks et al., 2014). Seagrass metabolism can be conditioned by abiotic parameters such as temperature and can be assessed through the changes in concentration of dissolved oxygen in water. Water temperature has an effect on the air-water exchange by modifying oxygen solubility and affects ecosystem metabolism (Brown et al., 2004). In addition, anthropogenic pressures such as eutrophication (Paerl, 2006) or climate change are affecting oxygen cycling (Keeling et al., 2002; Conley et al., 2009; Keeling et al., 2010) and dissolved oxygen is one of the environmental parameters that has changed more drastically in a short period of time (Diaz et al., 1995; Diaz, 2001), with potential catastrophic consequences for marine life (Vaquer-Sunyer et al., 2008). In coastal ecosystems, increased nutrient inputs contribute to higher organic production and oxygen demand with a consequently greater likelihood of hypoxia (Karim et al., 2003; Zhang et al., 2010). Measuring dissolved oxygen concentrations in seagrass meadows allows to infer metabolic parameters such as Gross Primary Production

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Deleted: (McLeod et al., 2011; Fourqurean et al., 2012). Assessing their metabolism is crucial to understand their contribution as blue carbon sinks and water oxygenators... Seagrass metabolism is conditioned by abiotic parameters such as temperature and can be assessed through the changes in concentration of dissolved oxygen in water. Water temperature has an effect on... the air-water exchange by modifying oxygen solubility and affects an impact on oxygen dynamics by affecting the... ecosystem metabolism (Brown et al., 2004). In addition, anthropogenic pressures such as eutrophication (Paerl, 2006) or climate change are affecting oxygen cycling (... [5])

500 (GPP)(Duarte et al., 2010)) for the meadow community. Metabolic community status is defined by the Net Community Production (NCP), the difference between GPP and Community Respiration (CR). When a community exports organic carbon to adjacent systems, it is considered as net autotrophic (NCP > 0), on the other hand if the community gets external organic carbon inputs to sustain its own metabolism, it is considered as net heterotrophic (NCP < 0) (Champenois et al., 2012). (Duarte et al., 2010)(Gullström et al., 2018).

505 The dominant seagrass species in the Mediterranean Sea are *Cymodocea nodosa* and *Posidonia oceanica*, inhabiting a region that has been defined as a “hotspot for climate change” (Giorgi, 2006) with warming rates of two- to four-fold higher than in other regions (Vargas-Yáñez et al., 2008; Vaquer-Sunyer et al., 2010; Burrows et al., 2011). Jordà et al. (2012) An increase in the seasonal average temperature of 2.2°C in winter and 3.4°C in summer is projected for the end of this century for the (Belkin, 2009; Richon et al., 2019)Nykjaer (2009)Western Basin Amitai et al. (2020) of the Mediterranean Sea in a scenario with

510 moderated greenhouse gasses emissions (Furthermore, extreme thermal events are expected to be more intense and frequent in the Mediterranean region (IPCC, 2021) while the basin is not subject to the (Béthoux et al., 1986; Pasqualini et al., 1998)(Bonacorsi et al., 2013)(Telesca et al., 2015)same rates of warming, with indications that the (Waycott et al., 2009)Eastern Mediterranean is (Boudouresque et al., 2009; Marbà et al., 2014; Telesca et al., 2015)warming faster than the Western Mediterranean (Telesca et al., 2015). Climate warming can impact *P. oceanica* meadows negatively, as higher

515 temperatures stress the species physiologically (Marbà et al., 2010), with shoot mortality increasing during heat waves exceeding 28°C, at the end of summer (Diaz-Almela et al., 2007). (Jordà et al., 2012)The total surface area occupied by *P. oceanica* meadows is estimated to range between 1 to 2% of the total surface area of the Mediterranean Sea, although this number is uncertain. The distribution has been estimated as 510.710 ha in the Western and 713.992 ha in the Eastern Mediterranean basin, which might be conservative due to lack of data, with much more data available in the Western basin

520 compared with the Eastern part where absence of data is common. Contrary to other European seagrasses with decreasing loss rates (the extent of *P. oceanica* meadows is decreasing considerably with between 13 as-50% areal extent lost since the 1960s. *C. nodosa* meadows have a higher thermal tolerance and are supposed to cope better with increasing temperatures (Egea et al., 2018)Olsen et al. (2012), even though high temperatures during heat waves over the coming decades might increase the annual mean temperature with 4°C and will probably exceed the limit beyond which *C. nodosa* losses can be expected in the

525 Mediterranean Sea (Olsen et al., 2012). Also, all Mediterranean water bodies are affected by anthropogenic CO₂ emissions, however more so in the Eastern basin, demonstrated by decreasing values of pH ranging with -0.14 to -0.005 pH units drops since the beginning of the industrial era to 2001, higher than elsewhere in the open ocean (Touratier et al., 2011). Therefore, ocean acidification is a climate change indicator that has been characterized as one of the most important for the Mediterranean Sea, together with temperature and UV radiation (Micheli et al., 2013). In addition to climate change, the Mediterranean Sea

530 is likely to be more impacted by human disturbances (Giorgi et al., 2008; Richon et al., 2019)(e.g., overfishing, increasing pollution (Lejeune et al., 2010)from wastewater outfalls, riverine, farmland, runoff, fish farming (Apostolaki et al., 2007; IPCC, 2013; Powley et al., 2016)and the introduction of alien species than other seas. With these multiple pressures increasing it is crucial to evaluate the functions and services provided by key coastal ecosystems such as seagrasses.

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Seagrass metabolism has classically been measured using closed benthic chambers. However, the spatial heterogeneity of these ecosystems (Gazeau et al., 2005) and their high temporal variability cannot be easily estimated with this approach (Karl et al., 2003). For this purpose, using sensors can be more suitable as dissolved oxygen concentrations can be evaluated for longer periods of time. Additionally, the aquatic eddy covariance technique can give even more precise values for productivity, although spatially limited, nevertheless so far there has only been one study including *P. oceanica* in the Mediterranean Sea (Koopmans et al., 2020). GPP values obtained with the use of benthic chambers could provide an underestimate as a result of photorespiration, while the use of multiparametric probes measuring oxygen in the canopy probably provides more realistic GPP values (Champenois et al., 2012). The use of multiparametric probes to measure O₂ also provides the opportunity to measure metabolic rates without damaging roots or rhizomes. In river and lake ecosystems, the measurement of metabolism by oxygen probes and loggers is a commonly used method (Cole et al., 2000; Coloso et al., 2008), while it is not as wide spread in coastal waters (Odum et al., 1958; Odum et al., 1962; Ziegler et al., 1998; Vaquer-Sunyer et al., 2012) due to the higher lateral transport rates of water in these systems.

The aim of this study is to evaluate the potential carbon capture of the dominant Mediterranean Sea seagrass (*Posidonia oceanica* and *Cymodocea nodosa*) communities, through their metabolic activity, comparing two methodologies (benthic chambers and multiparametric probes) and evaluate the spatial and temporal differences between Mediterranean regions. We do so by conducting field measurements amended by published data compiled from the literature.

2 Methods

2.1 Data compilation

Data for the metabolic parameters was extracted from the literature, through a literature search on SCOPUS and the Web of Science using the keywords “Posidonia”, OR “Cymodocea”, OR “Seagrass”, AND “Productivity”, OR “Metabolism” and manually screened for data on metabolism in the Mediterranean basin. This database was extended with submitted data and data from dedicated sampling campaigns in 2016 in Mallorca (Western Mediterranean) and 2017 in the Eastern basin (Crete and Cyprus, see Table 1, Fig. 1). We also compiled data from multiparametric sensors collected during different periods ranging from 2011 to 2019 (for details see Table 1). While data using the benthic chambers methodology had a higher number of literature studies, with a total of 12 publications with data for *P. oceanica* and/or *C. nodosa* meadows (for details see Table 2), and a wider temporal cover with studies carried out from 1982 to 2019. Importantly, this study adds new data on Mediterranean seagrasses metabolism in the Eastern Mediterranean Basin (Crete, Cyprus; Table 1), where little data has been published before. Data available as oxygen concentration over time was processed and analysed to obtain the metabolic parameters, when this was not available, we used the reported metabolic rates.

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2.2 Site description

Data from multiparametric probes in either *Posidonia oceanica* and/or *Cymodocea nodosa* meadows came from one site in France (Corsica, literature), eight sites in Spain (Mallorca, of which one collected for this study), three in Crete (Greece) and one in Cyprus (Republic of Cyprus) the last four all collected for this study. (see Table 1).

All were shallow sites, ranging from 2.9 metres depth (Punta Negra, Mallorca) to 15.7 metres depth (Cap Enderrocat, Mallorca). Extracted data from Corsica came from Cape Revellata, a protected area. The site in Limassol (Cyprus) is adjacent to the second largest city in Cyprus and it is considered an impacted area affected by high anthropogenic pressures related to intense tourism and the construction of extensive coastal infrastructures. Marathi and Kalami are located close to each other next (< 10 km) to the Port of Souda in Western Crete, both sampling sites have similar environmental conditions and are impacted by notably sewage discharge, agriculture and industrial/chemical pollution. Simbora et al. (2016) (Maridati, in Eastern Crete, is a pristine bay but affected by intermittent discharges of an ephemeral stream. In Mallorca, multiparametric probes were

in sites with a range of environmental impacts, encompassing sites with protection like Cap Enderrocat, which forms part of an SPA (Special Protection Area) under the Birds Directive and is a SIC (Site of Community Importance, Natura 2000), as well as Son Veri and Cala Blava, which are also protected and host 1.5% of the total *Posidonia* meadows within the Marine Protected Area of Cap Enderrocat - Cap Blanc. Even though the locations are protected, the bay of Palma is influenced by various outlets of waste water treatment plants. On the opposite site in the bay of Palma Punta Negra is considered a Natural Area of Special Interest (SPA) and a natural space protected by law by the Government of the Balearic Islands). Magaluf (Mallorca, Bay of Palma) is in front of a touristic beach but the location of the sensors was sheltered behind an island (Isla Sa Porrassa). Sant Elm (Mallorca) is located in a relatively pristine area but near a sewage plant effluent. Pollença (Mallorca) is in an enclosed bay affected by considerable organic input from the s'Albufereta wetlands, an effluent of the sewage plant, nearby harbour and urban area. The least impacted site would be Sta. Maria, a bay located on the coast of Cabrera island and the most pristine sampling area. Cabrera island is part of a Maritime and Terrestrial National Park located at the Cabrera Archipelago, and recognized internationally as special protection zones with importance for the Mediterranean and SAC (Special Areas of Conservation). The sampling sites where sensors were deployed in the Mediterranean therefore include sites with different degrees of human impact and protected areas with very low anthropogenic impact.

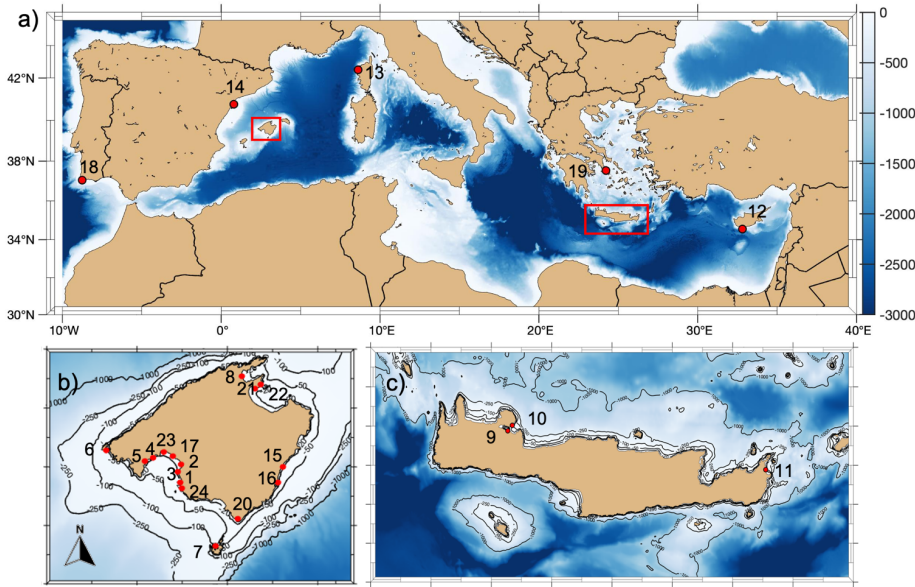
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The sampling ...ite in Cyprus was located in ...imassol (Cyprus) is adjacent to the second largest city in Cyprus and it is, East Akrotiri bay...considered an impacted area affected by high anthropogenic pressures related to intense tourism and the construction of extensive coastal infrastructures. In Crete, ...arathi and Kalami are located considered as a single sampling site due to the proximity and similarity of the environmental factors of both sampling sites. This sampling station, located in Western Crete ...lose to each other next (< 10 km) to the Port of Souda in Western Crete, both sampling sites have similar environmental conditions and are...impacted by notably sewage discharge, agriculture and industrial/chemical pollution; according to ... ADDIN EN.CITE <EndNote><Cite considered to have a moderate pressure index. ...Maridati, the second station located ...n Eastern Crete,...is situated on the East side of the Island, in ... pristine bay with no human coastal activity ...ut affected by intermittent discharges of an ephemeral stream. In Mallorca, multiparametric probes were. [9]

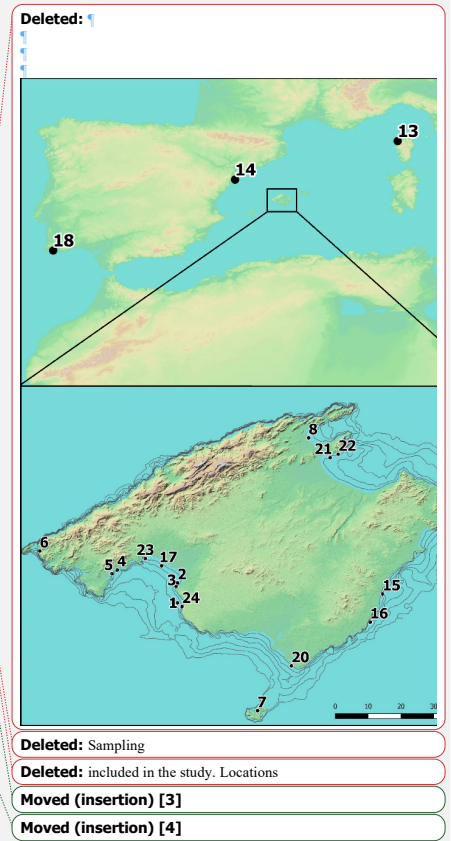
Deleted: The Mallorca sampling sites ranged from pristine to impacted, Magaluf site is in front of a very famous and touristic beach but it was protected from the "open bay" due to the sensors location behind an island (Isla Sa Porrassa). Sant Elm site is located in a relatively pristine area near a small harbour, this location includes a sewage plant emissary. Pollença is in an enclosed bay without high anthropogenic pressure but affected by considerable organic input from the s'Albufereta wetlands, the emissary of the sewage plant, the Port and the sewer of the urban area. ...ap Enderrocat, which forms together with Son Veri and Cala Blava, are part of an SPA (Special Protection Areas... under the Birds Directive and is a SIC (Site of Community Importance, Natura 2000), as well as Son Veri and Cala Blava, which are also protected and host sites) figures that grant a special protection to these areas and count with ...1.5% of the total *Posidonia* meadows of the total flora ...ithin the Marine Protected Area of ZEPA...Cap Enderrocat - Cap Blanc. Even though the locations are protected, the bay of Palma is influenced by various outlets of waste water treatment plants. On the opposite site in the bay of Palma area. ...unta Negra is considered as a Natural Area of Special Interest (SPA) and a natural space protected by law by the Government of the Balearic Islands). Magaluf (Mallorca, Bay of Palma) is in front of a touristic beach but the location of the sensors was sheltered behind an island (Isla Sa Porrassa). Sant Elm (Mallorca) is located in a relatively pristine area but near a sewage plant effluent. Pollença (Mallorca) is in an enclosed bay affected by considerable organic input from the s'Albufereta wetlands, an effluent of the sewage plant, nearby [10]



405 **Figure 1.** Location of sampling sites with numbered ID as described in Table 1 and Table 2 included in this compilation (map generated with Matlab (2012). M_Map: A mapping package for Matlab).

Table 1. Characteristics of sampling stations where multiparametric probes were deployed. Temperature and salinity represent average values during the deployment.

Region	Station	ID	Date	Species	Depth (m)	Temperature (°C)	Salinity
Mallorca	Cap Enderrocat ¹	1	25/8/2016-	<i>Posidonia oceanica</i>	14.6	26.6	40.1
			26/8/2016				
			18/8/2016-				
Mallorca	Son Veri ²	2	5/06/2012-	<i>Posidonia oceanica</i>	7.3	23.4	40.8
			11/06/2012				



			<u>5/06/2012-</u> <u>8/06/2012</u>		<u>5.4</u>	<u>23.4</u>	<u>40.8</u>			
Mallorca	Cala Blava ²	3	<u>6/06/2012-</u> <u>12/06/2012</u>	<i>Posidonia oceanica</i>	<u>5.9</u>	<u>23.8</u>	<u>38.9</u>			
			<u>5/6/2012-</u> <u>11/6/2012</u>		<u>4.4</u>	<u>23.8</u>	<u>39</u>			
Mallorca	Pta. Negra ³	4	<u>2/07/2019-</u> <u>3/07/2019</u>	<i>Cymodocea nodosa</i>	<u>2.9</u>	<u>15.4</u>	<u>36.8</u>			
			<u>11/04/2019-</u> <u>12/04/2019</u>	<i>Posidonia oceanica</i>	<u>3.3</u>	<u>15.3</u>	<u>37.1</u>			
Mallorca	Magalluf ⁵	5	<u>20/9/2011-</u> <u>23/9/2011</u>	<i>Posidonia oceanica</i>	<u>6.3</u>	<u>26.3</u>	<u>40.5</u>			
Mallorca	St. Elm ²	6	<u>13/09/2011-</u> <u>16/09/2011</u>	<i>Posidonia oceanica</i>	<u>9.4</u>	<u>26.8</u>	<u>40.3</u>			
Mallorca	Cabrera ²	7	<u>6/9/2011-</u> <u>9/9/2011</u>	<i>Posidonia oceanica</i>	<u>7.2</u>	<u>26.6</u>	<u>40.2</u>			
Mallorca	Pollença ⁴	8	<u>16/10/2018-</u> <u>17/10/2018</u>	<i>Cymodocea nodosa</i>	<u>6.4</u>	<u>23</u>	<u>38.6</u>			
			<u>16/7/2018-</u> <u>17/7/2018</u>	<i>Posidonia oceanica</i>	<u>6.1</u>	<u>24</u>	<u>39</u>			
			<u>15/1/2019-</u> <u>16/1/2019</u>	<i>Posidonia oceanica</i>	<u>7.1</u>	<u>13.2</u>	<u>36.9</u>			
			<u>15/1/2019-</u> <u>16/1/2019</u>	<i>Cymodocea nodosa</i>	<u>7.7</u>	<u>13.2</u>	<u>37</u>			
			<u>18/4/2018-</u> <u>19/4/2018</u>	<i>Cymodocea nodosa</i>	<u>6.8</u>	<u>16.1</u>	<u>37.7</u>			
			<u>18/4/2018-</u> <u>19/4/2018</u>	<i>Posidonia oceanica</i>	<u>6.5</u>	<u>16.1</u>	<u>38.4</u>			
			<u>25/06/2015-</u> <u>30/06/2015</u>	<i>Cymodocea nodosa</i>	<u>8</u>	<u>25.7</u>	<u>40.6</u>			
			<u>25/06/2015-</u> <u>1/7/2015</u>	<i>Posidonia oceanica</i>	<u>4.5</u>	<u>25.8</u>	<u>40.9</u>			
			Crete	Marathi ¹	9	<u>18/7/2017-</u> <u>20/7/2017</u>	<i>Posidonia oceanica</i>	<u>4.7</u>	<u>26.3</u>	<u>40.5</u>
						<u>18/7/2017-</u> <u>20/7/2017</u>	<i>Cymodocea nodosa</i>	<u>5.4</u>	<u>27</u>	<u>40</u>

			<u>21/7/2017-</u> <u>23/7/2017</u>	<u><i>Cymodocea nodosa</i></u>	<u>6.2</u>	<u>25.2</u>	<u>40.5</u>
	Maridati ¹	11	<u>21/7/2017-</u> <u>23/7/2017</u>	<u><i>Posidonia oceanica</i></u>	<u>8.9</u>	<u>25.1</u>	<u>40.7</u>
Cyprus	Limassol ¹	12	<u>4/09/2017-</u> <u>7/09/2017</u>	<u><i>Cymodocea nodosa</i></u>	<u>3.2</u>	<u>27.3</u>	<u>40.2</u>
Corsica	Revelatta ⁵	13	<u>2006-2016</u>	<u><i>Posidonia oceanica</i></u>	<u>NA</u>	<u>18.7</u>	<u>NA</u>
Corsica	Revelatta ⁶	13	<u>2006-2009</u>	<u><i>Posidonia oceanica</i></u>	<u>NA</u>	<u>18.6</u>	<u>NA</u>

Source: 1. Unpublished data., 2., 3. Marx et al., 2021, 4. Hendriks et al., submitted. 5, 6.

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420 **Table 2.** Characteristics of sampling stations with data for benthic chamber deployments.

<u>Region</u>	<u>Station</u>	<u>ID</u>	<u>Season</u>	<u>Year</u>	<u>Species</u>	<u>Depth</u> <u>(m)</u>	<u>Temperature</u> <u>(°C)</u>	<u>Salinity</u>
Corsica	Bay of Calvi ¹	13	Annual	<u>1982-</u> <u>1984</u>	<u><i>Posidonia oceanica</i></u>			
Spain	Ebro Delta ²	14	Summer	<u>2000</u>	<u><i>Cymodocea nodosa</i></u>			
Mallorca	Magalluf ⁵	<u>5</u>	Annual	<u>2001</u>	<u><i>Posidonia oceanica</i></u>			
Mallorca	Magalluf ⁴	5	Summer/Spring	<u>2001</u>	<u><i>Posidonia oceanica</i></u>		<u>27.5</u>	
Mallorca	Cabrera ⁵	7	Summer	<u>2000</u>	<u><i>Cymodocea nodosa</i></u>		<u>18</u>	<u>38</u>
Mallorca	Sa Paret ⁵	15	Summer	<u>2000</u>	<u><i>Posidonia oceanica</i></u>		<u>18</u>	<u>38</u>
Mallorca	Porto Colom ⁵	16	Summer	<u>2000</u>	<u><i>Posidonia oceanica</i></u>		<u>18</u>	<u>38</u>
Mallorca	Sta Maria ⁵	7	Summer	<u>2000</u>	<u><i>Posidonia oceanica</i></u>		<u>18</u>	<u>38</u>
Mallorca	Magalluf ⁵	<u>5</u>	Annual	<u>2002</u>	<u><i>Posidonia oceanica</i></u>			
Mallorca	Magalluf ⁵	<u>5</u>	Annual	<u>2002</u>	<u><i>Posidonia oceanica</i></u>			
Mallorca	Cap Encerroc ⁶	1	Annual	<u>2002</u>	<u><i>Posidonia oceanica</i></u>			
Mallorca	Bay of Palma ⁶	17	Annual	<u>2002</u>	<u><i>Posidonia oceanica</i></u>			
Portugal	Ria Formosa ⁷	18	Summer	<u>2002</u>	<u><i>Cymodocea nodosa</i></u>			
Greece	Sounion ⁸	19	Annual	<u>2006</u>	<u><i>Posidonia oceanica</i></u>			
Mallorca	Es Cargol ⁹	20	Annual	<u>2006</u>	<u><i>Posidonia oceanica</i></u>			
Greece	Sounion ⁸	19	Winter/Spring	<u>2007</u>	<u><i>Posidonia oceanica</i></u>			
Corsica	Revellata ¹⁰	13	Summer/Winter	<u>2007-</u> <u>2009</u>	<u><i>Posidonia oceanica</i></u>			
Corsica	Revellata ¹¹	13	Fall	<u>2012</u>	<u><i>Posidonia oceanica</i></u>			
Mallorca	Alcanada ¹²	21	Fall	<u>2012</u>	<u><i>Posidonia oceanica</i></u>		<u>18</u>	<u>36.6</u>

Mallorca	Alcanada ¹²	21	Winter	2012	<i>Posidonia oceanica</i>		13	35.94
Mallorca	Albufera ¹²	22	Summer	2012	<i>Posidonia oceanica</i>		25.5	38.27
Mallorca	Calanova ¹²	23	Summer	2012	<i>Posidonia oceanica</i>		23.5	38.14
Mallorca	Alcanada ¹²	21	Summer	2012	<i>Posidonia oceanica</i>		25.25	38.23
Mallorca	Arenal ¹²	24	Summer	2013	<i>Posidonia oceanica</i>		24.25	38.08
Mallorca	Alcanada ¹²	21	Spring	2013	<i>Posidonia oceanica</i>		18.8	37.7
Mallorca	Arenal ¹²	24	Summer	2013	<i>Posidonia oceanica</i>		27.6	37.7
Mallorca	Calanova ¹²	23	Summer	2013	<i>Posidonia oceanica</i>		28.3	37.6
Mallorca	Albufera ¹²	22	Summer	2013	<i>Posidonia oceanica</i>		23.8	38
Mallorca	Alcanada ¹²	21	Summer	2013	<i>Posidonia oceanica</i>		23.5	38
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Posidonia oceanica</i>	2.79	26.06	37.79
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Cymodocea nodosa</i>	5.66	15.85	37.01
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Cymodocea nodosa</i>	3.40	15.33	37.42
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Cymodocea nodosa</i>	3.40	15.85	37.02
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Cymodocea nodosa</i>	2.84	26.19	37.75
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Cymodocea nodosa</i>	2.79	26.06	37.79
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Cymodocea nodosa</i>	2.79	26.06	37.79
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Cymodocea nodosa</i>	2.84	26.19	37.75
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Posidonia oceanica</i>	3.40	15.33	37.42
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Cymodocea nodosa</i>	3.40	15.33	37.42
Mallorca	Pt. Negra ¹³	4	Fall	2019	<i>Posidonia oceanica</i>			
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Posidonia oceanica</i>	2.84	26.19	37.75
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Posidonia oceanica</i>	2.84	26.19	37.75
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Posidonia oceanica</i>	3.40	15.85	37.02
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Posidonia oceanica</i>	3.40	15.85	37.02
Mallorca	Pt. Negra ¹³	4	Summer	2019	<i>Posidonia oceanica</i>	2.79	26.06	37.79
Mallorca	Pt. Negra ¹³	4	Spring	2019	<i>Posidonia oceanica</i>	3.40	15.33	37.42
Mallorca	Pt. Negra ¹³	4	Fall	2019	<i>Cymodocea nodosa</i>			

Source: 1. Frankignoulle et al., 1987, 2. Barrón et al., 2004, 3. Barrón et al., 2009, 4. Barrón et al., 2006, 5. Holmer et al., 2004, 6. Gazeau et al., 2005, 7. Santos et al., 2004, 8. Apostolaki et al., 2010, 9. Gacia et al., 2012, 10. Champenois et al., 2012, 11. Olivé et al., 2016, 12. Agawin et al., 2017, 13. Marx et al., 2021.

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425 2.3 Data analysis

Reported values from the literature were used for benthic chambers, in these articles Net Community Production (NCP) was generally estimated from changes in dissolved oxygen using the Winkler titration spectrophotometric method (Labasque et al., 2004). Benthic chambers enclose a section of the seagrass meadow, and flexible fitted plastic bags, not permeable for gases,

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assure the possibility of movement of the shoots inside, see details in the method section of each paper for the exact construction used. NCP, GPP and CR data were extracted from literature as well as accompanying biotic parameters. The benthic chamber methodology has been more generally used to assess metabolism of seagrass meadows and the database of this study contains a total of 100 NCP estimations. We compare the data obtained between both methodologies, however for the paper reporting sensor data, we have calculated metabolism from raw oxygen profiles obtained with the multiparametric sensors where possible (including for published and new data described in 2.1), and only used directly reported productivity values for the data obtained from Champenois et al., 2012 and 2019.

2.3.1 Metabolic rate calculations from multiparametric probes

Where available, we used time series of dissolved oxygen (DO, in mg/L), pH_{NBS} , salinity and temperature ($^{\circ}C$), measured in *P. oceanica* and/or *C. nodosa* meadows with multiparametric sensors (OTT Hydrolab DSX5 and HL4). pH accuracy for both sensors is ± 0.2 , while the accuracy for dissolved oxygen is ± 0.2 mg/L. The duration of the data collection was different depending on the site, from 1 full day to 4 consecutive days (see Table 1), while 24-h periods were used for calculations.

Sensors were deployed 0.2 m above the seafloor in seagrass meadows. Data was recorded every 15 minutes except in Cap Enderrocat where readings were taken every 10 minutes (Table 1). Biological metadata detailing habitat traits, was obtained following the methodology described by

Sensors were calibrated before each deployment with a two-point pH calibration, with 7.00 and 10.00 NIST traceable pH buffers (Hendriks et al., 2014). Oxygen sensors (Hach LDO™) were calibrated using the water saturated air method calibration. For validation of salinity, specific conductance calibrations were performed with 50.000uS/cm buffers. For depth measurements, pressure readings were corrected for specific conductance.

Meteorological data for the deployment was obtained from the Agencia Estatal de Meteorología (AEMET) for the stations in Mallorca, from the Cyprus Department of Meteorology for Cyprus sampling sites and from the Hellenic National Meteorological Service for the locations in Crete (see Table A1 in the Appendix).

With input parameters dissolved oxygen (DO), temperature ($^{\circ}C$) and salinity we calculated the metabolic rates of the seagrass habitats using a modification of the model of, implemented in MATLAB (version 7.5, the Mathworks Inc.) explained in detail in. For each station, we manually introduced the Mixed Layer Depth (MLD), the latitude, and year, day and time as day fraction. For wind speed (m/s) we used the *k660* calculations based on. Net community production (NCP) was calculated as Gross Primary Production (GPP) - Community Respiration (CR), taking into account diffusive exchange with the atmosphere (D) following Eq. (1):

$$DO = NCP + D + A. \quad (1)$$

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The diffusion with the atmosphere is regulated by the difference in DO concentration linked to atmospheric equilibrium (DO sat) and the air-sea gas velocity transfer for oxygen (k) at a given temperature according to Eq. (2).

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$$D = k (DO_{sat} - DO), \quad (2)$$

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where D can be positive (DO addition to the system) or negative (DO removal from the system). Wind speed was estimated at each station for 15 minutes intervals (10 minutes for the Cap Enderrocat station) to predict k_{660} (air-sea gas transfer velocity for O_2 at 20° C and salinity 35) based on and Schmidt number equations for seawater according to Wanninkhof (1992) were used for the k calculation from k_{660} . As the cubic model equals the model proposed by for short-term winds this parameterization by is used.

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The model assumes that the only metabolic activity during the night is respiration (Community Respiration; CR) as in the absence of sunlight there is no photosynthetic production. CR can be extracted from the change in O_2 concentration during the night (Net Community Production at night = CR), from 1 h past sunset to 1 h before sunrise. During the day light period Net

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Community Production (NCP) is considered to be the result of the balance between Gross Primary Production (GPP) and CR. NCP was calculated using the rate of change of DO within the interval of 24 hours, while CR is calculated from night values and converted to hourly rates. As is general, we assumed that CR rates during the light period equal those at night and use the equivalent hourly values of CR for the light period to estimate GPP, adding the oxygen consumption (CR) for this period to NCP to get GPP. GPP and CR could be underestimated since it is likely that CR during daytime exceeds CR at night (Grande et al., 1989; Pace et al., 2005; Pringault et al., 2007) but this underestimation would not affect NCP values (Cole et al., 2000). Individual estimates of CR, NCP and GPP within the measured intervals obtained from the multiparametric probes were calculated over a 24h period for each day and station. As we did not dispose of vertical profiles of Conductivity, Temperature and Depth (CTD) for each station to calculate the Mixed Layer Depth, we used the model of to calculate the MLD following Eq. (3):

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$$S = \frac{\rho C_p U_2}{g \alpha H Q}, \quad (3)$$

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where S represents the non-dimensional parameter of the ratio of the input of kinetic energy by the wind to the input of potential energy by solar radiation. ρ is the density, calculated from the salinity, temperature and pressure collected by the *in situ* multiparametric sensor following the formula of. C_p represents the specific heat, considered here to be 3850 J kg⁻¹ °C⁻¹ as the relative value for seawater. U_2 refers to the diurnally averaged wind speed specified here to be measured 2 m above the water body. In our case, the wind data was measured at 10 m above the upstream edge of the water body and was converted, according to the wind profile power law. Eq. (4):

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515 $\frac{\vartheta}{\vartheta r} = \left(\frac{z}{zr}\right)^\alpha$ (4)

Moved down [20]: $\frac{\vartheta}{\vartheta r} = \left(\frac{z}{zr}\right)^\alpha$.

520 with ϑ as the wind speed (in meters per second) at a determined height z (metres) and ϑr the speed that is known at a reference height (zr). The exponential α is a coefficient derived empirically which varies upon the stability of the atmosphere. In our case, neutral stability is assumed and within those conditions α is approximately 0.143, g (Eq. (3)), corresponding to the gravitational acceleration (9.8 m. s^{-1}). α (Eq. (3)) represents the thermal expansion coefficient which was calculated as a function of the absolute salinity, *in situ* temperature and pressure. This function is included in the Gibbs-SeaWater (GSW) Oceanographic Toolbox (McDougall et al., 2011), and evaluates the thermal expansion coefficient α' in respect with the *in situ* temperature (t), from equation (2.18.1) of the TEOS-10 Manual (IOC, 2015) following Eq. (5):

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525 $\alpha' = \left(\frac{1}{v} \frac{\partial v}{\partial T}\right) S_A, p = \frac{\vartheta r p}{g p}$ (5)

Moved down [22]: $\alpha' = \alpha'(S_A, t, p) = -\frac{1}{v} \frac{\partial \rho}{\partial T} |_{S_A, p} = \frac{1}{v} \frac{\partial v}{\partial T} |_{S_A, p} = \frac{\vartheta r p}{g p}$

This function uses the full TEOS-10 Gibbs function $g(S_A, t, p)$ of as the sum of the and Gibbs functions.

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Finally, H , Eq. (3) equals the average water depth (in m) and Q Eq. (3) the diurnally averaged shortwave radiative heat flux (Wm^{-2}). Then, the surface mixed layer (z_s) was approximated following Eq.(6) by :

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530 $z_s = ((2.9 - 0.20 \ln S) \pm 0.04)$, the interval from 9:00 to 16:00 hours into account for the wind data. This interval resulted to be the more accurate (highest R^2 obtained for that interval, $R^2=0.9$) for the wind data, based on the linear regressions between zH/S obtained with the different wind and radiation intervals.

Moved down [26]: $z_s = ((2.9 - 0.20 \ln S) \pm 0.04)$. (6)

To be as accurate as possible, we tried different intervals for the wind and radiation data. Taking in account that stratification starts to develop between 09:00 and 10:00 hours and reaches its maximum around 16:00 hours (Condie et al., 2001), we decided to take

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535 2.3.2 Statistical analysis

We used mixed linear models with package lme4 in the R environment (R core team, 2021) to evaluate differences between methods, regions and species. To reflect the variability between study approaches and sampling procedures and therefore variability in the precision of outcome of each study, we used a linear model where publication was included as random effect unless specified differently. We also analysed abiotic (wind, pH, depth) parameters related to sensor data as there was more additional data associated to these measurements. As the data was not normally distributed according to the Shapiro-Wilk test, we log transformed data for GPP, and CR before analysis. NCP could not be log transformed due to negative values.

Moved up [3]: [†] Table 1.

Deleted: Characteristics of sampling stations for multiparametric probes. Temperature and salinity are average values during the deployment.[†]

Region ... [11]

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(Hendriks et al., 2014)(Champenois et al., 2019)(Champenois et al., 2012)(Coloso et al. (2008)(Vaquer-Sunyer et al. (2012)(Kihm et al. (2010) $DO = NCP + D + A, D = k (DO_{sat} - DO)$, Kihm et al. (2010)(Cole et al. (1998)(Kihm et al. (2010)(Wanninkhof et al. (1999)(Kihm et al. (2010)(Cole et al., 2000; Hanson et al., 2003; Lauster et al., 2006)(Condie et al.

565 (2001) $S = \frac{\rho C_p U_2}{g \alpha H Q}$, Fofonoff et al. (1983). C_p represents the specific heat, considered here to be $3850 \text{ J kg}^{-1} \text{ }^\circ\text{C}^{-1}$ as the relative value for seawater. U_2 refers to the diurnally averaged wind speed specified here to be measured 2 m above the water body (Simpson et al., 1974; Holloway, 1980). In our case, the wind data was measured at 10 m above the upstream edge of the water body. So, to convert it, we used the wind profile power law. $\frac{\theta}{z} = \left(\frac{z}{z_s}\right)^\alpha$

$$\alpha^t = \alpha^t (S_A, t, p) = -\frac{1}{v} \frac{\partial \rho}{\partial T} \left[S_A, p = \frac{1}{v} \frac{\partial v}{\partial T} \right] S_A, p = \frac{g T v}{g p} \text{ (IOC, 2015)(IAPWS, 2008)(IAPWS, 2009)Condie et al. (2001)} z_s =$$

570 $((2.9 - 0.20 \ln S) \pm 0.04)$. (6)

To be as accurate as possible, we tried different intervals for the wind and radiation data. Taking in account that stratification starts to develop between 09:00 and 10:00 hours and reaches its maximum around 16:00 hours (Condie et al., 2001), we decided to take (Frankignoulle et al., 1987)(Barrón et al., 2004)(Barrón et al., 2009)(Barrón et al., 2006)(Holmer et al., 2004)(Gazeau et al., 2005)(Santos et al., 2004)(Apostolaki et al., 2010)(Gacia et al., 2012)(Champenois et al., 2012)(Olivé et al., 2016)(Agawin et al., 2017) **3 Results**

575 (Apostolaki et al., 2010) We compiled 133 CR, 141 GPP and 168 NCP estimates, most of them (86.4 %) restricted to seagrass meadows located in the Western Mediterranean. The studied meadows were situated at water depths between 0.5 and 22 m (Table 1, 2) where water salinity ranged from 35.94 to 40.98 (Table 1, 2). The majority (50.0 %) of the metabolic rates were assessed in summer, 19.9% of data was sampled in spring, 10.6% in fall and 7.2% in winter, with seawater temperatures during the measurements varying between 13 °C and 28.5 °C (average $23.2^\circ\text{C} \pm 4.4 \text{ SD}$) between locations (Table 1, 2). Estimates of seagrass metabolic rates in Mediterranean seagrass meadows span from 1982 to 2019 (Table 1, 2), but most measurements were conducted after the year 2007 for benthic chambers and even later, after 2015 for sensors. Benthic chamber deployments were concentrated in the Western basin (72 metabolic measurements) with only 6 measurements in the Eastern basin. While 55 metabolic measurements were made in the Western basin with multiparametric sensors, compared to 14 in the Eastern basin.

585 Table 1. Summary of metabolic rates ($\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$), for the different methodologies, per region, season, and when possible per species.

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	NCP	SE	CR	SE	GPP	SE	P/R	SE
benthic chambers	18.75	3.80	41.18	4.55	55.31	6.39	1.57	0.12
<i>Cymodocea nodosa</i>	-9.18	5.29	30.64	7.48	22.01	5.21	1.49	0.34
WEST	-9.18	5.29	30.64	7.48	22.01	5.21	1.49	0.34
Fall	-1.40	0.00	3.50	0.00	2.00	0.00	0.57	0.00
Spring	-0.44	1.01	6.86	3.42	6.43	2.62	1.05	0.19
Summer	-12.23	7.05	39.37	9.06	27.90	6.35	1.68	0.46
<i>Posidonia oceanica</i>	25.47	4.21	45.45	5.55	68.77	7.94	1.60	0.10
EAST	39.36	5.61	52.60	11.73	93.20	17.67	1.86	0.14
Fall	27.04		47.92		74.96		1.56	
Spring	46.03		42.94		88.97		2.07	
Summer	48.64	15.22	82.38	24.27	134.74	43.20	1.62	0.05
Winter	32.92	3.85	29.99	4.44	62.91	0.59	2.14	0.30
WEST	24.33	4.51	44.40	6.15	65.19	8.66	1.56	0.11
Annual	20.55		95.55		115.75		1.21	
Fall	16.47	8.78	57.96	18.26	79.64	24.01	1.44	0.32
Spring	27.82	7.68	31.92	9.31	53.80	18.17	1.68	0.16
Summer	19.88	4.62	45.40	9.75	68.51	13.58	1.61	0.20
Winter	48.79	29.72	31.35	9.29	40.52	9.49	1.39	0.17
sensors	143.22	28.21	229.91	25.57	329.21	29.91	2.11	0.26
EAST	-236.12	19.83	429.01	69.27	192.90	61.66	0.41	0.08
Summer	-236.12	19.83	429.01	69.27	192.90	61.66	0.41	0.08
WEST	182.12	23.20	207.78	24.98	341.60	31.61	2.31	0.27
Fall	133.62	47.09	151.13	30.72	185.86	36.18	1.59	
Spring	-62.19	47.08	444.88	76.32	382.68	41.28	0.89	0.46
Summer	228.98	25.05	187.77	26.82	408.11	52.01	2.68	0.08
Winter	182.52	30.52	125.40	23.30	325.75	26.41	2.65	0.35

The amount of CR estimates assessed with multiparametric probes (66) and benthic chambers (67) was similar whereas GPP was more often estimated using multiparametric sensors (74) compared to benthic chambers (67). For net community productivity (NCP) benthic chambers (99) were preferred over sensors (69 measurements). However, we found negative respiration rates (oxygen production) at night for many sensor deployments, an indication for the influence of lateral advection and passing of different water masses. Therefore, we trimmed the dataset to contain only measurements where this influence was not detected (see number of measurements in each Figure). Since benthic chambers and multiparametric sensors yielded such different CR with 41.2 ± 4.55 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for benthic chambers and 229.9 ± 25.57 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for sensors ($t_{df=84.86}=-9.57, p<0.0001$), with almost an order of magnitude difference for NCP as well (18.8 ± 3.80 and 143.2 ± 28.21 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for benthic chambers and sensors respectively; $t_{df=25.61}=2.78, p<0.001$) and GPP (55.3 ± 6.39 and 329.2 ± 29.91 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for chambers and sensors; $t_{df=101.05}=11.14, p<0.0001$) in a mixed model, with as only factor methodology and as random effect study (Fig. 2) we decided to analyse the metabolic rates estimated using benthic chambers and multiparametric sensors separately.

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3.3.1 Data analysis⁴

First, we compared results for GPP, CR and NCP between the two studied methodologies: benthic chambers and sensors. We found significant differences for NCP and GPP ($p<0.001$). (Fig. 2). We therefore analysed data from benthic chambers and from multiparametric probes separately.

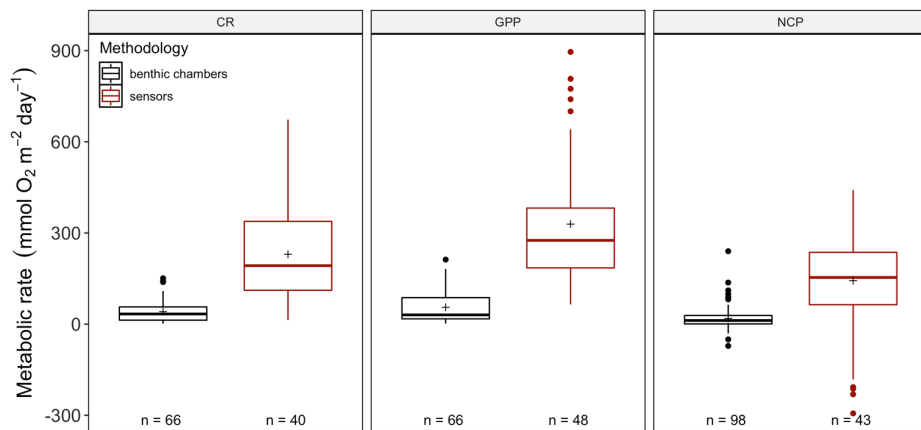
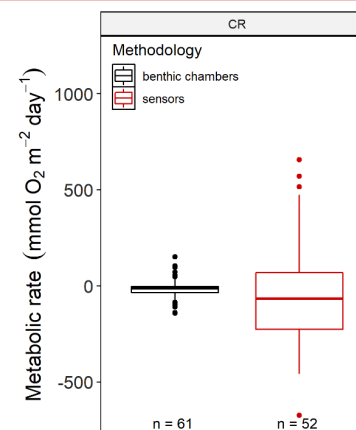


Figure 2. Comparison between benthic chamber (black) and sensor data (red) for CR, GPP and NCP (mmol O₂ m⁻² day⁻¹) for the full dataset. Upper and lower hinges correspond to the upper and lower quartiles, the line inside the boxes correspond to the median, the mean is marked by a crosshair and the error bars are based on minimum and maximum standard deviation for each parameter. We found differences for CR, GPP and NCP ($p < 0.001$).

3.1 Multiparametric sensors

Sensor data were collected in the water column, with lateral movement between habitats of water masses, and there were no significant differences in GPP ($t_{df=31.75} = -0.16, p = 0.87$), CR ($t_{df=32.46} = 0.91, p = 0.37$) and NCP ($t_{df=32.30} = 0.21, p = 0.84$) between the two species (*P. oceanica* and *C. nodosa*), tested in a mixed model with "Site" as random factor, including depth, region, and seasons. Therefore, we didn't divide the sensor data for the two species. GPP ($t_{df=2.93} = 0.84, p = 0.47$), and CR ($t_{df=3.78} = -1.37, p = 0.25$) were similar between the Eastern and Western Mediterranean basins (Fig. 3, Table 1), but NCP was higher the Western basin ($t_{df=3.63} = 3.25, p = 0.04$). No significant influence of depth was identified for any of the metabolic parameters, nor season for CR or GPP, however NCP was lower in spring ($t_{df=17.72} = -3.60, p < 0.01$). In spring, we also found the highest GPP rates (Mean \pm SE) with 382.68 ± 41.28 mmol O₂ m⁻² day⁻¹, however, the corresponding CR rates for spring were 444.88 ± 76.32 mmol O₂ m⁻² day⁻¹ respectively, leading to a negative NCP of -62.19 ± 47.08 mmol O₂ m⁻² day⁻¹. For the rest of the seasons productivity was higher than respiration, reflected in positive averaged NCP rates and confirming that seagrass meadows



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normally tend to be autotrophic ecosystems with a mean P/R ratio above 1 (2.1 ± 0.26), confirming the tendency of net autotrophy. In the Eastern Mediterranean basin, only data recorded with sensors in summer was available to compare to measurements in the Western basin. Average GPP in the Western basin in summer was 408.11 ± 52.01 (SE) $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$, and while the average yearly GPP did not differ between basins, the productivity in summer is significantly different from the Eastern basin, with a lower average of 192.90 ± 61.66 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$. Average NCP in the Eastern basin (summer) was negative with -236.12 ± 19.83 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$, based on only 4 measurements, and in the Western basin positive with 182.12 ± 23.20 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$ averaged over the year and 228.98 ± 25.05 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$ in summer. The negative NCP rates in the Eastern basin are the result of the high CR measured there, with 429.01 ± 69.27 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$ more than twice the CR measured in summer for the Western basin of 187.77 ± 26.82 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$. This led to low P/R ratios, with an average 0.41 ± 0.08 in the Eastern basin in summer. In the Western basin in summer, the seagrass communities tended to be net autotrophic, reflected in an average P/R ratio of 2.31 ± 0.27 . In general, for both basins, the threshold GPP where the ecosystem switched between net heterotrophy and net autotrophy (NCP=0) was 254.03 $\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$.

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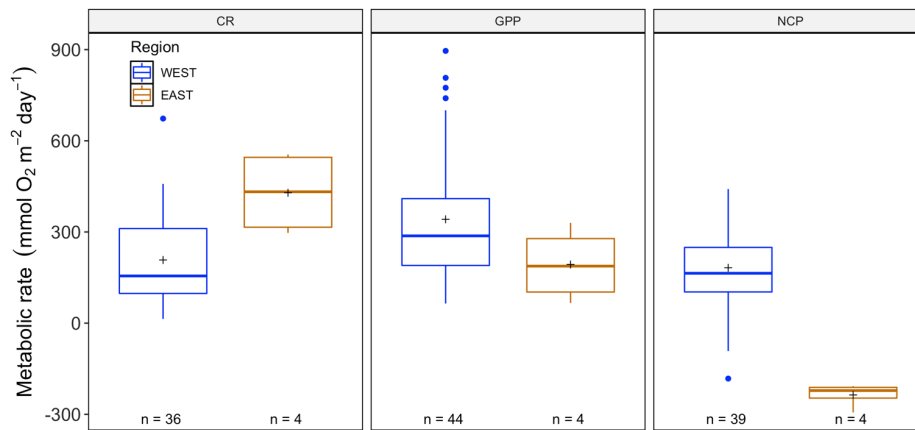


Figure 3. Averaged GPP, NCP and CR ($\text{mmol O}_2 \text{m}^{-2} \text{day}^{-1}$) values for Eastern (blue) and Western (orange) Mediterranean basins calculated from measurements of multiparametric sensors. Upper and lower hinges correspond to the upper and lower quartiles, the lines inside the boxes correspond to the median, the mean is marked by a crosshair and the error bars are based on minimum and maximum standard deviation for each parameter. We found differences with $p < 0.05$ for NCP between the regions.

The temperature recorded during the highest GPP measurement in *P. oceanica* in the Western basin was 26.6°C , which is close, even though a bit higher, to the optimal value reported for *P. oceanica* of 25.8°C (Savva et al., 2018). For the Eastern

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Mediterranean basin, the highest GPP obtained was 329.94 mmol O₂ m⁻² day⁻¹ at Maridati (Crete) during July, and the *in situ* temperature registered at that moment was 25.0 °C, which was not the highest temperature registered in the Eastern basin (28.5°C) and lower than the mean temperature in the Eastern basin during the summer sampling campaign (25.9 ± 0.8 °C). The lowest GPP values found in the Western and Eastern regions were similar, we found the lowest value for GPP of 64.72 mmol O₂ m⁻² day⁻¹ for the Western basin in the the bay of Pollença (Mallorca) during fall, whereas the lowest GPP value in the Eastern basin was 66.19 mmol O₂ m⁻² day⁻¹ in Maridati (Crete) in summer, temperatures during both measurements were different, with 2.5 degree Celsius of difference between them: 25.4 °C in Maridati station (Crete) and 22.9°C in Pollença (Mallorca). We tested with individual regression models for the effect of temperature, which did not significantly affect GPP (t_{df=63}=-1.22, p=0.23), however NCP increased (t_{df=63}=2.46, p=0.02) with increasing temperatures while, surprisingly, CR decreased (t_{df=34.5}=-2.24, p=0.03) (See Appendices, Fig. A4). Windspeed did not drive metabolic rates with t_{df=10.7}=-0.69, p=0.51; t_{df=14.5}=0.86, p=0.41 and t_{df=7.1}=1.07, p=0.32 respectively for GPP, NCP and CR. Over the 12 year of data available for sensor measurements (2007 – 2019), we found an increase of CR (t_{df=12.8}=2.82, p<0.05), but no significant changes in GPP (t_{df=31.18}=1.23, p=0.23) nor NCP (t_{df=28.9}=-0.57, p=0.57; Figure A6).

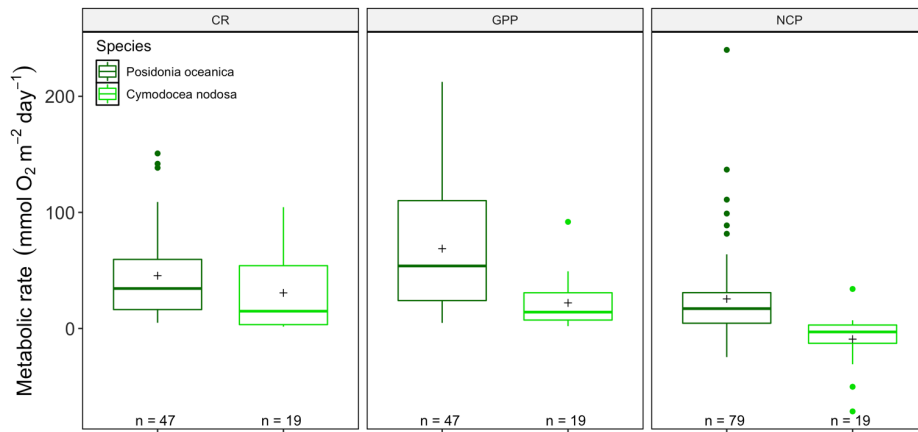
3.2 Benthic chambers

4) between *P. oceanica* and *C. oceanica* communities to be net autotrophic. We found significant differences for CR (t_{df=15.3}=4.05, p<0.01, and GPP (t_{df=15.3}=5.2, p<0.001) but not NCP (t_{df=22.7}=1.19, p=0.25; Fig. *nodosa* productivity, in a model including depth and season, and study as random factor. At a seasonal scale, there were no significant differences for NCP, or CR for *C. nodosa* with NCP (γ²=0.22, p=0.90), CR (γ²=2.63, p=0.27) but there was for GPP, with higher values during summer (γ²=6.29, p=0.04). GPP was lower than CR during all seasons for which measurements were available, reflected in the averaged NCP, with a negative rate (-9.2 ± 5.29 SE mmol O₂ m⁻² day⁻¹), revealing that the *C. nodosa* community tends to be net heterotrophic. The threshold GPP to switch from a heterotrophic to an autotrophic system (NCP=0) was 23.12 O₂ m⁻² day⁻¹ for *C. nodosa*.

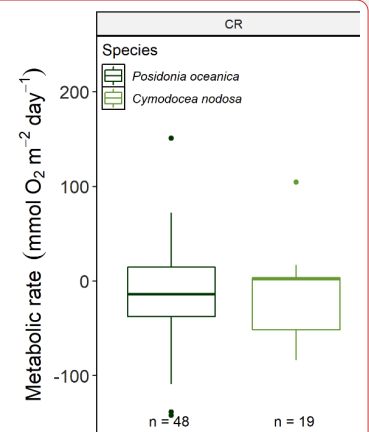
There were no significant differences between NCP (γ²=3.87, p=0.42) and CR (γ²=8.57, p=0.07) across seasons (with year as random factor) for *P. oceanica*, but there were for GPP (γ²=17.43, p<0.01, Figure A5). As we did not have *C. nodosa* data for the Eastern Mediterranean basin we only examined *P. oceanica* to distil patterns between Eastern and Western Mediterranean regions. There were no significant differences for NCP (t_{df=7.48}=-0.32, p=0.76), GPP (t_{df=8.04}=-0.65, p=0.54) or CR (t_{df=8.04}=-0.71, p=0.50) in *Posidonia* incubations between Eastern and Western regions (Fig. 5), due to the high variability between sites, which was incorporated in the model as a random factor. For the Western basin, averaged NCP was 24.33 ± 4.51 SE mmol O₂ m⁻² day⁻¹, with the average GPP (65.19 ± 8.66 mmol O₂ m⁻² day⁻¹) higher than the CR rate (44.4 ± 6.15 mmol O₂ m⁻² day⁻¹), reflecting the tendency of *P.* This was also the case for the Eastern basin, with average NCP even higher at 39.36 ± 5.61 SE mmol O₂ m⁻² day⁻¹, average GPP (93.20 ± 17.67 mmol O₂ m⁻² day⁻¹), higher than the CR rate (52.60 ± 11.73 mmol O₂ m⁻² day⁻¹).

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1). The threshold GPP to switch from a heterotrophic to an autotrophic system (NCP=0) was $36.64 \text{ O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for *P. oceanica*, with both basins combined. Contrary to the sensor data, temperature was not correlated with any metabolic rate, with NCP ($t_{df=17.2}=0.02, p=0.84$), GPP ($t_{df=16.14}=1.65, p=0.12$), and CR ($t_{df=16.58}=1.29, p=0.21$; Figure A4). For chamber incubations we found a tendency over time, albeit not significant, (See Appendices Fig. A6) of decreasing GPP ($t_{df=5.34}=-2.39, p=0.06$) and CR ($t_{df=3.02}=-3.117, p=0.05$) but not NCP ($t_{df=7.96}=0.40, p=0.70$).



2685 **Figure 4.** Metabolic rates, GPP, CR and NCP ($\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$) for *Cymodocea nodosa* (light green) and *Posidonia oceanica* (dark green) for the benthic chambers dataset in the Western Mediterranean basin. Upper and lower hinges correspond to the upper and lower quartiles, the line inside the boxes correspond to the median, the mean is marked by a crosshair and the error bars are based on minimum and maximum standard deviation for each parameter (Rates were different with $p < 0.001$ for GPP and CR $p < 0.01$).



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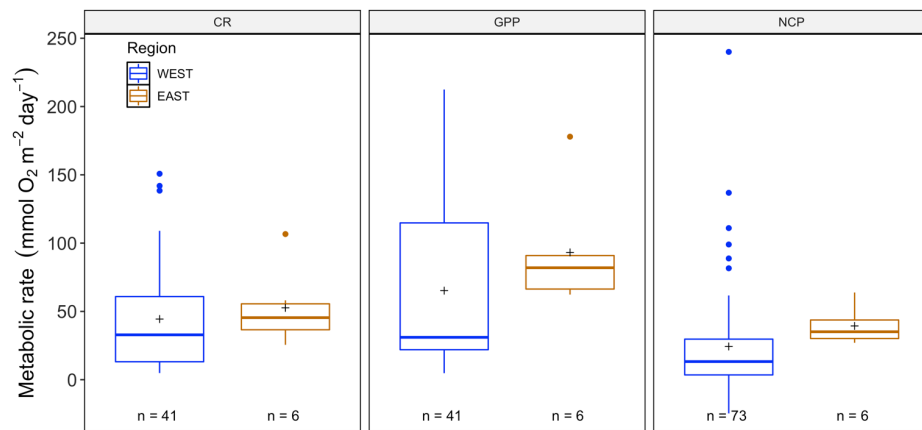
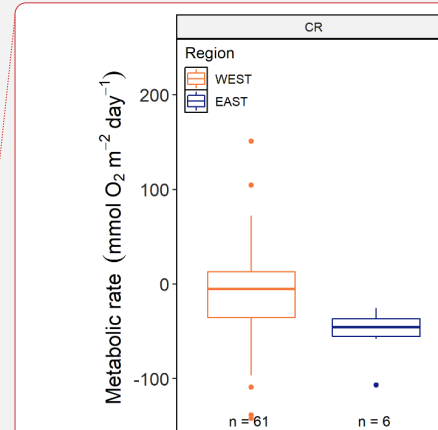


Figure 5. Metabolic rates GPP, NCP and CR ($\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$) for the Eastern (blue) and Western (orange) Mediterranean as obtained from the benthic chamber dataset for *Posidonia oceanica*. Upper and lower hinges correspond to the upper and lower quartiles. The line inside the boxes correspond to the median, the mean is marked by a crosshair and the error bars are based on minimum and maximum standard deviation for each parameter.



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4 Discussion

In this study we found significant differences in metabolic rates between *Cymodocea nodosa* and *Posidonia oceanica* in benthic chambers, while no species-specific pattern could be distilled with sensor data. Only significant differences in NCP estimated with sensor data were found between the Eastern and Western Mediterranean basins, which might be due to the persistence of a much lower number of observations in the Eastern basin, with subsequent loss of statistical power to detect differences. The bias toward a higher number of observations in summer compared to other seasons could have prevented detection of seasonal patterns, with only lower NCP in spring detected with sensors and a higher GPP in summer with benthic chambers and similar metabolic rates for the rest of the seasons. Over half of NCP measurements was done in summer with 55.1% for benthic chamber data and 69.8% for sensor data. Over three quarter (80.4%) of the data for *P. oceanica* and *C. nodosa* communities show that these seagrass meadows are net autotrophic in almost all seasons and locations and are capable to act as carbon sinks and modify pH on diurnal an annual time scale. When this productivity is buried as biomass, carbon could be fixed over long time scales, highlighting the role of these seagrass meadows in climate change mitigation. The threshold GPP where the ecosystem switched between net heterotrophy and net autotrophy (NCP=0) was $254.03 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for measurements from sensors, which is higher than the estimate of $186 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for different seagrass species and regions pooled by

Duarte et al. (2010). For estimates from benthic chambers, this threshold was much lower, $36.64 \text{ O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for *P. oceanica* and $23.12 \text{ O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for *C. nodosa*.

4.1 Multiparametric Sensors

Due to the effect of lateral advection and mixing of water masses, masking a species-specific signal, it was not possible to demonstrate differences in the metabolic rates between *Cymodocea nodosa* and *Posidonia oceanica* meadows, since the sensors are measuring a composed signal in the water column. Due to logistic constraints, sensor deployment in *C. nodosa* and *P. oceanica* meadows when both seagrass species were present in a same site, was separated by a distance of less than 10 m, which adds to the lack of differentiation of values found between the two studied species. Measurements with multiparametric probes should therefore be interpreted as measurement at an ecosystem level as the influence of oxygen dynamics of macrophytes near the measuring site cannot be separated. The influence of phytoplankton and other primary producers may affect sensors as well as benthic chamber measurements. During a spring bloom a relationship between Chl *a* in the water column and GPP has been shown for the bay of Palma. However, not always a correlation with planktonic Chl *a* can be demonstrated (Gazeau et al., 2005); for instance, during a study of annual patterns in the Bay of Revellata (Italy), Champenois et al. (2012) the highest GPP values recorded in a *P. oceanica* meadow were found when planktonic Chl *a* was particularly low and the highest values of Chl *a* did not reflect an increase in GPP and NCP values. Sensor measurements in meadows of both seagrass species allowed us to estimate the metabolic activity of the whole ecosystem and compare between regions, showing similar rates for CR and GPP between the Eastern and Western Mediterranean basins, while NCP was higher in the Western basin, with negative values for the Eastern basin (Table 1). This difference is caused by the relatively high CR rates in the Eastern basin of on average 429.0 ± 69.27 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$, two times higher than the averaged CR rate in the Western basin 207.78 ± 24.98 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$. No significant differences were found for GPP, which has relatively low values in the Eastern basin of 192.90 ± 61.66 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ compared to a yearly average of 341.60 ± 31.61 (SE) $\text{mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ for the Western Mediterranean due to the low sample size ($n=4$), limited measurements over different seasons and high variability of measurements in the East. When we use GPP of the Western basin in summer only, there is a significant difference in GPP between the basins. More measurements are necessary in the Eastern basin, during all seasons in order to obtain a more robust comparison.

The highest GPP was recorded in Cap Enderrocat (Mallorca, Spain) during summer in a *Cymodocea nodosa* meadow with a production of $895.78 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$. Even if these values are high, this is lower than the $1338.0 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ measured at the bay of Revellata (Corsica) by Champenois et al. (2012). Champenois et al. (2012) These authors suggest that extreme GPP values in *P. oceanica* meadows may be rare events that are hardly captured by the classic benthic chambers methodology and the presence of high values measured with multiparametric sensors in this database might reflect that these events could be less uncommon than previously thought. We find the highest GPP values during the summer months, and the highest CR rates in spring (Fig. A5), with a positive relationship with increasing temperatures up to an optimum temperature (Fig. A4), confirming that increasing temperatures enhance metabolic rates (Brown et al., 2004) until a threshold is reached. Abiotic and

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biotic factors that drive seagrass community metabolism differ between regions. In the Eastern basin, GPP was affected by temperature ($p < 0.05$, Fig. A4). No effect was found of water depth on metabolic rates, while depth determines light availability, which in turn determines seagrass distribution, biomass and productivity (Dennison, 1987). This lack of effect is probably due to the limited depth range of the sites in the database (max. 22m, min. 0.6m depth), with measurements mainly in shallow sites, with an average depth of 8.7 ± 0.61 (SE) m. There was a relation between temperature and NCP and CR for the sensor data, with increasing Net Production with rising temperatures, but surprisingly lower Community Respiration rates.

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4.2 Benthic chambers

Due to the effective enclosure with benthic chambers, it was possible to assess the productivity of *Posidonia oceanica* and *Cymodocea nodosa* communities separately, confirming higher CR and GPP in *P. oceanica* communities (Fig. 4). Estimates are for the whole community and include epiphyte and bacterial communities associated to each seagrass species. The higher Gross Productivity and Community Respiration, calculated per surface area (m^2) is logical as *P. oceanica* in general has a higher biomass per m^2 and therefore is more productive relative to *C. nodosa*. Caution should be taken in interpreting these results, as no data for *C. nodosa* from the Eastern basin was available and the database contained a higher number of *P. oceanica* estimates (n=42 for CR, GPP; n=79 for NCP), compared to *C. nodosa* (n=19). Apostolaki et al. (2010) (Champenois et al., 2012, 2019) (Champenois et al., 2019) (Duarte et al., 2010; Champenois et al., 2012, 2019) There was a tendency for GPP and CR to decrease over the progressing years (2001-2019) for incubations of *P. oceanica* (Figure A6), however, our analysis with mixed models and each study as random factor did not indicate significant differences. With a simpler model (linear model) the decrease in CR would have been significant ($t_{df=45} = -6.08$, $p < 0.001$) as well as for GPP ($t_{df=45} = -6.19$, $p < 0.001$) but not for the longer time series (1982-2019) of NCP. The decrease in CR is in contrast with the increase in CR found through time with sensor data (2007-2019), these differences may be due to the fact that sensors also detect trends from other photosynthetic organisms, or limitations for seagrass communities in benthic chambers as water renewal is limited. No differences could be demonstrated in NCP and CR for both species through the seasons, however GPP was higher in summer. There were remarkable individual differences between the two species with an average positive NCP for *P. oceanica*, with only positive values found in benthic incubations and clear net autotrophic communities during the sampling periods in *P. oceanica* meadows. These meadows appear more productive than *C. nodosa* meadows, in agreement with previous studies, which had a higher incidence of heterotrophic communities.

4.3 Sensors vs Benthic chambers

Significant different GPP, NCP and CR were obtained for the different methods, with values almost an order of magnitude larger when estimated from sensor data (Table 1) compared to estimations from benthic chambers as previously reported by Champenois et al. (2012). This difference may be due to a possible underestimation of the metabolic rates assessed by the

benthic chambers methodology or an overestimation associated to water renovation at the placement of sensors. There are some limitations linked to the methodology using benthic chambers as, even if most incubations use flexible material for the bags, which allows for movement and some mixing, there is no real interchange with the water column, and nutrient limitation could occur. (Alcoverro et al., 2001) However the effect of oxygen or nutrient limitation should be limited when incubations are short (24h) (Barrón et al., 2009). The reduction in water motion could lead to the increase of the width of the diffusive boundary layer (DBL) between a seagrass leaf and the water column and slower exchange of nutrients and CO₂ with the water column, since water velocity determines DBL boundary thickness. Another possible explanation for the underestimation in benthic chambers of metabolic rates could be the fact that the insertion of the base of the benthic chambers into the sediment may cut the roots and rhizomes but this should be considered a rare event as most of the biomass of the belowground tissues of *P. oceanica* and *C. nodosa* is located at deeper strata. For the seagrass physiology, rhizomes play an important role as they translocate resources between shoots (Marbà et al., 2002), affecting therefore seagrass metabolism if they are severed. Another reason that may explain a possible underestimation in metabolic rates is the fact that pH may increase, together with O₂ during the day; those two factors, together with a high irradiance conducts the Ribulose-1.5. biphosphate-carboxylase-oxygenase enzyme to change from carboxylase to oxygenase (Heber et al., 1996). Under this reaction there is a higher consumption of O₂ and a CO₂ exudation which may conduce to a lower GPP estimation from the change in O₂ (Champenois et al., 2012). (Enriquez et al., 2006; Hendriks et al., 2017) Nonetheless, benthic chambers can provide measurements for meadows of a single species when enclosures are properly selected. Multiparametric sensors measure a composed signal affected by all surrounding photosynthetic (and heterotrophic) organisms and measured metabolic rates reflect an ecosystem estimation. Measurements with the eddy covariance methodology, (Koopmans et al., 2020) providing estimates on shorter time scales and therefore limiting the effect of lateral transport of water masses. Koopmans et al. (2020) have led to estimations of NCP for *P. oceanica* ranging from 85 to 119 mmol O₂ m⁻² d⁻¹ in nearshore meadows. These estimates are closer to our estimates obtained from sensors, which on average were between 1.7 and 1.2 times higher, while the values obtained from benthic chambers are much lower, with Eddy Covariance estimates 4.5 – 6.3 times higher than the NCP obtained from benthic chambers. The used method should therefore be selected depending on the study objectives taking the focus of the study into account, whether it is more important to attribute productivity a certain species or surface or an ecosystem estimate is required. Independent of the method used, two main limitations remain: the lower amount of available data within the Eastern Mediterranean and the higher sampling frequency during summer compared to other seasons. More than half (55% for benthic chambers and 70% for sensor data) of the data has been collected in summer, due to the logistic restraints of underwater observations. The lack of data for the Eastern basin is specifically urgent to solve, as climate change does not act homogeneously on the two regions and warming is faster for the Eastern basin (; . Failing to collect actual data on metabolic rates could be detrimental for our knowledge on the rates of change in the Mediterranean in the future. We also highlight the lack of data for *C. nodosa* compared to *P. oceanica*. This is probably due to the fact that *C. nodosa* has not had a marked historical presence in many locations, especially in the Western Mediterranean. Their current expanse and apparent Jess

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sensitivity to higher temperatures compared to *P. oceanica* convert *C. nodosa* meadows in potential important players governing coastal metabolic signals deserving a closer look into productivity of these meadows and controlling factors.

3675 4.4 Seagrass metabolism and carbon burial

680 More than three quarters, 80.9% of the NCP values were positive, reflecting the strong capacity of seagrass meadows to act as carbon sinks, which is also exemplified by the high number of P/R ratios above one for both methodologies (Table 1). *P. oceanica* communities tended to be net autotrophic. The exception for this net autotrophic averaged NCP values was found in the Eastern basin, in Maridati (Crete, Greece), where the averaged NCP was $-236.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$ during July 2017. This value is in agreement with the low decadal carbon burial rates and stocks measured by at the same site. This station is located nearby a temporary stream and receive its discharges which implies an extra nutrient input into this area. In 1980's there was a massive sediment input that may have caused mortality and physiological stress to the seagrass meadow and this may be still reflected in the net heterotrophic metabolism observed 2-3 decades later. We also saw heterotrophic meadows in the bay of Pollença (Mallorca, Spain) during spring 2018 (on average $-137.1 \text{ mmol O}_2 \text{ m}^{-2} \text{ day}^{-1}$). This sampling site is located nearby, 685 a nutrient source with high input of organic matter from the s'Albufereta coastal lagoon. Additionally, the organic matter input from the nearby harbour and the sewage systems from urban areas and hotels may have affected the metabolism of the seagrasses in this site. (Borges et al., 2013) Sampling for additional parameters like nutrient values in the water column and sedimentation of organic matter and nutrients at the sites of the metabolism measurements could add important information enabling the explanation of deviant metabolic rates. Seagrass ecosystems are mainly net autotrophic and hence act as carbon 690 sinks but might be threatened and disappear due to high organic inputs and other anthropic threats (e.g., mechanic destruction of the seagrass meadows).

5 Conclusions

695 Seagrass metabolic rates (Net Community Production, Gross Primary Production and Community Respiration) are significantly different depending on the methodology used. The rates obtained with benthic chambers are lower than those obtained with multiparametric sensors. With the benthic chamber methodology seagrass metabolism at a species level can be compared, with demonstrated differences between *Posidonia oceanica* and *Cymodocea nodosa* for GPP and CR. With *P. oceanica* the more productive species compared to *C. nodosa*, but also with higher respiration rates. Multiparametric sensors can assess metabolism at an ecosystem level, and showed NCP was higher in the Western Mediterranean basin compared to 700 the Eastern basin. Benthic chamber measurements could not demonstrate a link between temperature and metabolic rates, while sensor data showed an increase in NCP and an unexpected decrease in CR with higher temperatures. When we plot our data according to the year, we see an increase in CR calculated from sensor data while benthic chamber rates have been

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775 decreasing for CR and GPP over the years. However, care should be taken in interpreting these trends as this is inconclusive
 due to the variability in seasonal measurements and measurement sites.

780 There is a publication bias with a higher number of observations in the Western region and a more elevated number of
 observations for summer compared to other seasons. The possibility to deploy multiparametric sensors for longer periods than
 benthic chambers allows for longer observational periods and detection of high GPP values that could be underestimated due
 to possible nutrient limitation or missed due to the shorter incubation time of the benthic chamber technique. Sampling during
 785 different time periods confirmed the switch between negative and positive NCP values, with changes between autotrophy and
 heterotrophy in a same location during different periods of the year, therefore reinforcing the importance of monitoring during
 the whole year and not only summer. The high percentage of autotrophic meadows highlights their key role for climate change
 mitigation, by acting as carbon sinks through growth as well as through accumulation of allochthonous carbon through particle
 retention. Therefore, it is important to augment the knowledge on seagrass metabolism in regions and seasons where there is
 little data available, to prevent the deterioration of seagrass meadows in the context of climate change where they play an
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Code availability
Metabolic rates of the seagrass meadows were calculated using a modification of the model of Cole et al. (2000) implemented in MATLAB (version 7.5, the Mathworks Inc.) explained in detail in Vaquer-Sunyer et al. (2012)

3815

Data availability

The full dataset will be publicly available at digital.csic.es/handle/xxxxx/xxxxxx.

Executable research compendium (ERC)

3820 **Sample availability**

NA

Supplement link

3825 **Author contribution**

Conceptual idea IEH and NM. Data collection MW, SF, RVS, IEH, NM. Analyses IEH, AEM, SF. Literature compilation IEH and AEM. All authors have contributed to the writing of the article.

Competing interests

The authors declare that they have no conflict of interest.

3830 **Disclaimer**

Special issue statement

Sample availability

Acknowledgements

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References

- 3885 Agawin, N. S., Ferriol, P., Sintes, E., & Moyà, G. (2017). Temporal and spatial variability of in situ nitrogen fixation activities associated with the Mediterranean seagrass *Posidonia oceanica* meadows. *Limnology and Oceanography*, *62*(6), 2575-2592.
- Alcoverro, T., Duarte, C. M., & Romero, J. (1995). Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. *Marine Ecology Progress Series*, 203-210.
- 3890 Alcoverro, T., Manzanera, M., & Romero, J. (2001). Annual metabolic carbon balance of the seagrass *Posidonia oceanica*: the importance of carbohydrate reserves. *Marine Ecology Progress Series*, *211*, 105-116.
- Alongi, D., Murdiyarso, D., Fourqurean, J., Kauffman, J., Hutahaean, A., Crooks, S., . . . Fortes, M. (2016). Indonesia's blue carbon: a globally significant and vulnerable sink for seagrass and mangrove carbon. *Wetlands Ecology and Management*, *24*(1), 3-13.
- 3895 Amitai, Y., Yam, R., Montagna, P., Devoti, S., Correa, M. L., & Shemesh, A. (2020). Spatial and temporal variability in Mediterranean climate over the last millennium from vermetid isotope records and CMIP5/PMIP3 models. *Global and Planetary Change*, *189*, 103159. doi:<https://doi.org/10.1016/j.gloplacha.2020.103159>
- Apostolaki, E. T., Tsagaraki, T., Tsapakis, M., & Karakassis, I. (2007). Fish farming impact on sediments and macrofauna associated with seagrass meadows in the Mediterranean. *Estuarine, Coastal and Shelf Science*, *75*(3), 408-416. doi:<https://doi.org/10.1016/j.eess.2007.05.024>
- 3900 Apostolaki, E. T., Holmer, M., Marbà, N., & Karakassis, I. (2010). Metabolic imbalance in coastal vegetated (*Posidonia oceanica*) and unvegetated benthic ecosystems. *Ecosystems*, *13*(3), 459-471.
- Armitage, A., & Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Ifldr Import 2019-10-08 Batch 5*.
- Aufdenkampe, A. K., Mayorga, E., Raymond, P. A., Melack, J. M., Doney, S. C., Alin, S. R., . . . Yoo, K. (2011). Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere. *Frontiers in Ecology and the Environment*, *9*(1), 53-60.
- 3905 Barrón, C., Marbè, N., Terrados, J., Kennedy, H., & Duarte, C. M. (2004). Community metabolism and carbon budget along a gradient of seagrass (*Cymodocea nodosa*) colonization. *Limnology and Oceanography*, *49*(5), 1642-1651.
- Barrón, C., Duarte, C. M., Frankignoulle, M., & Borges, A. V. (2006). Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (*Posidonia oceanica*), meadow. *Estuaries and Coasts*, *29*(3), 417-426.
- 3910 Barrón, C., & Duarte, C. M. (2009). Dissolved organic matter release in a *Posidonia oceanica* meadow. *Marine Ecology Progress Series*, *374*, 75-84.
- Bay, D. (1984). A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) delile in Calvi Bay, Corsica. *Aquatic Botany*, *20*(1), 43-64. doi:[https://doi.org/10.1016/0304-3770\(84\)90026-3](https://doi.org/10.1016/0304-3770(84)90026-3)
- 3915 Belkin, I. M. (2009). Rapid warming of large marine ecosystems. *Progress in Oceanography*, *81*(1-4), 207-213.
- Béthoux, J. P., & Copin-Montégut, G. (1986). Biological fixation of atmospheric nitrogen in the Mediterranean Sea. *Limnology and Oceanography*, *31*(6), 1353-1358. doi:10.4319/lo.1986.31.6.1353
- Bonacorsi, M., Pergent-Martini, C., Breand, N., & Pergent, G. (2013). Is *Posidonia oceanica* regression a general feature in the Mediterranean Sea? *Mediterranean Marine Science*, *14*(1), 193-203.
- Borges, A., & Champenois, W. (2013). Seasonal and inter-annual variations of gross primary production, community respiration, and net community production of a seagrass meadow.
- 3920 Boudouresque, C. F., Bernard, G., Pergent, G., Shili, A., & Verlaque, M. (2009). Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. *Botanica Marina*, *52*(5), 395-418.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771-1789.
- 3925 Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., . . . Halpern, B. S. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, *334*(6056), 652-655.
- Cebrian, J. (1999). Patterns in the fate of production in plant communities. *The American Naturalist*, *154*(4), 449-468.

- Cebrián, J., Duarte, C. M., Marbà, N., & Enriquez, S. (1997). Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. *Marine Ecology Progress Series*, 155, 29-44.
- 3930 Champenois, W., & Borges, A. V. (2012). Seasonal and interannual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnology and Oceanography*, 57(1), 347-361. doi:10.4319/lo.2012.57.1.0347
- Champenois, W., & Borges, A. V. (2019). Inter-annual variations over a decade of primary production of the seagrass *Posidonia oceanica*. *Limnology and Oceanography*, 64(1), 32-45. doi:10.1002/lno.11017
- 3935 Cole, J., Pace, M., Carpenter, S., & Kitchell, J. (2000). Cole JJ, Pace ML, Carpenter SR, Kitchell JF. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulation. *Limnol Oceanogr*. *Limnology and Oceanography - LIMNOL OCEANOGR*, 45, 1718-1730. doi:10.4319/lo.2000.45.8.1718
- Cole, J. J., & Caraco, N. F. (1998). Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF₆. *Limnology and Oceanography*, 43(4), 647-656.
- 3940 Coloso, J., Cole, J., Hanson, P., & Pace, M. (2008). Depth-integrated, continuous estimates of metabolism in a clear-water lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 712-722. doi:10.1139/f08-006
- Condie, S., & Webster, I. (2001). Estimating stratification in shallow water bodies from mean meteorological conditions. *Journal of Hydraulic Engineering*, 127(4), 286-292.
- Conley, D. J., Carstensen, J., Vaquer-Sunyer, R., & Duarte, C. M. (2009). Ecosystem thresholds with hypoxia. In *Eutrophication in coastal ecosystems* (pp. 21-29): Springer.
- 3945 Dennison, W. C. (1987). Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany*, 27(1), 15-26. doi:[https://doi.org/10.1016/0304-3770\(87\)90083-0](https://doi.org/10.1016/0304-3770(87)90083-0)
- Diaz-Almela, E., Marbà, N., & Duarte, C. M. (2007). Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. *Global Change Biology*, 13(1), 224-235. doi:10.1111/j.1365-2486.2006.01260.x
- 3950 Diaz, R. J., & Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and marine biology. An annual review*, 33, 245-203.
- Diaz, R. J. (2001). Overview of hypoxia around the world. *Journal of environmental quality*, 30(2), 275-281.
- Duarte, C. M., Middelburg, J. J., & Caraco, N. (2004). Major role of marine vegetation on the oceanic carbon cycle.
- 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 Biogeochemical Cycles*, 24(4).
- 3955 Duarte, C. M., Hendriks, I. E., Moore, T. S., Olsen, Y. S., Steckbauer, A., Ramajo, L., . . . McCulloch, M. (2013). Is Ocean Acidification an Open-Ocean Syndrome? Understanding Anthropogenic Impacts on Seawater pH. *Estuaries and Coasts*, 36(2), 221-236. doi:10.1007/s12237-013-9594-3
- Egea, L. G., Jimenez-Ramos, R., Vergara, J. J., Hernandez, I., & Brun, F. G. (2018). Interactive effect of temperature, acidification and ammonium enrichment on the seagrass *Cymodocea nodosa*. *Mar Pollut Bull*, 134, 14-26. doi:10.1016/j.marpolbul.2018.02.029
- 3960 Enriquez, S., & Rodríguez-Román, A. (2006). Effect of water flow on the photosynthesis of three marine macrophytes from a fringing-reef lagoon. *Marine Ecology Progress Series*, 323, 119-132.
- Fofonoff, N. P., & Millard Jr, R. (1983). Algorithms for the computation of fundamental properties of seawater.
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., . . . Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5(7), 505-509. doi:10.1038/ngeo1477
- 3965 Frankignoulle, M., & Bouquegneau, J.-M. (1987). Seasonal variation of the diel carbon budget of a marine macrophyte ecosystem. *Marine Ecology Progress Series*, 38, 197-199.
- Gacia, E., Marbà, N., Cebrián, J., Vaquer-Sunyer, R., Garcias-Bonet, N., & Duarte, C. M. (2012). Thresholds of irradiance for seagrass *Posidonia oceanica* meadow metabolism. *Marine Ecology Progress Series*, 466, 69-79. Retrieved from <https://www.int-res.com/abstracts/meps/v466/p69-79/>
- 3970 Gazeau, F., Duarte, C. M., Gattuso, J.-P., Barrón, C., Navarro, N., Ruiz, S., . . . Frankignoulle, M. (2005). Whole-system metabolism and CO₂ fluxes in a Mediterranean Bay dominated by seagrass beds (Palma Bay, NW Mediterranean). *Biogeosciences*, 2(1), 43-60.
- Giorgi, F. (2006). Climate change hot-spots. *Geophysical Research Letters*, 33(8).
- Giorgi, F., & Lionello, P. (2008). Climate change projections for the Mediterranean region. *Global and Planetary Change*, 63(2-3), 90-104.
- 3975 Gobert, S., Cambridge, M., Velimirov, B., Pergent, G., Lepoint, G., Bouquegneau, J., . . . Walker, D. (2006). Biology of *Posidonia*, Seagrasses: Biology, Ecology, and Conservation. In: Springer, Dordrecht, The Netherlands.
- Grande, K. D., Marra, J., Langdon, C., Heinemann, K., & Bender, M. L. (1989). Rates of respiration in the light measured in marine phytoplankton using an 18O isotope-labelling technique. *Journal of Experimental Marine Biology and Ecology*, 129(2), 95-120.
- Greiner, J. T., McGlathery, K. J., Gunnell, J., & McKee, B. A. (2013). Seagrass restoration enhances "blue carbon" sequestration in coastal waters. *PLoS One*, 8(8), e72469. doi:10.1371/journal.pone.0072469
- 3980 Gullström, M., Lyimo, L. D., Dahl, M., Samuelsson, G. S., Eggertsen, M., Anderberg, E., . . . Björk, M. (2018). Blue Carbon Storage in Tropical Seagrass Meadows Relates to Carbonate Stock Dynamics, Plant–Sediment Processes, and Landscape Context: Insights from the Western Indian Ocean. *Ecosystems*, 21(3), 551-566. doi:10.1007/s10021-017-0170-8

- Gutiérrez, J., Jones, C., Byers, J., Arkema, K., Berkenbusch, K., Commito, J., . . . Hendriks, I. (2011). 7.04—Physical ecosystem engineers and the functioning of estuaries and coasts. *Treatise on estuarine and coastal science*, 53-81.
- 3985 Hanson, P. C., Bade, D. L., Carpenter, S. R., & Kratz, T. K. (2003). Lake metabolism: relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography*, 48(3), 1112-1119.
- Heber, U., Bligny, R., Streb, P., & Douce, R. (1996). Photorespiration is essential for the protection of the photosynthetic apparatus of C3 plants against photoinactivation under sunlight. *Botanica Acta*, 109(4), 307-315.
- 3990 Hendriks, I. E., & Duarte, C. M. (2008). Allocation of effort and imbalances in biodiversity research. *Journal of Experimental Marine Biology and Ecology*, 360(1), 15-20.
- Hendriks, I. E., Duarte, C. M., & Álvarez, M. (2010). Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine, Coastal and Shelf Science*, 86(2), 157-164.
- Hendriks, I. E., Olsen, Y. S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T. S., . . . Duarte, C. M. (2014). Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences*, 11(2), 333-346. doi:10.5194/bg-11-333-2014
- 3995 Hendriks, I. E., Duarte, C. M., Marbà, N., & Krause-Jensen, D. (2017). pH gradients in the diffusive boundary layer of subarctic macrophytes. *Polar Biology*, 40(12), 2343-2348. doi:10.1007/s00300-017-2143-y
- Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., . . . Takeshita, Y. (2011). High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PLoS one*, 6(12).
- Holloway, P. E. (1980). A criterion for thermal stratification in a wind-mixed system. *Journal of Physical Oceanography*, 10(6), 861-869.
- 4000 Holmer, M., Duarte, C. M., Boschker, H. T. S., & Barrón, C. (2004). Carbon cycling and bacterial carbon sources in pristine and impacted Mediterranean seagrass sediments. *Aquatic Microbial Ecology*, 36(3), 227-237.
- IAPWS. (2008). Release on the IAPWS Formulation 2008 for the Thermodynamic Properties of Seawater. The International Association for the Properties of Water and Steam. Berlin, Germany, September 2008, available from www.iapws.org.
- IAPWS. (2009). Supplementary Release on a Computationally Efficient Thermodynamic Formulation for Liquid Water for Oceanographic Use. The International Association for the Properties of Water and Steam. Doorwerth, The Netherlands, September 2009, available from <http://www.iapws.org>.
- 4005 IOC, S. a. I. (2015). The International thermodynamic equation of seawater–2010: calculation and use of thermodynamic properties.[includes corrections up to 31st October 2015].
- 4010 IPCC. (2013). Climate change 2013: The physical science basis. *Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change* [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex & P.M. Midgley], 1535.
- Jordà, G., Marbà, N., & Duarte, C. M. (2012). Mediterranean seagrass vulnerable to regional climate warming. *Nature Climate Change*, 2(11), 821-824.
- 4015 Karim, M. R., Sekine, M., Higuchi, T., Imai, T., & Ukita, M. (2003). Simulation of fish behavior and mortality in hypoxic water in an enclosed bay. *Ecological Modelling*, 159(1), 27-42.
- Karl, D. M., Laws, E. A., Morris, P., Williams, P. J. I., & Emerson, S. (2003). Metabolic balance of the open sea. *Nature*, 426(6962), 32-32. doi:10.1038/426032a
- Keeling, R., Körtzinger, A., & Gruber, N. (2010). Ocean Deoxygenation in a Warming World. *Ann. Rev. Mar. Sci.*
- 4020 Keeling, R. F., & Garcia, H. E. (2002). The change in oceanic O2 inventory associated with recent global warming. *Proceedings of the National Academy of Sciences*, 99(12), 7848-7853.
- Kelly, M. W., & Hofmann, G. E. (2013). Adaptation and the physiology of ocean acidification. *Functional Ecology*, 27(4), 980-990.
- Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., & Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24(4).
- 4025 Kihm, C., & Körtzinger, A. (2010). Air-sea gas transfer velocity for oxygen derived from float data. *Journal of Geophysical Research: Oceans*, 115(C12).
- 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. *Frontiers in Marine Science*, 7.
- Labasque, T., Chaumery, C., Aminot, A., & Kergoat, G. (2004). Spectrophotometric Winkler determination of dissolved oxygen: re-examination of critical factors and reliability. *Marine Chemistry*, 88(1), 53-60. doi:<https://doi.org/10.1016/j.marchem.2004.03.004>
- 4030 Lacoue-Labarthe, T., Nunes, P. A., Ziveri, P., Cinar, M., Gazeau, F., Hall-Spencer, J. M., . . . Sauzade, D. (2016). Impacts of ocean acidification in a warming Mediterranean Sea: An overview. *Regional Studies in Marine Science*, 5, 1-11.
- Lauster, G. H., Hanson, P. C., & Kratz, T. K. (2006). Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 63(5), 1130-1141.
- 4035 Lavery, P. S., Mateo, M.-Á., Serrano, O., & Rozaimi, M. (2013). Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS One*, 8(9).
- Lejeune, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., & Pérez, T. (2010). Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in ecology & evolution*, 25(4), 250-260.

- Lo Iacono, C., Mateo, M. A., Gracia, E., Guasch, L., Carbonell, R., Serrano, L., . . . Danobeitia, J. (2008). Very high-resolution seismic-acoustic imaging of seagrass meadows (Mediterranean Sea): Implications for carbon sink estimates. *Geophysical Research Letters*, 35(18).
- 1040 Marbà, N., Diaz-Almela, E., & Duarte, C. M. (2014). Mediterranean seagrass (*Posidonia oceanica*) loss between 1842 and 2009. *Biological Conservation*, 176, 183-190.
- Marbà, N., Hemminga, M. A., Mateo, M. A., Duarte, C. M., Mass, Y. E., Terrados, J., & Gacia, E. (2002). Carbon and nitrogen translocation between seagrass ramets. *Marine Ecology Progress Series*, 226, 287-300.
- 1045 Marbà, N., & Duarte, C. M. (2010). Mediterranean warming triggers seagrass (*Posidonia oceanica*) shoot mortality. *Global Change Biology*, 16(8), 2366-2375.
- Mateo, M., Romeo, J., Pérez, M., Littler, M. M., & Littler, D. S. (1997). Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuarine, Coastal and Shelf Science*.
- Mateo, M., Cebrián, J., Dunton, K., & Mutchler, T. (2006). Carbon flux in seagrass ecosystems. *Seagrasses: biology, ecology and conservation*, 159-192.
- 1050 McDougall, T. J., & Barker, P. M. (2011). Getting started with TEOS-10 and the Gibbs Seawater (GSW) oceanographic toolbox. *SCOR/IAPSO WG*, 127, 1-28.
- McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., . . . Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9(10), 552-560.
- 1055 Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., . . . Rosenberg, A. A. (2013). Cumulative Human Impacts on Mediterranean and Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. *PLoS One*, 8(12), e79889. doi:10.1371/journal.pone.0079889
- Nykjaer, L. (2009). Mediterranean Sea surface warming 1985–2006. *Climate Research*, 39(1), 11-17. Retrieved from <https://www.int-res.com/abstracts/cr/v39/n1/p11-17/>
- 1060 Odum, H. T., & Hoskin, C. M. (1958). Comparative studies on the metabolism of marine waters. *Publications of the Institute of Marine Science, Texas*, 5, 16-46.
- Odum, H. T., & Wilson, R. F. (1962). Further studies on reaeration and metabolism of Texas bays, 1958-1960.
- Olivé, I., Silva, J., Costa, M. M., & Santos, R. (2016). Estimating Seagrass Community Metabolism Using Benthic Chambers: The Effect of Incubation Time. *Estuaries and Coasts*, 39(1), 138-144. doi:10.1007/s12237-015-9973-z
- 1065 Olsen, Y. S., Sánchez-Camacho, M., Marbà, N., & Duarte, C. M. (2012). Mediterranean Seagrass Growth and Demography Responses to Experimental Warming. *Estuaries and Coasts*, 35(5), 1205-1213. doi:10.1007/s12237-012-9521-z
- Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., . . . Williams, S. L. (2006). A Global Crisis for Seagrass Ecosystems. *Bioscience*, 56(12), 987-996. doi:10.1641/0006-3568(2006)56[987:Agcfse]2.0.Co;2
- 1070 Pace, M. L., & Prairie, Y. T. (2005). Respiration in lakes. *Respiration in aquatic ecosystems*, 1, 103-122.
- Paerl, H. W. (2006). Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations. *Ecological Engineering*, 26(1), 40-54.
- Pasqualini, V., Pergent-Martini, C., Clabaut, P., & Pergent, G. (1998). Mapping of *Posidonia oceanica* causing Aerial Photographs and Side Scan Sonar: Application off the Island of Corsica (France). *Estuarine, Coastal and Shelf Science*, 47(3), 359-367.
- 1075 Pergent, G., Rico-Raimondino, V., & Pergent-Martini, C. (1997). Fate of primary production in *Posidonia oceanica* meadows of the Mediterranean. *Aquatic Botany*, 59(3), 307-321. doi:[https://doi.org/10.1016/S0304-3770\(97\)00052-1](https://doi.org/10.1016/S0304-3770(97)00052-1)
- Powley, H. R., Dürr, H. H., Lima, A. T., Krom, M. D., & Van Cappellen, P. (2016). Direct discharges of domestic wastewater are a major source of phosphorus and nitrogen to the Mediterranean Sea. *Environmental science & technology*, 50(16), 8722-8730.
- 1080 Pringault, O., Tassas, V., & Rochelle-Newall, E. (2007). Consequences of respiration in the light on the determination of production in pelagic systems.
- Ricart, A. M., Pérez, M., & Romero, J. (2017). Landscape configuration modulates carbon storage in seagrass sediments. *Estuarine, Coastal and Shelf Science*, 185, 69-76.
- Richon, C., Dutay, J.-C., Bopp, L., Le Vu, B., Orr, J. C., Somot, S., & Dulac, F. (2019). Biogeochemical response of the Mediterranean Sea to the transient SRES-A2 climate change scenario. *Biogeosciences*, 16(1).
- 1085 Romero, J., Pérez, M., Mateo, M. A., & Sala, E. (1994). The belowground organs of the Mediterranean seagrass *Posidonia oceanica* as a biogeochemical sink. *Aquatic Botany*, 47(1), 13-19. doi:[https://doi.org/10.1016/0304-3770\(94\)90044-2](https://doi.org/10.1016/0304-3770(94)90044-2)
- Samper-Villarreal, J., Lovelock, C. E., Saunders, M. I., Roelfsema, C., & Mumby, P. J. (2016). Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnology and Oceanography*, 61(3), 938-952.
- 1090 Santos, R., Silva, J., Alexandre, A., Navarro, N., Barrón, C., & Duarte, C. M. (2004). Ecosystem metabolism and carbon fluxes of a tidally-dominated coastal lagoon. *Estuaries*, 27(6), 977-985. doi:10.1007/BF02803424
- Savva, I., Bennett, S., Roca, G., Jordà, G., & Marbà, N. (2018). Thermal tolerance of Mediterranean marine macrophytes: Vulnerability to global warming. *Ecology and evolution*, 8(23), 12032-12043. doi:10.1002/ece3.4663

- 4095 Serrano, O., Lavery, P. S., Rozzaimi, M., & Mateo, M. Á. (2014). Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles*, 28(9), 950-961.
- Serrano, O., Lavery, P. S., López-Merino, L., Ballesteros, E., & Mateo, M. A. (2016). Location and Associated Carbon Storage of Erosional Escarpments of Seagrass *Posidonia* Mats. *Frontiers in Marine Science*, 3(42). doi:10.3389/fmars.2016.00042
- Simboura, N., Pavlidou, A., Bald, J., Tsapakis, M., Pagou, K., Zeri, C., . . . Panayotidis, P. (2016). Response of ecological indices to nutrient and chemical contaminant stress factors in Eastern Mediterranean coastal waters. *Ecological Indicators*, 70, 89-105. doi:<https://doi.org/10.1016/j.ecolind.2016.05.018>
- 1100 Simpson, J., & Hunter, J. (1974). Fronts in the Irish sea. *Nature*, 250(5465), 404-406.
- Telesca, L., Belluscio, A., Criscoli, A., Ardizzone, G., Apostolaki, E. T., Fraschetti, S., . . . Pergent, G. (2015). Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Scientific Reports*, 5, 12505.
- 1105 Touratier, F., & Goyet, C. (2011). Impact of the Eastern Mediterranean Transient on the distribution of anthropogenic CO₂ and first estimate of acidification for the Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 58(1), 1-15. doi:<https://doi.org/10.1016/j.dsr.2010.10.002>
- Trevathan-Tackett, S. M., Kelleway, J., Macreadie, P. I., Beardall, J., Ralph, P., & Bellgrove, A. (2015). Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology*, 96(11), 3043-3057.
- 1110 Vaquer-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences*, 105(40), 15452-15457.
- Vaquer-Sunyer, R., Duarte, C. M., Santiago, R., Wassmann, P., & Reigstad, M. (2010). Experimental evaluation of planktonic respiration response to warming in the European Arctic Sector. *POLAR BIOLOGY*, 33(12), 1661-1671.
- Vaquer-Sunyer, R., Duarte, C. M., Jordà, G., & Ruiz-Halpern, S. (2012). Temperature Dependence of Oxygen Dynamics and Community Metabolism in a Shallow Mediterranean Macroalgal Meadow (*Caulerpa prolifera*). *Estuaries and Coasts*, 35(5), 1182-1192. doi:10.1007/s12237-012-9514-y
- 1115 Vargas-Yáñez, M., García, M. J., Salat, J., García-Martínez, M., Pascual, J., & Moya, F. (2008). Warming trends and decadal variability in the Western Mediterranean shelf. *Global and Planetary Change*, 63(2-3), 177-184.
- Wanninkhof, R. (1992). Relationship between wind speed and gas exchange over the ocean. *Journal of Geophysical Research: Oceans*, 97(C5), 7373-7382.
- 1120 Wanninkhof, R., & McGillis, W. R. (1999). A cubic relationship between air-sea CO₂ exchange and wind speed. *Geophysical Research Letters*, 26(13), 1889-1892.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., . . . Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30), 12377-12381. doi:10.1073/pnas.0905620106
- 1125 Zhang, J., Gilbert, D., Gooday, A., Levin, L., Naqvi, S., Middelburg, J., . . . Dewitte, B. (2010). Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development.
- Ziegler, S., & Benner, R. (1998). Ecosystem metabolism in a subtropical, seagrass-dominated lagoon. *Marine Ecology Progress Series*, 173, 1-12.
- 130 [Agawin, N. S., Ferriol, P., Sintes, E., & Moyà, G. \(2017\). Temporal and spatial variability of in situ nitrogen fixation activities associated with the Mediterranean seagrass *Posidonia oceanica* meadows. *Limnology and Oceanography*, 62\(6\), 2575-2592.](#)
- [Alcoverro, T., Duarte, C. M., & Romero, J. \(1995\). Annual growth dynamics of *Posidonia oceanica*: contribution of large-scale versus local factors to seasonality. *Marine Ecology Progress Series*, 203-210.](#)
- 135 [Alcoverro, T., Manzanera, M., & Romero, J. \(2001\). Annual metabolic carbon balance of the seagrass *Posidonia oceanica*: the importance of carbohydrate reserves. *Marine Ecology Progress Series*, 211, 105-116.](#)
- [Amitai, Y., Yam, R., Montagna, P., Devoti, S., Correa, M. L., & Shemesh, A. \(2020\). Spatial and temporal variability in Mediterranean climate over the last millennium from vermetid isotope records and CMIP5/PMIP3 models. *Global and Planetary Change*, 189, 103159. doi:<https://doi.org/10.1016/j.gloplacha.2020.103159>](#)
- 140 [Apostolaki, E. T., Tsagaraki, T., Tsapakis, M., & Karakassis, I. \(2007\). Fish farming impact on sediments and macrofauna associated with seagrass meadows in the Mediterranean. *Estuarine, Coastal and Shelf Science*, 75\(3\), 408-416. doi:<https://doi.org/10.1016/j.ecss.2007.05.024>](#)

- Apostolaki, E. T., Holmer, M., Marbà, N., & Karakassis, I. (2010). Metabolic imbalance in coastal vegetated (*Posidonia oceanica*) and unvegetated benthic ecosystems. *Ecosystems*, 13(3), 459-471.
- 145 Armitage, A., & Fourqurean, J. W. (2016). Carbon storage in seagrass soils: long-term nutrient history exceeds the effects of near-term nutrient enrichment. *Biogeosciences* 13, 313-321
- Aufdenkampe, A. K., Mayorga, E., Raymond, P. A., Melack, J. M., Doney, S. C., Alin, S. R., . . . Yoo, K. (2011). Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere. *Frontiers in Ecology and the Environment*, 9(1), 53-60.
- 150 Barrón, C., Marbè, N., Terrados, J., Kennedy, H., & Duarte, C. M. (2004). Community metabolism and carbon budget along a gradient of seagrass (*Cymodocea nodosa*) colonization. *Limnology and Oceanography*, 49(5), 1642-1651.
- Barrón, C., Duarte, C. M., Frankignoulle, M., & Borges, A. V. (2006). Organic carbon metabolism and carbonate dynamics in a Mediterranean seagrass (*Posidonia oceanica*), meadow. *Estuaries and Coasts*, 29(3), 417-426.
- Barrón, C., & Duarte, C. M. (2009). Dissolved organic matter release in a *Posidonia oceanica* meadow. *Marine Ecology Progress Series*, 374, 75-84.
- 155 Bay, D. (1984). A field study of the growth dynamics and productivity of *Posidonia oceanica* (L.) delile in Calvi Bay, Corsica. *Aquatic Botany*, 20(1), 43-64. doi:[https://doi.org/10.1016/0304-3770\(84\)90026-3](https://doi.org/10.1016/0304-3770(84)90026-3)
- Belkin, I. M. (2009). Rapid warming of large marine ecosystems. *Progress in Oceanography*, 81(1-4), 207-213.
- Béthoux, J. P., & Copin-Montégut, G. (1986). Biological fixation of atmospheric nitrogen in the Mediterranean Sea. *Limnology and Oceanography*, 31(6), 1353-1358. doi:10.4319/lo.1986.31.6.1353
- 160 Bonacorsi, M., Pergent-Martini, C., Breand, N., & Pergent, G. (2013). Is *Posidonia oceanica* regression a general feature in the Mediterranean Sea? *Mediterranean Marine Science*, 14(1), 193-203.
- Borges, A., & Champenois, W. (2013). Seasonal and inter-annual variations of gross primary production, community respiration, and net community production of a seagrass meadow.
- 165 Boudouresque, C. F., Bernard, G., Pergent, G., Shili, A., & Verlaque, M. (2009). Regression of Mediterranean seagrasses caused by natural processes and anthropogenic disturbances and stress: a critical review. *Botanica Marina*, 52(5), 395-418.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771-1789.
- 170 Burrows, M. T., Schoeman, D. S., Buckley, L. B., Moore, P., Poloczanska, E. S., Brander, K. M., . . . Halpern, B. S. (2011). The pace of shifting climate in marine and terrestrial ecosystems. *Science*, 334(6056), 652-655.
- Cebrian, J. (1999). Patterns in the fate of production in plant communities. *The American Naturalist*, 154(4), 449-468.
- Cebrián, J., Duarte, C. M., Marbà, N., & Enríquez, S. (1997). Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. *Marine Ecology Progress Series*, 155, 29-44.
- 175 Champenois, W., & Borges, A. V. (2012). Seasonal and interannual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnology and Oceanography*, 57(1), 347-361. doi:10.4319/lo.2012.57.1.0347

- Champanois, W., & Borges, A. V. (2019). Inter-annual variations over a decade of primary production of the seagrass *Posidonia oceanica*. *Limnology and Oceanography*, 64(1), 32-45. doi:10.1002/lno.11017
- Chefaoui, R. M., Duarte, C. M., & Serrão, E. A. (2018). Dramatic loss of seagrass habitat under projected climate change in the Mediterranean Sea. *Global Change Biology*, 24(10), 4919-4928. doi:https://doi.org/10.1111/gcb.14401
- Cole, J. J., Pace, M., Carpenter, S., & Kitchell, J. (2000). Cole JJ, Pace ML, Carpenter SR, Kitchell JF. 2000. Persistence of net heterotrophy in lakes during nutrient addition and food web manipulation. *Limnology and Oceanography*, 45, 1718-1730. doi:10.4319/lo.2000.45.8.1718
- Cole, J. J., & Caraco, N. F. (1998). Atmospheric exchange of carbon dioxide in a low-wind oligotrophic lake measured by the addition of SF6. *Limnology and Oceanography*, 43(4), 647-656.
- Coloso, J., Cole, J., Hanson, P., & Pace, M. (2008). Depth-integrated, continuous estimates of metabolism in a clear-water lake. *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 712-722. doi:10.1139/f08-006
- Condie, S., & Webster, I. (2001). Estimating stratification in shallow water bodies from mean meteorological conditions. *Journal of Hydraulic Engineering*, 127(4), 286-292.
- Conley, D. J., Carstensen, J., Vaquer-Sunyer, R., & Duarte, C. M. (2009). Ecosystem thresholds with hypoxia. In *Eutrophication in coastal ecosystems* (pp. 21-29): Springer.
- de los Santos, C. B., Krause-Jensen, D., Alcoverro, T., Marbà, N., Duarte, C. M., van Katwijk, M. M., . . . Santos, R. (2019). Recent trend reversal for declining European seagrass meadows. *Nature Communications*, 10(1), 3356. doi:10.1038/s41467-019-11340-4
- Dennison, W. C. (1987). Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany*, 27(1), 15-26. doi:https://doi.org/10.1016/0304-3770(87)90083-0
- Diaz-Almela, E., Marbà, N., & Duarte, C. M. (2007). Consequences of Mediterranean warming events in seagrass (*Posidonia oceanica*) flowering records. *Global Change Biology*, 13(1), 224-235. doi:10.1111/j.1365-2486.2006.01260.x
- Diaz, R. J., & Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and marine biology. An annual review*, 33, 245-203.
- Diaz, R. J. (2001). Overview of hypoxia around the world. *Journal of environmental quality*, 30(2), 275-281.
- Duarte, C. M., Middelburg, J. J., & Caraco, N. (2004). Major role of marine vegetation on the oceanic carbon cycle. *Biogeosciences* 2, 1-8
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., & Apostolaki, E. T. (2010a). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4), n/a-n/a. doi:10.1029/2010gb003793
- Duarte, C. M., Marbà, N., Gacia, E., Fourqurean, J. W., Beggins, J., Barrón, C., & Apostolaki, E. T. (2010b). Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles*, 24(4).

- 210 [Duarte, C. M., Hendriks, I. E., Moore, T. S., Olsen, Y. S., Steckbauer, A., Ramajo, L., . . . McCulloch, M. \(2013\). Is Ocean Acidification an Open-Ocean Syndrome? Understanding Anthropogenic Impacts on Seawater pH. *Estuaries and Coasts*, 36\(2\), 221-236. doi:10.1007/s12237-013-9594-3](#)
- [Egea, L. G., Jimenez-Ramos, R., Vergara, J. J., Hernandez, I., & Brun, F. G. \(2018\). Interactive effect of temperature, acidification and ammonium enrichment on the seagrass *Cymodocea nodosa*. *Mar Pollut Bull*, 134, 14-26. doi:10.1016/j.marpolbul.2018.02.029](#)
- 215 [Enríquez, S., & Rodríguez-Román, A. \(2006\). Effect of water flow on the photosynthesis of three marine macrophytes from a fringing-reef lagoon. *Marine Ecology Progress Series*, 323, 119-132.](#)
- [Fofonoff, N. P., & Millard Jr, R. \(1983\). Algorithms for the computation of fundamental properties of seawater.](#)
- [Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Serrano, O. \(2012\). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, 5\(7\), 505-509. doi:10.1038/ngeo1477](#)
- 220 [Frankignoulle, M., & Bouquegneau, J.-M. \(1987\). Seasonal variation of the diel carbon budget of a marine macrophyte ecosystem. *Marine Ecology Progress Series*, 38, 197-199.](#)
- [Gacia, E., Marbà, N., Cebrián, J., Vaquer-Sunyer, R., Garcias-Bonet, N., & Duarte, C. M. \(2012\). Thresholds of irradiance for seagrass *Posidonia oceanica* meadow metabolism. *Marine Ecology Progress Series*, 466, 69-79.](#)
- 225 [Gazeau, F., Duarte, C. M., Gattuso, J.-P., Barrón, C., Navarro, N., Ruiz, S., . . . Frankignoulle, M. \(2005\). Whole-system metabolism and CO₂ fluxes in a Mediterranean Bay dominated by seagrass beds \(Palma Bay, NW Mediterranean\). *Biogeosciences*, 2\(1\), 43-60.](#)
- [Giorgi, F. \(2006\). Climate change hot-spots. *Geophysical Research Letters*, 33\(8\).](#)
- [Giorgi, F., & Lionello, P. \(2008\). Climate change projections for the Mediterranean region. *Global and Planetary Change*, 63\(2-3\), 90-104.](#)
- 230 [Gober, S., Cambridge, M., Velimirov, B., Pergent, G., Lepoint, G., Bouquegneau, J., . . . Walker, D. \(2006\). Biology of *Posidonia*, Seagrasses: Biology, Ecology, and Conservation. In: Springer, Dordrecht, The Netherlands.](#)
- [Grande, K. D., Marra, J., Langdon, C., Heinemann, K., & Bender, M. L. \(1989\). Rates of respiration in the light measured in marine phytoplankton using an ¹⁸O isotope-labelling technique. *Journal of Experimental Marine Biology and Ecology*, 129\(2\), 95-120.](#)
- 235 [Greiner, J. T., McGlathery, K. J., Gunnell, J., & McKee, B. A. \(2013\). Seagrass restoration enhances "blue carbon" sequestration in coastal waters. *PLoS One*, 8\(8\), e72469. doi:10.1371/journal.pone.0072469](#)
- [Gullström, M., Lyimo, L. D., Dahl, M., Samuelsson, G. S., Eggertsen, M., Anderberg, E., . . . Björk, M. \(2018\). Blue Carbon Storage in Tropical Seagrass Meadows Relates to Carbonate Stock Dynamics, Plant-Sediment Processes, and Landscape Context: Insights from the Western Indian Ocean. *Ecosystems*, 21\(3\), 551-566. doi:10.1007/s10021-017-0170-8](#)
- 240 [Gutiérrez, J., Jones, C., Byers, J., Arkema, K., Berkenbusch, K., Commito, J., . . . Hendriks, I. \(2011\). 7.04—Physical ecosystem engineers and the functioning of estuaries and coasts. *Treatise on estuarine and coastal science*, 53-81.](#)

- 245 [Hanson, P. C., Bade, D. L., Carpenter, S. R., & Kratz, T. K. \(2003\). Lake metabolism: relationships with dissolved organic carbon and phosphorus. *Limnology and Oceanography*, 48\(3\), 1112-1119.](#)
- [Heber, U., Bligny, R., Streb, P., & Douce, R. \(1996\). Photorespiration is essential for the protection of the photosynthetic apparatus of C3 plants against photoinactivation under sunlight. *Botanica Acta*, 109\(4\), 307-315.](#)
- [Hendriks, I. E., & Duarte, C. M. \(2008\). Allocation of effort and imbalances in biodiversity research. *Journal of Experimental Marine Biology and Ecology*, 360\(1\), 15-20.](#)
- 250 [Hendriks, I. E., Duarte, C. M., & Álvarez, M. \(2010\). Vulnerability of marine biodiversity to ocean acidification: a meta-analysis. *Estuarine, Coastal and Shelf Science*, 86\(2\), 157-164.](#)
- [Hendriks, I. E., Olsen, Y. S., Ramajo, L., Basso, L., Steckbauer, A., Moore, T. S., . . . Duarte, C. M. \(2014\). Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences*, 11\(2\), 333-346. doi:10.5194/bg-11-333-2014](#)
- 255 [Hendriks, I. E., Duarte, C. M., Marbà, N., & Krause-Jensen, D. \(2017\). pH gradients in the diffusive boundary layer of subarctic macrophytes. *Polar Biology*, 40\(12\), 2343-2348. doi:10.1007/s00300-017-2143-y](#)
- [Hofmann, G. E., Smith, J. E., Johnson, K. S., Send, U., Levin, L. A., Micheli, F., . . . Takeshita, Y. \(2011\). High-frequency dynamics of ocean pH: a multi-ecosystem comparison. *PloS one*, 6\(12\).](#)
- [Holloway, P. E. \(1980\). A criterion for thermal stratification in a wind-mixed system. *Journal of Physical Oceanography*, 10\(6\), 861-869.](#)
- 260 [Holmer, M., Duarte, C. M., Boschker, H. T. S., & Barrón, C. \(2004\). Carbon cycling and bacterial carbon sources in pristine and impacted Mediterranean seagrass sediments. *Aquatic Microbial Ecology*, 36\(3\), 227-237.](#)
- [IAPWS. \(2008\). Release on the IAPWS Formulation 2008 for the Thermodynamic Properties of Seawater. The International Association for the Properties of Water and Steam. Berlin, Germany, September 2008, available from \[www.iapws.org\]\(http://www.iapws.org\).](#)
- 265 [IAPWS. \(2009\). Supplementary Release on a Computationally Efficient Thermodynamic Formulation for Liquid Water for Oceanographic Use. The International Association for the Properties of Water and Steam. Doorwerth, The Netherlands, September 2009, available from <http://www.iapws.org>.](#)
- [IOC, S. a. I. \(2015\). The International thermodynamic equation of seawater–2010: calculation and use of thermodynamic properties.\[includes corrections up to 31st October 2015\].](#)
- 270 [IPCC. \(2013\). Climate change 2013: The physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change \[Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex & P.M. Midgley\], 1535.](#)
- [Jordà, G., Marbà, N., & Duarte, C. M. \(2012\). Mediterranean seagrass vulnerable to regional climate warming. *Nature Climate Change*, 2\(11\), 821-824.](#)
- 275 [Karim, M. R., Sekine, M., Higuchi, T., Imai, T., & Ukita, M. \(2003\). Simulation of fish behavior and mortality in hypoxic water in an enclosed bay. *Ecological Modelling*, 159\(1\), 27-42.](#)

- 280 [Karl, D. M., Laws, E. A., Morris, P., Williams, P. J. I., & Emerson, S. \(2003\). Metabolic balance of the open sea. *Nature*, 426\(6962\), 32-32. doi:10.1038/426032a](#)
- [Keeling, R., Körtzinger, A., & Gruber, N. \(2010\). Ocean Deoxygenation in a Warming World. *Ann. Rev. Mar. Sci.* 2, 199-229](#)
- [Keeling, R. F., & Garcia, H. E. \(2002\). The change in oceanic O₂ inventory associated with recent global warming. *Proceedings of the National Academy of Sciences*, 99\(12\), 7848-7853.](#)
- [Kelly, M. W., & Hofmann, G. E. \(2013\). Adaptation and the physiology of ocean acidification. *Functional Ecology*, 27\(4\), 980-990.](#)
- 285 [Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marbà, N., & Middelburg, J. J. \(2010\). Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*, 24\(4\).](#)
- [Kihm, C., & Körtzinger, A. \(2010\). Air-sea gas transfer velocity for oxygen derived from float data. *Journal of Geophysical Research: Oceans*, 115\(C12\).](#)
- [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. *Frontiers in Marine Science*, 7.](#)
- 290 [Labasque, T., Chaumery, C., Aminot, A., & Kergoat, G. \(2004\). Spectrophotometric Winkler determination of dissolved oxygen: re-examination of critical factors and reliability. *Marine Chemistry*, 88\(1\), 53-60. doi:https://doi.org/10.1016/j.marchem.2004.03.004](#)
- 295 [Lacoue-Labarthe, T., Nunes, P. A., Ziveri, P., Cinar, M., Gazeau, F., Hall-Spencer, J. M., . . . Sauzade, D. \(2016\). Impacts of ocean acidification in a warming Mediterranean Sea: An overview. *Regional Studies in Marine Science*, 5, 1-11.](#)
- [Lauster, G. H., Hanson, P. C., & Kratz, T. K. \(2006\). Gross primary production and respiration differences among littoral and pelagic habitats in northern Wisconsin lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 63\(5\), 1130-1141.](#)
- 300 [Lejeusne, C., Chevaldonné, P., Pergent-Martini, C., Boudouresque, C. F., & Pérez, T. \(2010\). Climate change effects on a miniature ocean: the highly diverse, highly impacted Mediterranean Sea. *Trends in ecology & evolution*, 25\(4\), 250-260.](#)
- [Lo Iacono, C., Mateo, M. A., Gracia, E., Guasch, L., Carbonell, R., Serrano, L., . . . Danobeitia, J. \(2008\). Very high-resolution seismo-acoustic imaging of seagrass meadows \(Mediterranean Sea\): Implications for carbon sink estimates. *Geophysical Research Letters*, 35\(18\).](#)
- 305 [MATLAB and Statistics Toolbox Release \(2012\), The MathWorks, Inc., Natick, Massachusetts, United States.](#)
- [Marbà, N., Díaz-Almela, E., & Duarte, C. M. \(2014\). Mediterranean seagrass \(*Posidonia oceanica*\) loss between 1842 and 2009. *Biological Conservation*, 176, 183-190.](#)
- 310 [Marbà, N., Hemminga, M. A., Mateo, M. A., Duarte, C. M., Mass, Y. E., Terrados, J., & Gacia, E. \(2002\). Carbon and nitrogen translocation between seagrass ramets. *Marine Ecology Progress Series*, 226, 287-300.](#)

- 315 [Marbà, N., & Duarte, C. M. \(2010\). Mediterranean warming triggers seagrass \(*Posidonia oceanica*\) shoot mortality. *Global Change Biology*, 16\(8\), 2366-2375.](#)
- [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 \(mallorca\). *Frontiers in Marine Science*. doi:http://dx.doi.org/10.3389/fmars.2021.746379](#)
- [Mateo, M., Romeo, J., Pérez, M., Littler, M. M., & Littler, D. S. \(1997\). Dynamics of millenary organic deposits resulting from the growth of the Mediterranean seagrass *Posidonia oceanica*. *Estuarine, Coastal and Shelf Science*, 44\(1\), 103-110](#)
- 320 [Mateo, M., Cebrián, J., Dunton, K., & Mutchler, T. \(2006\). Carbon flux in seagrass ecosystems. *Seagrasses: biology, ecology and conservation* \(Springer\), 159-192.](#)
- [McDougall, T. J., & Barker, P. M. \(2011\). Getting started with TEOS-10 and the Gibbs Seawater \(GSW\) oceanographic toolbox. *SCOR/IAPSO WG*, 127, 1-28.](#)
- [McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., . . . Silliman, B. R. \(2011\). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO₂. *Frontiers in Ecology and the Environment*, 9\(10\), 552-560.](#)
- 325 [Micheli, F., Halpern, B. S., Walbridge, S., Ciriaco, S., Ferretti, F., Fraschetti, S., . . . Rosenberg, A. A. \(2013\). Cumulative Human Impacts on Mediterranean and Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. *PLoS One*, 8\(12\), e79889. doi:10.1371/journal.pone.0079889](#)
- [Nykjaer, L. \(2009\). Mediterranean Sea surface warming 1985–2006. *Climate Research*, 39\(1\), 11-17.](#)
- 330 [Odum, H. T., & Hoskin, C. M. \(1958\). Comparative studies on the metabolism of marine waters. *Publications of the Institute of Marine Science, Texas*, 5, 16-46.](#)
- [Odum, H. T., & Wilson, R. F. \(1962\). Further studies on reaeration and metabolism of Texas bays, 1958-1960.](#)
- [Olivé, I., Silva, J., Costa, M. M., & Santos, R. \(2016\). Estimating Seagrass Community Metabolism Using Benthic Chambers: The Effect of Incubation Time. *Estuaries and Coasts*, 39\(1\), 138-144. doi:10.1007/s12237-015-9973-z](#)
- 335 [Olsen, Y. S., Sánchez-Camacho, M., Marbà, N., & Duarte, C. M. \(2012\). Mediterranean Seagrass Growth and Demography Responses to Experimental Warming. *Estuaries and Coasts*, 35\(5\), 1205-1213. doi:10.1007/s12237-012-9521-z](#)
- [Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., . . . Williams, S. L. \(2006\). A Global Crisis for Seagrass Ecosystems. *Bioscience*, 56\(12\), 987-996. doi:10.1641/0006-3568\(2006\)56\[987:Agcfse\]2.0.Co;2](#)
- 340 [Pace, M. L., & Prairie, Y. T. \(2005\). Respiration in lakes. *Respiration in aquatic ecosystems*, 1, 103-122.](#)
- [Paerl, H. W. \(2006\). Assessing and managing nutrient-enhanced eutrophication in estuarine and coastal waters: Interactive effects of human and climatic perturbations. *Ecological Engineering*, 26\(1\), 40-54.](#)

- 345 Pasqualini, V., Pergent-Martini, C., Clabaut, P., & Pergent, G. (1998). Mapping of *Posidonia oceanica* using Aerial Photographs and Side Scan Sonar: Application off the Island of Corsica (France). *Estuarine, Coastal and Shelf Science*, 47(3), 359-367.
- Pergent, G., Rico-Raimondino, V., & Pergent-Martini, C. (1997). Fate of primary production in *Posidonia oceanica* meadows of the Mediterranean. *Aquatic Botany*, 59(3), 307-321. doi:[https://doi.org/10.1016/S0304-3770\(97\)00052-1](https://doi.org/10.1016/S0304-3770(97)00052-1)
- 350 Powley, H. R., Dürr, H. H., Lima, A. T., Krom, M. D., & Van Cappellen, P. (2016). Direct discharges of domestic wastewater are a major source of phosphorus and nitrogen to the Mediterranean Sea. *Environmental science & Technology*, 50(16), 8722-8730.
- Pringault, O., Tassas, V., & Rochelle-Newall, E. (2007). Consequences of respiration in the light on the determination of production in pelagic systems. *Biogeosciences*, 4, 105–114. <https://doi.org/10.5194/bg-4-105-2007>
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 355 Ricart, A. M., Pérez, M., & Romero, J. (2017). Landscape configuration modulates carbon storage in seagrass sediments. *Estuarine, Coastal and Shelf Science*, 185, 69-76.
- Richon, C., Dutay, J.-C., Bopp, L., Le Vu, B., Orr, J. C., Somot, S., & Dulac, F. (2019). Biogeochemical response of the Mediterranean Sea to the transient SRES-A2 climate change scenario. *Biogeosciences*, 16(1).
- 360 Romero, J., Pérez, M., Mateo, M. A., & Sala, E. (1994). The belowground organs of the Mediterranean seagrass *Posidonia oceanica* as a biogeochemical sink. *Aquatic Botany*, 47(1), 13-19. doi:[https://doi.org/10.1016/0304-3770\(94\)90044-2](https://doi.org/10.1016/0304-3770(94)90044-2)
- Samper-Villarreal, J., Lovelock, C. E., Saunders, M. I., Roelfsema, C., & Mumby, P. J. (2016). Organic carbon in seagrass sediments is influenced by seagrass canopy complexity, turbidity, wave height, and water depth. *Limnology and Oceanography*, 61(3), 938-952.
- 365 Santos, R., Silva, J., Alexandre, A., Navarro, N., Barrón, C., & Duarte, C. M. (2004). Ecosystem metabolism and carbon fluxes of a tidally-dominated coastal lagoon. *Estuaries*, 27(6), 977-985. doi:10.1007/BF02803424
- Savva, I., Bennett, S., Roca, G., Jordà, G., & Marbà, N. (2018). Thermal tolerance of Mediterranean marine macrophytes: Vulnerability to global warming. *Ecology and evolution*, 8(23), 12032-12043. doi:10.1002/ece3.4663
- 370 Serrano, O., Lavery, P. S., Rozaimi, M., & Mateo, M. Á. (2014). Influence of water depth on the carbon sequestration capacity of seagrasses. *Global Biogeochemical Cycles*, 28(9), 950-961.
- Serrano, O., Lavery, P. S., López-Merino, L., Ballesteros, E., & Mateo, M. A. (2016). Location and Associated Carbon Storage of Erosional Escarpments of Seagrass *Posidonia* Mats. *Frontiers in Marine Science*, 3(42). doi:10.3389/fmars.2016.00042
- 375 Simboura, N., Pavlidou, A., Bald, J., Tsapakis, M., Pagou, K., Zeri, C., . . . Panayotidis, P. (2016). Response of ecological indices to nutrient and chemical contaminant stress factors in Eastern Mediterranean coastal waters. *Ecological Indicators*, 70, 89-105. doi:<https://doi.org/10.1016/j.ecolind.2016.05.018>

- Simpson, J., & Hunter, J. (1974). Fronts in the Irish sea. *Nature*, 250(5465), 404-406.
- Telesca, L., Belluscio, A., Criscoli, A., Ardizzone, G., Apostolaki, E. T., Fraschetti, S., . . . Pergent, G. (2015). Seagrass meadows (*Posidonia oceanica*) distribution and trajectories of change. *Scientific Reports*, 5, 12505.
- 380 Touratier, F., & Goyet, C. (2011). Impact of the Eastern Mediterranean Transient on the distribution of anthropogenic CO₂ and first estimate of acidification for the Mediterranean Sea. *Deep Sea Research Part I: Oceanographic Research Papers*, 58(1), 1-15. doi:https://doi.org/10.1016/j.dsr.2010.10.002
- Trevathan-Tackett, S. M., Kelleway, J., Macreadie, P. I., Beardall, J., Ralph, P., & Bellgrove, A. (2015). Comparison of marine macrophytes for their contributions to blue carbon sequestration. *Ecology*, 96(11), 3043-3057.
- 385 Vaquer-Sunyer, R., & Duarte, C. M. (2008). Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences*, 105(40), 15452-15457.
- Vaquer-Sunyer, R., Duarte, C. M., Jordà, G., & Ruiz-Halpern, S. (2012). Temperature Dependence of Oxygen Dynamics and Community Metabolism in a Shallow Mediterranean Macroalgal Meadow (*Caulerpa prolifera*). *Estuaries and Coasts*, 35(5), 1182-1192. doi:10.1007/s12237-012-9514-y
- 390 Vaquer-Sunyer, R., & Duarte, C. M. (2013). Experimental evaluation of the response of coastal Mediterranean planktonic and benthic metabolism to warming. *Estuaries and Coasts*, 36(4), 697-707.
- Vargas-Yáñez, M., García, M. J., Salat, J., García-Martínez, M., Pascual, J., & Moya, F. (2008). Warming trends and decadal variability in the Western Mediterranean shelf. *Global and Planetary Change*, 63(2-3), 177-184.
- Wanninkhof, R. (1992). Relationship between wind speed and gas exchange over the ocean. *Journal of Geophysical Research: Oceans*, 97(C5), 7373-7382.
- 395 Wanninkhof, R., & McGillis, W. R. (1999). A cubic relationship between air-sea CO₂ exchange and wind speed. *Geophysical Research Letters*, 26(13), 1889-1892.
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., . . . Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30), 12377-12381. doi:10.1073/pnas.0905620106
- 400 Wesselmann, M., Gerdali, N. R., Duarte, C. M., Garcia-Orellana, J., Díaz-Rúa, R., Arias-Ortiz, A., . . . Marbà, N. (2021). Seagrass (*Halophila stipulacea*) invasion enhances carbon sequestration in the Mediterranean Sea. *Global Change Biology*, 27(11), 2592-2607.
- Zhang, J., Gilbert, D., Gooday, A., Levin, L., Naqvi, S., Middelburg, J., . . . Dewitte, B. (2010). Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. *Biogeosciences*, 7, 1443-1467
- 405 Ziegler, S., & Benner, R. (1998). Ecosystem metabolism in a subtropical, seagrass-dominated lagoon. *Marine Ecology Progress Series*, 173, 1-12.

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