

Abstract

Estimates of dissolved organic carbon (DOC) release by marine macrophyte communities (seagrass meadows and macroalgal beds) were obtained experimentally using in situ benthic chambers. The effect of light availability on DOC release by macrophyte communities was examined in two communities both by comparing net DOC release under light and dark, and by examining the response of net DOC release to longer-term (days) experimental shading of the communities. All most 85 % of the seagrass communities and almost all of macroalgal communities examined acted as net sources of DOC. There was a weak tendency for higher DOC fluxes under light than under dark conditions in seagrass meadow. There is no relationship between net DOC fluxes and gross primary production (GPP) and net community production (NCP), however, this relationship is positive between net DOC fluxes and community respiration. Net DOC fluxes were not affected by shading of a *T. testudinum* community in Florida for 5 days, however, shading of a mixed seagrass meadow in the Philippines led to a significant reduction on the net DOC release when shading was maintained for 6 days compared to only 2 days of shading. Based on published and unpublished results we also estimate the global net DOC production by marine macrophytes. The estimated global net DOC flux, and hence export, from marine macrophyte is about $0.197 \pm 0.015 \text{ Pg C yr}^{-1}$ or $0.212 \pm 0.016 \text{ Pg C yr}^{-1}$ depending if net DOC flux by seagrass meadows was estimated by taking into account the low or high global seagrass area, respectively.

1 Introduction

Marine macrophytes (macroalgae and angiosperms) form highly productive ecosystems in the coastal ocean (Gattuso et al., 1998; Hemminga and Duarte, 2000; Barrón et al., 2006; Duarte et al., 2010). Marine macrophyte communities tend to produce excess organic matter that can be stored in sediments or exported to adjacent ecosystems (Duarte and Cebrián, 1996; Gattuso et al., 1998; Barrón et al., 2003; Duarte et al., 2005; Barrón and Duarte, 2009). Macroalgae and seagrasses store about 0.4 %

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and 16 % of their net primary production in the sediments, respectively (Duarte and Cebrián, 1996), and some of the excess organic matter they produce can be exported to adjacent waters (Duarte et al., 2005; Barrón and Duarte, 2009).

The release of dissolved organic matter has been reported to account, on average, for 25 % and 44 % of the net primary production of macroalgae and seagrass, respectively (Duarte and Cebrián, 1996), although the form, particulate or dissolved, of this release has not been resolved. Release of dissolved organic carbon (DOC) by marine macrophytes has been examined largely in experiments with isolated plants (Brilinsky, 1977; Wetzel and Penhalel 1979; Moriarty et al., 1986). However, extrapolation of DOC release by individual plants does not allow estimation of community net release, and hence total DOC export, because it neglects DOC release by other community components such as epiphytes, or leaching of DOC from material decomposing in the sediments, and it neglects consumption, of DOC by bacteria and possibly metazoans. Indeed, some marine macrophyte communities may possibly act as DOC sinks, consuming more carbon than they produce, a possibility that cannot be ascertained from consideration of DOC release by individual plants alone. Thus, the capacity to export DOC is best assessed through the examination of net DOC production by intact macrophyte communities. Regrettably, very few studies have examined DOC release by marine macrophyte communities in situ (Ziegler and Benner, 1999a; Barrón et al., 2003, 2004; Barrón and Duarte, 2009; Apostolaki et al., 2010a, b; Maher and Eyre, 2010).

Seasonal DOC release by marine macrophyte communities (Ziegler and Benner, 1999a; Suzuki et al., 2003; Barrón and Duarte, 2009; Ziegler et al., 2004; Apostolaki et al., 2010a) suggests a dependence of DOC release on light availability. Most marine macrophyte communities examined displayed net DOC uptake during dark incubations and net DOC release during light (Maher and Eyre, 2010). Indeed, DOC release was on annual scale 12 % higher in the light than in the dark in a *Posidonia oceanica* meadow (Apostolaki et al., 2010b). Further, bacterial production in the water column of seagrass beds has been reported to vary diurnally (Chin-Leo and Benner,

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1991), suggesting a light-dependence of seagrass DOC release. Additional evidence was provided by Ziegler and Benner (1999a), who reported bacterial production and net benthic DOC production to vary between a sunny and a subsequent cloudy day. In addition, Maher and Eyre (2010) report a tight coupling between DOC fluxes and bacterial biomass. These results suggest a dependence of net DOC release on light availability.

Here we experimentally quantify and synthesize available estimates of the net dissolved organic carbon (DOC) fluxes by marine macrophyte (seagrass and macroalgae) communities, and test its hypothesized light dependence. The effect of light availability on DOC release by macrophyte communities was examined both by comparing net community DOC release under light and dark, and by examining the response of net DOC release to longer-term (days) experimental shading of the communities. We combined experimental results, derived from a broad range of marine macrophyte communities (seagrass meadows and macroalgal beds) using in situ benthic chambers, and published and unpublished estimates to provide a first assessment of the global net DOC production by marine macrophyte communities.

2 Methods

2.1 Net DOC fluxes from marine macrophytes

Estimates of net DOC fluxes in seagrass derived experimentally here were amended with estimates derived from in situ benthic chambers reported in the literature, including a total of 66 estimates (Table 1), seven of which corresponded to DOC fluxes in macroalgal communities (Table 2). The net DOC flux of seagrass and macroalgal communities was evaluated in situ using benthic chambers (three–four replicates) set up by SCUBA divers. The benthic chambers consisted of a PVC cylinder inserted about 7–10 cm in the sediment and fitted with a polyethylene plastic bag by the divers. When growing on hard substratum, e.g. the *Fucus serratus* community, the chambers were attached to the substratum using a cement mix (cf. Barrón et al., 2003). The

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polyethylene plastic bags had a sampling port to collect the water samples with acid-washed syringes. Most of the DOC fluxes during dark were collected from incubations during night. However, sometimes night incubations could not be set up and dark DOC fluxes were collected from short-term (less than 6 h) incubations of benthic chambers covered by dark plastic bags, run in parallel to clear ones. The only exception was the benthic chamber covered by the dark plastic bags conducted with *Cymodocea nodosa*, which lasted for around 24 h (Barrón et al., 2004). Hourly dark and light DOC rates were converted to daily rates by multiplying the hourly rates by the number of night and light hours during the day. The polyethylene plastic bags allowed mixing in the interior of the benthic chamber due to the flexible nature of this material. The mixing times were assessed by injecting a fluorescent dye (fluorescein) in the chambers and found to be around 5 s.

The volume of each chamber was estimated by injecting a phosphate solution (0.25 mol l^{-1}) at the end of the incubation. Five ml of the phosphate solution was injected in each chamber and allowed to mix for 5 min before sampling. The water samples collected were kept frozen until the spectrophotometric determination of the phosphate concentration (Hansen and Koroleff, 1999). The volume of each benthic chamber was calculated from the difference between the phosphate concentration in the solution injected and the water sample collected from the benthic chambers. Although phosphate is a non-conservative species, we selected it because of ease of preservation of the samples, standardization and measurement. Considering maximum phosphate uptake rates for seagrass of $50 \mu\text{mol g DW}^{-1} \text{ d}^{-1}$ (Duarte, 1995), the plants would be able to remove, at the maximum biomass in the chambers, $5.6 \mu\text{mol}$ of phosphate in the 5 min of mixing time. This maximum seagrass uptake in the benthic chambers represents 0.4 % of the input of $1250 \mu\text{mol}$ into the chamber, so that the effect of plant removal would be negligible and cannot possibly affect our results and conclusions. The volume of the benthic chambers ranged from 5 to 20 l.

Fluxes of dissolved organic carbon (DOC) were based on the rate of change in concentration between initial and final samples. Water samples from the benthic chambers

were filtered through pre-combusted (450 °C for 4 h) GF/F filters. DOC samples were kept frozen in acid washed glass vials with silicone-teflon caps until analyses. DOC samples retrieved subsequently were kept acidified with 2 mol l⁻¹ HCl at room temperature in acid-washed sealed ampoules, a procedure which improved accuracy in DOC determinations. DOC samples were analyzed on a Shimadzu TOC-5000A (Benner and Strom, 1993). DOC standards provided by Dennis A. Hansell and Wenhao Chen (University of Miami) of 44–45 2 μmol DOC were used to assess the accuracy of the analyses. Samples for DOC analyses from the experiments conducted in The Philippines were filtered through precombusted (400 °C for 2 h) GF/F filters, and kept frozen in precombusted glass ampoules until analysis. DOC was determined on 2 ml samples, after acidification with 10 μl of 85 % H₃PO₄ and sparging with N₂ for 5 min, by high temperature oxidation using an MQ1001 TOC Analyzer (Benner and Strom, 1993).

Net community production (NCP) was evaluated in parallel from dissolved oxygen (DO) changes in the benthic chambers. Hourly rates of respiration (*R*) and NCP were estimated from the difference in oxygen concentration change in the chambers during the night and the day, respectively. Hourly rates of gross primary production (GPP) were estimated as the sum of the hourly rates of *R* and NCP, and daily rates of GPP were calculated by multiplying the hourly GPP by the photoperiod. Daily *R* was calculated as hourly *R* multiplied by 24 h, and daily rates of NCP were estimated as the difference between daily GPP and *R*. Depending on the experimental location, DO concentration were determined by high-precision Winkler titration with a Mettler DL21 titrator (Carritt and Carpenter, 1966), with a reproducibility of 0.35 %, and other samples were measured using a spectrophotometric modification of the Winkler titration method (Pai et al., 1993; Roland et al., 1999). Metabolic rates in DO units were converted to carbon units assuming photosynthetic and respiratory quotients of 1, however, variability about these quotients may introduce errors in the estimates, as discussed in detail by Kirk (1983).

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2.2 Response of net DOC fluxes to shading

The effect of shading on net community DOC release was examined in March 2000 in a mixed seagrass meadow at Silaqui Island, Bolinao (Luzón, The Philippines), and in October 2003 at a *Thalassia testudinum* meadow in Homossassa, on the Gulf coast of Florida.

Nine separate 2.25 m² (1.5 m × 1.5 m) plots were set up in October 2003 in the *Thalassia testudinum* meadow in Homossassa in the Gulf coast of Florida, experimental details are reported in Calleja et al. (2006). The shading screens (dark gray fiberglass) were established 60 cm above the seagrass canopy. The light attenuation by the screen material was estimated by measuring the photosynthetically active radiation (PAR, 400–700 nm) at noon on a clear day by comparing 10-s averages from paired underwater LI-COR cosine collectors (model LI-192SA) positioned at canopy height beneath and outside the shaded areas with an ambient surface PAR sensor (model LI-190SA). Shade treatments were 0, 0.9, 20.7, 34.1, 47.6, 56.8, 84.0, 86.0, and 90.9% light reduction on the nine plots. Benthic chambers were set up in the center of the plot to estimate the DOM fluxes of the *T. testudinum* community after five days of shading. Benthic chambers consisted of transparent gas-tight polyethylene plastic bags (Hansen et al., 2000) with sampling ports, as described in Barrón et al. (2004). The benthic chambers were deployed for 2.5 to 4 h during day and night. To avoid gas over-saturation, the plastic bags were removed between day and night incubations. Net DOC fluxes were measured as described above.

Duplicate 2 m² plots with shading screens were set up in the mixed seagrass meadow at Silaqui Island (The Philippines), in each of the following treatments: 0, 50, 65, 84, 90, 95, and 98% of reduction of the light incident on the communities. Additional details on the experimental design are reported in Gacia et al. (2005). The DOC fluxes, after 2 and 6 days of shading, were estimated using transparent benthic chambers as described above. An additional series of four benthic chambers with thick black plastic bags fitted to the PVC ring were used to examine net DOC release in communities exposed to short-term (2–4 h) darkness.

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2.3 Statistical analyses

Least-squares linear regression analysis was used to describe the relationship between the net DOC fluxes and water column temperature in seagrass communities, the net DOC fluxes under light and dark conditions in seagrass and macroalgae communities and between metabolism and net DOC fluxes in macrophyte communities. This analysis was also used to test the relationship between the light reduction and the net DOC fluxes in the shading experiments. We used the Wilcoxon signed rank test to reveal a significant tendency for the DOM fluxes to be consistently positive or negative (i.e. release vs. uptake). The Wilcoxon ranked sign test was also used to compare the net DOC fluxes after 2 and 6 days of shading in the experiment conducted in The Philippines.

3 Results

The net DOC release by seagrass meadows averaged $11.1 \pm 2.7 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Table 1, Fig. 1a), with 85% of the seagrass meadows tested acting as sources of DOC to the surrounding waters (Fig. 1a). The maximum net DOC uptake ($-53.6 \pm 10.8 \text{ mmol C m}^{-2} \text{ d}^{-1}$) and the maximum net release ($81.6 \pm 13.9 \text{ mmol C m}^{-2} \text{ d}^{-1}$) were both observed in *Cymodocea nodosa* communities (Table 1, Fig. 1a). The net DOC fluxes in seagrass communities were significantly correlated ($r^2 = 0.34$, $p < 0.01$) with the water temperature, increasing by $1.07 \pm 0.28 \text{ mmol C m}^{-2} \text{ d}^{-1}$ by each $^{\circ}\text{C}$ temperature increase (Fig. 2). All macroalgal communities studied acted as net sources of DOC (Table 2, Fig. 1b), with a higher average ($\pm\text{SE}$) net DOC flux of $29.8 \pm 8.4 \text{ mmol C m}^{-2} \text{ d}^{-1}$ than that supported by seagrass meadows. DOC release ranged an order of magnitude across macroalgal communities from a net release of $8.4 \pm 1.6 \text{ mmol C m}^{-2} \text{ d}^{-1}$ in *Caulerpa prolifera* to $71.9 \pm 33.2 \text{ mmol C m}^{-2} \text{ d}^{-1}$ in *Halimeda tuna* (Table 2).

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Light and dark net DOC flux were significantly correlated in seagrass ($r^2 = 0.17$, $p < 0.05$) and macroalgal ($r^2 = 0.72$, $p < 0.05$) communities (Fig. 3), but the net flux of DOC tended to be higher under light than dark conditions in macroalgal communities (Wilcoxon ranked sign test, $p < 0.05$; Fig. 3a). However, although 30 out of 46 seagrass communities tended to support higher net DOC fluxes under light than under dark, this tendency was not statistically significant (Wilcoxon ranked sign test, $p > 0.05$; Fig. 3a). An important fraction, 40%, of the marine macrophyte communities studied had a net DOC flux under light conditions at least two fold higher than that in the dark (Fig. 3b). There was no significant correlation between either gross primary production (GPP) or net community production (NCP) and net DOC fluxes for both seagrass and macroalgal communities ($p > 0.05$, Fig. 4a, c). However, community respiration (R) and net DOC flux were significantly and positively correlated in seagrass communities ($r^2 = 0.12$, $p < 0.05$, Fig. 4b), but not in macroalgal communities.

Experimentally-shaded *Thalassia testudinum* communities in Homossassa (Florida) supported net DOC fluxes ranging from a net uptake of $-10.41 \text{ mmol C m}^{-2} \text{ d}^{-1}$ to a net DOC release of $31.94 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (Fig. 5), independently of the level of shading imposed ($r^2 = 0.12$, $p > 0.05$). However, the mixed seagrass meadow in the Philip-pines acted as a source of DOC under all irradiances after two days of shading, except for a small net DOC uptake of $-25.3 \text{ mmol C m}^{-2} \text{ d}^{-1}$ at 88.2% of light reduction. However, after 6 days of shading all the communities receiving $>10\%$ of incident light (7 plots in total) reverted to net DOC consumption, and only a net DOC release of $284.9 \text{ mmol C m}^{-2} \text{ d}^{-1}$ persisted at 98% shading (Fig. 6). Net DOC flux in the experimentally-shaded mixed meadow was independent of the level of shading imposed after 2 days of shading ($r^2 = 0.11$, $p > 0.05$) and after 6 days of shading ($r^2 = 0.11$, $p > 0.05$). However, the net DOC fluxes in this seagrass meadow were significantly reduced after 6 days of experimental shading (Wilcoxon ranked sign test, $p < 0.05$) compared to net DOC fluxes after 2 days of shading.

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4 Discussion

The results presented show that marine macrophyte (seagrass and macroalgal) communities generally act as net sources of DOC to the ecosystem, as more than 85 % of the marine macrophyte communities studied supported a net DOC release. Marine macrophyte communities are complex assemblages including microbes, metazoans and plants, all of which are involved in dissolved organic matter (DOM) fluxes. These communities can release DOM by different mechanisms, such as release from autotrophic organisms (seagrass, benthic macro- and micro-algae, phytoplankton and epiphytes), release by leaching, and decomposition of detritus and excretion by organisms all of which can be considered to be of autochthonous origin. DOM can also be produced from release and/or decomposition of organic matter produced elsewhere (i.e. of allochthonous origin), such as DOM derived from decomposition of sestonic material trapped in the sediments (Gacia et al., 2002; Hendriks et al., 2007). Most prior studies reported DOC release rates of macrophytes isolated under laboratory conditions using ^{14}C addition experiments, concluding that DOC release from macroalgae represented from 1 to 39 % of gross primary production (Khailov and Burlakova, 1969; Brilinsky, 1977; Pregnall, 1983) compared to <5 % from seagrasses (Brilinsky, 1977; Penhale and Smith, 1977; Moriarty et al., 1986). These techniques, however, can underestimate community DOC release rates because only the carbon recently incorporated by the plant as ^{14}C can be released as DO^{14}C , neglecting, therefore, leaching from all and decaying tissues, and because the use of isolated marine macrophytes excludes the contributions of other components and compartments (e.g. sediments) of the system.

Published measurements of DOC release by marine macrophyte communities were few prior to the present study (Tables 1 and 2). A variety of seagrass meadows were studied in the Southeastern coast of Australia by Maher and Eyre (2010). They reported net DOC release by the seagrass community studied ranging from 3.5 to 41.5 $\text{mmol C m}^{-2} \text{d}^{-1}$, except for a net DOC uptake of 8.1 $\text{mmol C m}^{-2} \text{d}^{-1}$ in *Halophila*

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sp. (Table 1). Ziegler and Benner (1999a) reported consistent net DOC release by a *Thalassia testudinum* community in the Gulf of Mexico, ranging from 3.6 to 24.9 mmol C m⁻² d⁻¹, substantially higher than estimates of net DOC fluxes in the *Thalassia testudinum* community studied here (Table 1). Velimirov (1986) reported a net DOC release by a Mediterranean *P. oceanica* community of 40.2 mmol C m⁻² h⁻¹ (Velimirov, 1986), which must be considered with caution as DOC concentrations in this report varied by almost 10 fold. Most (90%) of the experiments conducted in *P. oceanica* communities supported a net DOC release, with a maximum DOC release of 34.7 mmol C m⁻² d⁻¹. Barrón et al. (2004) reported a transition of communities of the seagrass *Cymodocea nodosa* in a Mediterranean Bay from a net sink to net source of DOC along the colonization process.

Although the rates for individual communities vary greatly, the results we report here are consistent with previously published reports of DOC fluxes in seagrass meadows (e.g. Ziegler and Benner, 1999a) in that most of the communities we examined showed a net DOC release. All the macroalgal communities were net sources of DOC to the ecosystem. Yet, information on DOC release rates by macroalgal communities was even more sparse than those for seagrasses, and the only published report we are aware of corresponds to an *Ulva lactuca* community reported to release dissolved organic nitrogen (DON) to the water column under laboratory conditions (Tyler et al., 2001).

Previous studies concluded that the net DOC release rates in a *T. testudinum* community were higher in the light, ranging between 8.4 to 22.9 mmol C m⁻² d⁻¹, while in the dark DOC fluxes varied from a net uptake of 7.7 to a net release of 8.4 mmol C m⁻² d⁻¹ (Ziegler and Benner, 1999a), with DOC fluxes under the light being significantly correlated with NCP. Our results also revealed a tendency for marine macrophyte communities to support higher net DOC fluxes under the light than in the dark, a tendency that was particularly weak in seagrass meadows. *P. oceanica* communities had higher net DOC release rates in summer than in winter when water temperature was colder (Barrón and Duarte 2009), despite the increase in bacterial carbon

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demand with increased temperature (Kritzberg et al., 2010). The absence of any significant relationship between net DOC fluxes and GPP or NCP across communities suggests a weak coupling between contemporaneous light availability and seagrass and community photosynthetic activity and net community DOC release. However, there was a significant relationship between community respiration and net DOC fluxes, as reported previously for a *Cymodocea nodosa* community (Barrón et al., 2004). Maie et al. (2006) reported high DOC release during decomposition of the seagrass *Thalassia testudinum*, with 80 % of the DOC leached over the first week of decomposition. This suggests that the relationship between community respiration rate and net DOC release rate may derive from high DOC release and respiration rate during decomposition of seagrass tissues.

Further insight into the relationship between incident irradiance, photosynthetic activity, and net DOC release was derived from the two shading experiments conducted here. Net DOC fluxes were not affected by shading for 5 days of a *T. testudinum* community (Fig. 5), whereas the GPP and NCP, but not respiration rates of this seagrass meadow were significantly reduced (Calleja et al., 2006). Shading of a mixed seagrass meadow in the Philippines did not lead to any significant reduction in net DOC release after two days of shading, but it led to a significant reduction of the net DOC release when shading was maintained for 6 days. These results suggest, therefore, that whereas net community DOC release is not supported by fresh photosynthetic activity, the necessary coupling between photosynthetic production and DOC release occurs at time scales of a few days in seagrass meadows. The reduction in net DOC fluxes after 6 days of shading could have been caused by a reduction of the net DOC release from seagrass communities or by an increase in DOC consumption due to mainly bacterial respiration as suggested above.

DOC release by a *Thalassia testudinum* community represented about 10 % of the net community production in Laguna Madre (Ziegler and Benner, 1999a). The rates of net DOC release by seagrass communities reported here represented on average 38 % of the GPP, but 83 % of their NCP. The net DOC release in macroalgal communities

represented on average 27 % of the GPP but more than 300 % of the NCP. Because carbon burial and particulate carbon export by macrophyte stands typically exceed 40 % of NPP (Duarte and Cebrián, 1996), the high net DOC release relative to NCP of the macrophyte communities studied here is unlikely to be supported by autochthonous photosynthetic production alone. Allochthonous inputs of sestonic materials, which are important in seagrass communities (e.g. Gacia et al., 2002; Hendriks et al., 2007) may play an important role in supporting the net DOC release of macrophyte communities through DOC leaching during decay of seston particles in seagrass sediments.

The total global net DOM flux from marine macrophytes was estimated using the average net DOM release by marine macrophytes derived here of $4047.85 \pm 967.25 \text{ mmol C m}^{-2} \text{ y}^{-1}$ and $10887.95 \pm 3047.75 \text{ mmol C m}^{-2} \text{ y}^{-1}$ for seagrass meadows and macroalgal communities, respectively, and the area estimated to be covered by macroalgae ($1.4 \times 10^{12} \text{ m}^2$, Duarte et al., 2005) and seagrass meadows [$0.3 \times 10^{12} \text{ m}^2$, (Duarte et al., 2005) to $0.6 \times 10^{12} \text{ m}^2$ (Charpy-Roubaud and Sournia, 1990)]. The estimated global net DOC flux, and hence export, from seagrass meadows ranged from $0.015 \pm 0.003 \text{ Pg C yr}^{-1}$ to $0.029 \pm 0.007 \text{ Pg C yr}^{-1}$ depending on whether the low or high estimates of global seagrass cover is used. This range encompasses the global net DOC flux of $0.019 \text{ Pg C yr}^{-1}$ estimated by Maher and Eyre (2010), who used data on net DOC fluxes from eleven seagrass meadows compiled from five references, while our estimate is based on 66 estimates. The global net DOC export from seagrass meadows reported here represents 41 % of the global NCP of seagrass meadows calculated by Duarte et al. (2010). The estimated global net DOC export from macroalgal beds is $0.18 \pm 0.051 \text{ Pg C yr}^{-1}$, well above that of seagrass meadows. Thus, the global net DOC release by marine macrophytes supports a net carbon export of about $0.197 \pm 0.015 \text{ Pg C yr}^{-1}$ to $0.212 \pm 0.016 \text{ Pg C yr}^{-1}$. The global net DOC export from macrophyte communities represents a modest flux relative to the metabolism of the coastal ocean, but is significant relative to the net community production of benthic habitats and of a similar magnitude as burial rates (Duarte et al., 2005). The fate of the DOM exported from marine macrophyte communities is, however, unknown. DOM

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release represents an important, but poorly understood flux from macrophyte communities that may contribute to support metabolism in adjacent pelagic ecosystems.

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Table 1. Net dissolved organic carbon (DOC) fluxes (mean \pm SE; rates in $\text{mmol C m}^{-2} \text{d}^{-1}$) in seagrass meadows. Negative values represent net uptake while positive values represent net release. The overall average of DOC fluxes are reported at the bottom.

Field site	Specie	Temp. °C	DOC \pm SE $\text{mmol C m}^{-2} \text{d}^{-1}$	Comments	Ref.
Bolinao, The Philippines	Mixed seagrass meadow <i>Enhalus acoroides</i>		76.36	March 2000	1
			18.88 \pm 16.48	March 2000	
Delta del Ebro, Spain	<i>Cymodocea nodosa</i>		-34.88 \pm 12.09	July 2000, 0.5 yr old	2
			38.17 \pm 2.43	July 2000, 3.3 yr old	
			12.75 \pm 7.71	July 2000, 2.3 yr old	
			81.57 \pm 13.89	July 2000, 6.1 yr old	
			75.23 \pm 22.55	July 2000, 3.8 yr old	
			-53.59 \pm 10.82	July 2000, 1.4 yr old	
Trondheim, Norway	<i>Zostera marina</i>		17.01 \pm 8.90	July 2000, 5.3 yr old	1
			10.61 \pm 2.18	September 2000	
Porto Colom, Mallorca I., Spain	<i>Posidonia oceanica</i>		6.96 \pm 1.29	September 2000	1
			1.82 \pm 1.39	May 2001	
Cabrera I. Spain	<i>Cymodocea nodosa</i>		5.93 \pm 1.68	May 2001	1
Santa María, Cabrera I., Spain	<i>Posidonia oceanica</i>		15.64 \pm 3.67	May 2001	
Port, Cabrera I., Spain	<i>Posidonia oceanica</i>		-1.05 \pm 2.26	May 2001	1
Cap Enderrocat, Mallorca I., Spain	<i>Posidonia oceanica</i>		4.99 \pm 2.59	March 2002	
Magaluf Bay, Mallorca I., Spain	<i>Posidonia oceanica</i>		13.83 \pm 3.94	June 2002	1
			-18.50 \pm 12.17	June 2002, at 22 m deep	
			1.44 \pm 2.65	June 2002, at 15 m deep	
			19.62 \pm 3.18	June 2002, at 4 m deep	

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Table 1. Continued.

Field site	Specie	Temp. °C	DOC ± SE mmol C m ⁻² d ⁻¹	Comments	Ref.
Magaluf Bay, Mallorca I., Spain	<i>Posidonia oceanica</i>		-20.75	March 2001	3
			3.00±1.78	April	
			13.73±2.24	May	
		22.64	17.40±3.37	June	
		25.08	10.57	July	
		27.2	34.23±8.47	August	
		25.69	12.18±4.25	September	
		23.6	10.79±3.37	October	
		18.63	8.04±1.22	November	
		15.63	2.79±5.43	December	
		13.93	2.11±0.35	January 2002	
		14.46	6.11±1.87	February	
		14.42	5.20±3.19	March	
		15.16	10.76±1.83	April	
		18.91	8.19±3.38	May	
Ria formosa, Portugal	<i>Zostera noltii</i> <i>Cymodocea nodosa</i>	22.38	34.68±4.11	June	4
		26.34	10.34±4.12	July	
		26	8.19±8.82	August	
		22.67	14.53±6.53	October	
			-13.25±9.69	July 2002	
	-3.61±4.57	July 2002			

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Table 1. Continued.

Field site	Specie	Temp. °C	DOC ± SE mmol C m ⁻² d ⁻¹	Comments	Ref.
Homossassa, Gulf of Florida, USA	<i>Thalassia testudinum</i>		-0.18	October 2003	1
	<i>Thalassia testudinum</i>		3.37	October 2003	
	<i>Thalassia testudinum</i>		-15.42±3.53	October 2003	
	<i>Syringodium filiforme</i>		32.99±10.03	October 2003	
	<i>Halodule wrightii</i>		21.67±32.10	October 2003	
Laguna Madre, USA	<i>Thalassia testudinum</i>	30.65	24.9±7.9	July 1996	5,6
		30.53	23±0.7	September	
		23.90	3.6±19.6	November	
		11.55	3.5±20.5	January 1997	
		20.67	14.2±11.7	March	
		27.30	5.6±16.1	June	
Sounion Aegaeen Sea (Greece)	<i>Posidonia oceanica</i>	13.93	4.62±3.17	April 2006	7
		23.41	4.98±3.54	June	
		25.78	7.21±2.65	August	
		21.29	12.55±4.50	October	
		16.14	1.66±1.12	December	
		14.05	-17.37±2.70	February 2007	
Southeastern coast of Australia	<i>Posidonia</i> sp.		6.37±5.13	April	8
	<i>Ruppia</i> sp.		26.10±3.70	sandy sediments	
	<i>Ruppia</i> sp.		22.40±16.40	muddy sediments	
	<i>Ruppia</i> sp.		26.1±8.4	muddy sediments	
	<i>Zostera</i> sp.		3.5±9	muddy sediments	
	<i>Zostera</i> sp.		41.5±19	sandy sediments	
	<i>Halophila</i> sp.		-8.1±4.2	muddy sediments	
<i>Halophila</i> sp.		15.1±11.4	sandy sediments		
Average			11.09±2.65		

Note: 1 Unpubl.; 2 Barrón et al., 2004; 3 Barrón and Duarte 2009; 4 Santos et al., 2004; 5 Ziegler et al., 1999a; 6 Ziegler et al., 2004; 7 Apostolaki et al., 2010a; 8 Maher and Eyre 2010.

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Table 2. Net dissolved organic carbon (DOC) fluxes (mean \pm SE; rates in $\text{mmol C m}^{-2} \text{d}^{-1}$) in macroalgal communities. Negative values represent a net uptake while positive values represent a net release. References (Ref.) are shown in the note below.

Field site	Specie	DOC \pm SE $\text{mmol C m}^{-2} \text{d}^{-1}$	Ref.
Bolinao, The Philippines	<i>Caulerpa racemosa</i>	37.66 \pm 6.15	1
	<i>Halimeda tuna</i>	71.89 \pm 33.06	
Oslofjord, Norway	<i>F. serratus</i>	35.15 \pm 5.49	1
Trondheim, Norway	Laminaria	30.62	
	<i>Fucus vesiculosus</i>	15.03 \pm 1.91	
Porto Colom, Mallorca I., Spain	<i>Caulerpa prolifera</i>	8.39 \pm 1.57	1
Southeastern coast of Australia	Habitat dominated by macroalgae	10.10 \pm 5.20	2
Average		29.83 \pm 8.35	

Note: 1 Unpubl.; 2 Maher and Eyre 2010.

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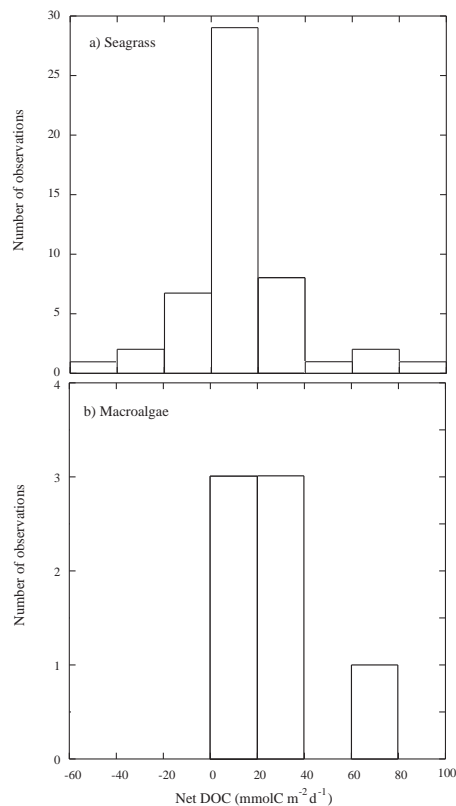


Fig. 1. Frequency distribution of the net daily DOC fluxes ($\text{mmol C m}^{-2} \text{d}^{-1}$) in **(a)** seagrass and **(b)** macroalgal communities. Average \pm SE shown. Data from Tables 1 and 2.

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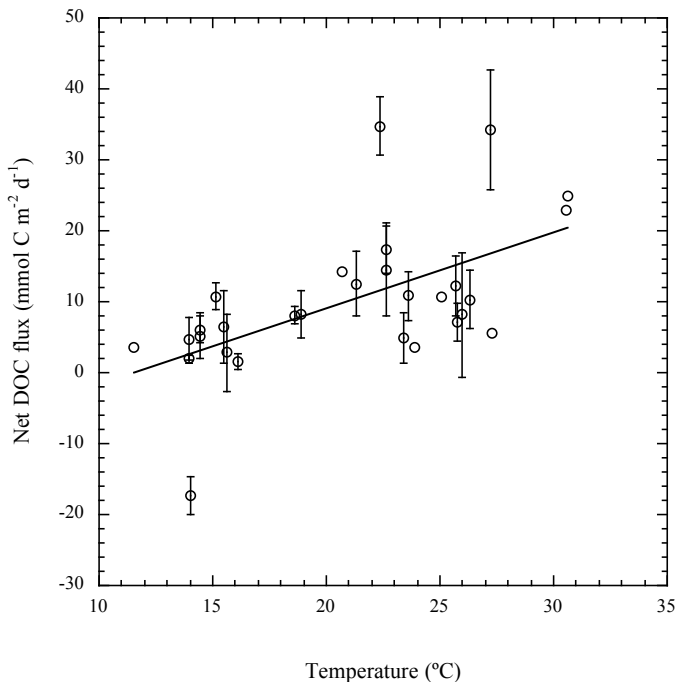


Fig. 2. The relationship between the net DOC flux ($\text{mmol C m}^{-2} \text{d}^{-1}$) in seagrass communities and in situ water temperature ($^{\circ}\text{C}$). The solid line represents the fitted linear regression equation $\text{Net DOC flux (mmol C m}^{-2} \text{d}^{-1}) = -12.30 (\pm 6.17) + 1.07 (\pm 0.28) T (^{\circ}\text{C})$, $r^2 = 0.34$, $p < 0.01$.

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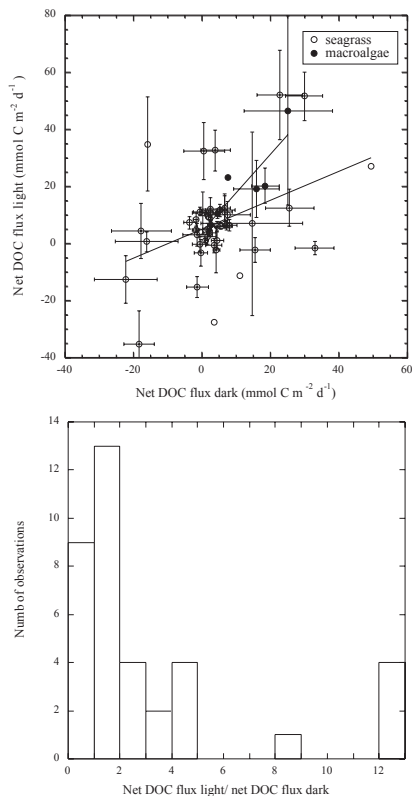


Fig. 3. (a) The relationship between net DOC flux under light and dark conditions in macroalgal and seagrass communities. The solid line represents the linear regression fitted for seagrass communities: $\text{Net DOC flux light (mmol C m}^{-2} \text{ d}^{-1}) = 4.70 (\pm 2.24) + 0.51 (\pm 0.17) \text{ Net DOC dark}$, $r^2 = 0.17$, $p < 0.01$. The dashed line represents the linear regression fitted for macroalgal communities: $\text{Net DOC flux light (mmol C m}^{-2} \text{ d}^{-1}) = 4.72 (\pm 6.10) + 1.34 (\pm 0.41) \text{ Net DOC dark}$, $r^2 = 0.72$, $p < 0.05$; Average \pm SE shown. **(b)** Frequency distribution of the ratio of net DOC fluxes in light and dark.

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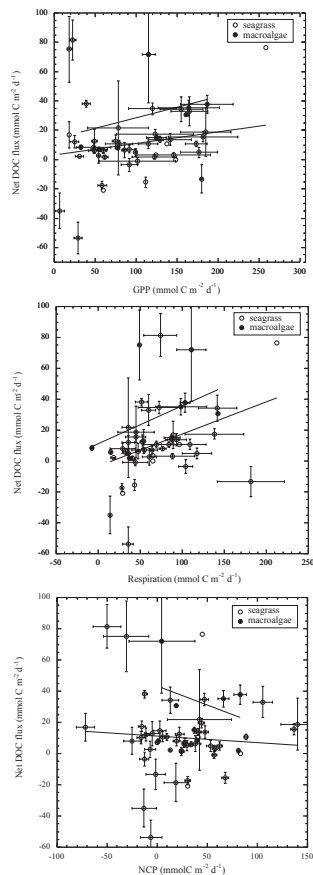


Fig. 4. The relationship between gross primary production (**a**; GPP), respiration (**b**; R) and net community production (**c**; NCP) and net DOC flux in seagrass and macroalgal communities. The solid line represents the linear regression fitted for both marine macrophyte communities. The only relationship that is significantly different from zero is R in seagrasses; Net DOC flux ($\text{mmol C m}^{-2} \text{d}^{-1}$) = $-2.54 (\pm 6.30) + 0.20 (\pm 0.08) R$, $r^2 = 0.12$, $p < 0.05$.

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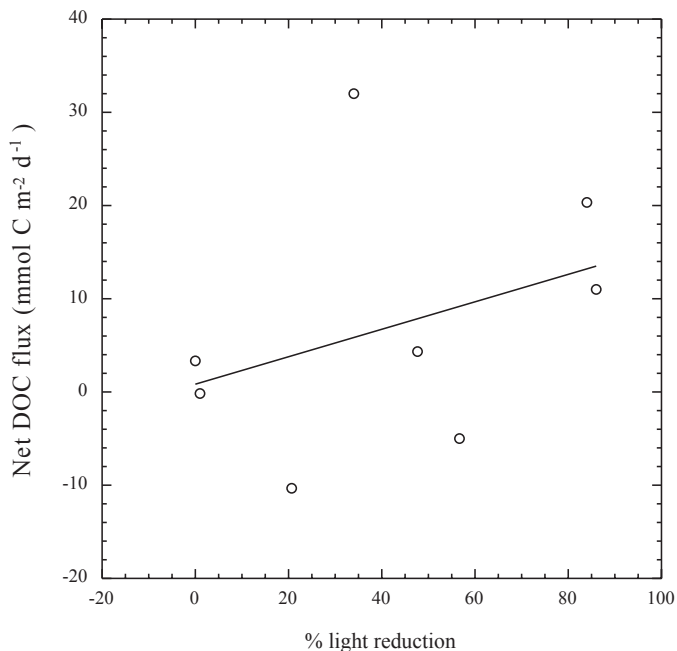


Fig. 5. The relationship between the net DOC flux ($\text{mmol C m}^{-2} \text{d}^{-1}$) and the experimental shading in the *Thalassia testudinum* meadow in Florida, after 5 days of shading. Negative values represent net DOC consumption. Net DOC fluxes ($\text{mmol C m}^{-2} \text{d}^{-1}$) = $0.84 (\pm 8.13) + 0.14 (\pm 0.16) \% \text{ light reduction}$, $r^2 = 0.13$, $p > 0.05$.

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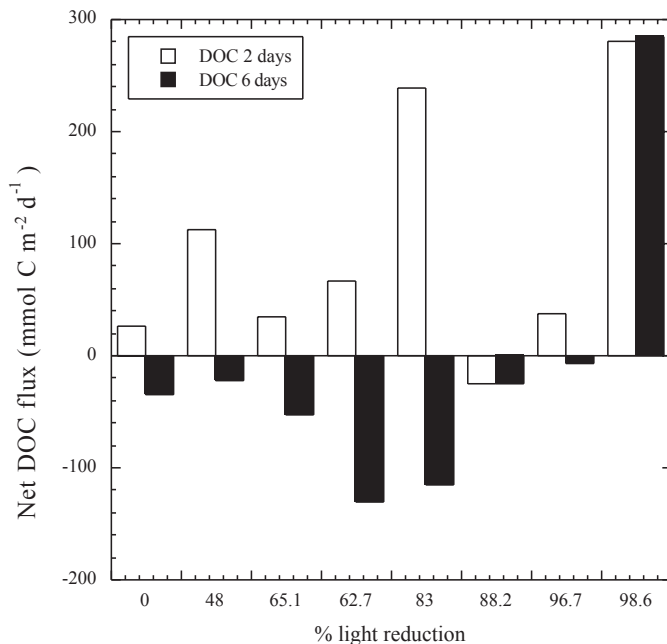


Fig. 6. The relationship between the net DOC flux under light conditions ($\text{mmol C m}^{-2} \text{d}^{-1}$) and the experimental shading in the mixed Philippine seagrass meadow after 2 days of shading; Net DOC fluxes ($\text{mmol C m}^{-2} \text{d}^{-1}$) = $20.59 (\pm 94.96) + 1.12 (\pm 1.27) \% \text{ light reduction}$, $r^2 = 0.11$, $p > 0.05$, and 6 days of shading Net DOC fluxes ($\text{mmol C m}^{-2} \text{d}^{-1}$) = $-102.79 (\pm 112.30) + 1.32 (\pm 1.51) \% \text{ light reduction}$, $r^2 = 0.11$, $p > 0.05$. Negative values represent net DOC consumption.

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