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Ecosystem metabolism along a colonization gradient of eelgrass (*Zostera marina*) measured by eddy correlation

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Abstract

The Virginia coastal bays experienced local extinction of eelgrass (*Zostera marina*) during the early 1930s, and restoration beginning in 2001 has generated an ecosystem state change from bare to vegetated sediments. Oxygen fluxes were measured seasonally using the eddy correlation technique at three sites representing different stages of seagrass colonization: unvegetated (bare), 5 yr, and 11 yr since seeding. Derived seasonal ecosystem respiration (R) and gross primary production (GPP) increased up to 10-fold and 25-fold, respectively, with meadow age. Although hourly oxygen (O_2) fluxes were highly correlated with light at the vegetated sites, no identifiable trends with light were observed at the bare site. The light compensation point where O_2 production and respiration are in balance increased from 46 μmol photons m^{-2} s^{-1} to 257 μmol photons m^{-2} s^{-1} and 63 μmol photons m^{-2} s^{-1} to 472 μmol photons m^{-2} s^{-1} at the 5 yr and 11 yr seagrass sites, respectively, with increasing seasonal temperatures from 12.3°C to 27.9°C and 9.3°C to 30.5°C, respectively. This suggests that more light, and thus more O_2 production, is required to offset increasing respiration with both temperature and meadow age. Photosynthesis–irradiance curves generated from hourly O_2 fluxes throughout the seasons were used to estimate annual net ecosystem metabolism (NEM). Annual NEM rates at the bare, 5 yr, and 11 yr sites were −7.6, 8.6, and −7.0 mol O_2 m^{-2} yr^{-1}, respectively. Although the system went through a period of net autotrophy during early stages of colonization, the ecosystem state change from unvegetated sediments to dense seagrass meadows changed the magnitude of both GPP and R, but not the overall metabolic balance of the system.

Seagrass decline has been well-documented worldwide (Waycott et al. 2009), and seagrass restoration via seeding or transplanting is used as a mechanism to reverse this trend and return important ecosystem services to coastal environments (McGlathery et al. 2012; Orth et al. 2012). Relative to unvegetated habitats, seagrasses are globally significant to carbon (C) sequestration (Duarte et al. 2010; Mcleod et al. 2011; Fourqurean et al. 2012) through high rates of primary productivity (Eyre et al. 2011; Hume et al. 2011) and organic matter deposition and burial (Gacia et al. 2002; Duarte et al. 2010; Greiner et al. 2013). Thus, a detailed understanding of the effect of seagrass colonization on ecosystem metabolism is important as a key component of coastal C dynamics.

Seagrass restoration is expected to alter coastal benthic ecosystem metabolism significantly by changing community structure and associated rates of metabolism. Seagrass meadows have higher production relative to unvegetated sediments (Barrón et al. 2004; Eyre et al. 2011; Hume et al. 2011) in part because they have greater primary producer and heterotrophic consumer biomass (Hemminga and Duarte 2000). In addition, changes in ecosystem structure through the development of a seagrass canopy can increase efficiency of light absorption on an ecosystem scale relative to unvegetated sites (Binzer et al. 2006; Ralph et al. 2007). Finally, seagrass communities affect flow conditions and create a depositional environment (Gacia and Duarte 2001; Hansen and Reidenbach 2012), increase sediment organic content (Fourqurean et al. 2012; McGlathery et al. 2012; Greiner et al. 2013), and change sediment oxygenation through release of oxygen from the roots and rhizomes (Frederiksen and Glud 2006).

The coastal lagoons of the Virginia Coast Reserve (VCR) have been the site of a successful large-scale seagrass restoration project (McGlathery et al. 2012; Orth et al. 2012). These coastal bays historically were colonized by eelgrass (*Zostera marina*), but underwent an ecosystem state change in the late 1920s and early 1930s when *Z. marina* was completely removed from the system as a result of disease (slime mold *Labrynthula zosterae*) and a hurricane in 1933 (Cottam and Munro 1954). Until the late 1990s, the lagoons were devoid of *Z. marina*, and between 2001 and 2008, a systematic restoration via seeding occurred and meadows have continued to expand by natural recruitment to cover over 17 km^2 by 2012 (Orth et al. 2012). The restoration design created a well-defined chronosequence in which the effects of seagrass colonization on the coastal lagoons can be studied (McGlathery et al. 2012). Recovery trajectories of seagrass in the coastal bays show the reinstatement of key ecosystem services with increased age (time since seeding), including seagrass productivity, enhanced sediment deposition, and sequestration of C and nutrients (McGlathery et al. 2012).

The eddy correlation technique (Berg et al. 2003) is a powerful approach to measure ecosystem metabolism because it provides the most direct and accurate measure of in situ oxygen fluxes. Compared to flux chamber methods, it can be deployed so that it does not alter the local hydrodynamics or ambient light (Berg et al. 2003). Additionally, O_2 fluxes can usually be extracted from

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15 min of data, allowing for high-resolution flux records that typically cannot be obtained with other methods (Lorrai et al. 2010). Finally, the seafloor area contributing to the measured flux covers many square meters and can integrate over most heterogeneous environments (Berg et al. 2007; Rheuban and Berg 2013). The eddy correlation technique has been used successfully in a number of environments where it is difficult to apply traditional flux methods, including seagrass meadows, permeable sediments, and coral reefs (Hume et al. 2011, Berg et al. 2013, Long et al. 2013).

Using the eddy correlation technique, we measured O_2 fluxes seasonally at three sites representing the chronosequence to determine how ecosystem metabolism changes with seagrass colonization. Based on O_2 fluxes, we quantified daily values of ecosystem respiration (R), gross primary production (GPP), and net ecosystem metabolism (NEM) throughout the year. In addition, we developed a non-linear regression model based on light availability to predict NEM continuously for 1 yr to estimate annual net metabolism for the different-aged sites.

Methods

Study sites—The study was conducted in the shallow lagoons of the Virginia Coast Reserve (VCR) Long Term Ecological Research (LTER) site, which are ~ 1 m deep at mean low water with a 1.2 m tidal range. Three sites were chosen that represent different stages of seagrass colonization: unvegetated sediments (no seeding), a young meadow (seeded in 2007), and an older meadow (seeded in 2001). The unvegetated sediment site (hereafter labeled as "bare") and the young meadow (hereafter labeled "5 yr") were located in Hog Island Bay (37°24′58.068″N, 75°42′35.33″W and 37°25′7.0788″N, 75°43′19.718″W for the bare and 5 yr site, respectively), and the older meadow (hereafter labeled "11 yr") was located in the adjacent South Bay (37°15′43.662″N, 75°48′54.554″W). Site characteristics of the two bays were not significantly different with respect to bathymetry, water depth, currents, and sediment and water-column parameters, and thus could be used as a chronosequence to compare the effects of seagrass colonization (McGlathery et al. 2012). The 11 yr site was the location of a previous eddy correlation study completed in 2007 (Hume et al. 2011), which allowed us to compare metabolism at the same site across different years. The seagrass sites were originally seeded in 0.4 ha plots with 100,000 *Z. marina* seeds per plot.

Data collection—Data were collected during four seasons related to *Z. marina* growth based on temperature: autumn regrowth after summer heat stress, low winter growth, early summer peak growth, and late summer heat stress (Orth and Moore 1986; Rheuban et al. 2014). The specific months sampled were early August 2011 at the 11 yr site (then 10 yr), and October 2011, February 2012, June 2012, and August 2012 at all three sites. The seasonal overlap (August 2011 and 2012) from the 11 yr site was designed to address interannual variation in metabolism rates.

Shoot density and benthic chlorophyll content were measured seasonally. Shoot density was measured by counting all shoots located within 4–10 haphazardly thrown 0.25 m^2 quadrats. During February 2012, because of logistical constraints of working at low temperatures, shoots were counted in eight replicate 0.125 m^2 quadrants. Benthic chlorophyll and phaeopigments were measured by collecting the top 1 cm of sediment in eight replicate 10 cm^3 syringe cores, and extracted in a 45:45 methanol : acetone solution as in McGlathery et al. (2012). Above- and belowground biomass and seagrass morphology data from K. J. McGlathery (unpubl.) were used from a larger annual survey in July 2011 and July 2012. Sediment permeability was measured at the bare site using a falling head permeameter (Klute and Dirksen 1986).

The eddy correlation instrument consisted of an acoustic Doppler velocimeter (ADV, Nortek-AS), coupled to a fast-responding (90% response time < 0.3 s) Clark-type O_2 microsensor (Unisense Science) via a submersible picoamp amplifier (McGinnis et al. 2011). These sensors are self-contained and mounted on a stainless steel tripod designed to minimize disturbance to the natural flow. The O_2 microsensor was set such that the sensing tip was located just outside the ~ 2 cm^3 measuring volume of the ADV, to minimize time lag between velocity and O_2 measurements. The measuring volume was adjusted such that it was located 31 cm, 26 cm, and 10 cm above the bottom at the 11 yr, 5 yr, and bare sites, respectively. These different measuring heights were chosen so that measurements were obtained above the seagrass canopy and not exposed at low tide because of small differences in water depth between sites. Care was taken to ensure the instruments were level and oriented into the dominant mean current direction at each site. The sensors recorded data continuously at 32 or 64 Hz in 14.5 min periods followed by a 0.5 min pause, and one flux value was extracted from each 14.5 min time period, producing four flux estimates h^{-1}. In each deployment, the eddy correlation instrument recorded data for 24 h with a 1–2 h gap between deployments to download data and to replace batteries and O_2 microsensors as needed. Deployments at each site ran for 3–8 d during each sampling season for 66 separate deployments. O_2 microsensors are fragile and often were destroyed mid-deployment; therefore, only 37 full 24 h data sets were collected to estimate daily metabolism.

Environmental state variables were also measured during deployments. Photosynthetically active radiation (PAR) was recorded every 15 min at the measurement height using a submersible planar 2π PAR sensor (Odyssey Data Recording) calibrated to a LI-193SA 4π scalar PAR sensor (LI-COR Biosciences; Long et al. 2012). Mean O_2 concentration and temperature were recorded every 15 min by either an optical Luminescent Dissolved Oxygen (LDO) probe (Hach Systems) mounted in a waterproof housing or a submersible optical dissolved oxygen datalogger (miniDOT, PME). Mean current velocity, direction, and water depth were extracted from the ADV data.

During June 2012, O_2 fluxes were also estimated from sediment core incubations for the bare site (Tyler et al. 2003) to compare with the eddy correlation fluxes. Six sediment cores (20 cm deep and 6 cm diameter) with overlying water and seawater from the site were collected

and kept on ice in the dark until returned to the lab. Sediment cores were bubbled with air and allowed to equilibrate overnight in an outdoor flowing seawater mesocosm to maintain in situ temperatures. After equilibration, the overlying water column was carefully siphoned off and replaced with filtered (Whatman, GF/C 0.2 μm) seawater from the site. Sediment cores were capped with lids in which magnetic stir bars were mounted, and care was taken so that no air bubbles were introduced into the cores. Six replicate sediment cores and two cores with only filtered seawater were incubated for 3 h in light at $\sim$ 600 μmol photons m^{-2} s^{-1}, after which the mesocosm was covered and cores were incubated for 3 h in dark. Water samples were collected every 0.5 h and replaced with an equal volume of filtered seawater from the site. Dissolved O_2 was measured with the LDO probe and concentration changes were corrected for additions of new filtered seawater to the cores. Oxygen fluxes were estimated from the measured concentration changes.

Data analysis—Oxygen fluxes, each covering 15 min periods, were extracted from the eddy correlation data using EddyFlux2.0 software (P. Berg unpubl.) following the procedure described in detail in Rheuban et al. (2014). Hourly averages of O_2 fluxes with associated standard errors (SE) were calculated from 15 min flux extractions and then grouped into "light" and "dark" data for regression analysis, where "light" was defined as PAR $\geq$ 1.0 μmol photons m^{-2} s^{-1} and "dark" was PAR $<$ 1.0 μmol photons m^{-2} s^{-1}. A few hourly fluxes were missing because of fouled or broken O_2 microsensors and were determined by interpolation using regressions from adjacent data. Daily GPP, R, and NEM were estimated using the equations from Hume et al. (2011). These equations assume that R is constant during the day and night, which may lead to underestimation of both GPP and R (Glud 2008); however, NEM is not affected because it is calculated directly from the eddy flux measurements.

Metabolism from the sediment core incubations was determined from the measured O_2 fluxes over the incubation period. Respiration was calculated from dark incubations, NEM was calculated from light and dark incubations scaled for hours of daylight, and GPP was calculated as

$$\mathrm{GPP} = |\mathrm{DARK}|h_l + \mathrm{LIGHT}h_l \quad (1)$$

where DARK and LIGHT are measured fluxes in the dark and light in units of mmol O_2 m^{-2} h^{-1}, and h_l is hours of light during the day.

PAR and O_2 flux values were used to determine photosynthesis–irradiance (P–I) relationships seasonally, with a hyperbolic tangent function (Jassby and Platt 1976) modified to account for respiration that was fit to the hourly O_2 flux values:

$$\mathrm{Flux} = P_{\max} \tanh \frac{I}{I_s} - R_I \quad (2)$$

where $P_{\max}$, I_S, and R_I are fitting constants that represent maximum photosynthetic rate, light saturation, and respiration, respectively; and I is available light (e.g., PAR_{canopy}, *see* below). If no light saturation is occurring, this function converges to a linear function. During seasons where the P–I response was linear, the best fit based on r^2 value between the Eq. (2) and a linear fit was chosen. Using all four seasonal P–I relationships for the seagrass sites, we calculated hourly NEM values throughout a year (November 2011 to October 2012) by interpolation between the midpoints of each season. The P–I relationships were driven by light measured at a meteorological tower ($\sim$ 6.5 km away from the 11 yr site) that was calibrated to concurrent light measured underwater above the seagrass canopy during deployment periods in October 2011, February 2012, and June 2012. During the August 2011 sampling, the meteorological station PAR sensor was inactive, and during the August 2012 sampling, fouling due to particle settling or macroalgal shading limited the number of underwater data available for this calibration. From the hourly NEM values covering the whole year, the cumulative annual NEM was determined. Because a weak or no relationship between light and metabolism was observed at the bare site, seasonally measured NEM was used to estimate NEM over the course of the year.

Results

Shoot density and benthic pigments were highly variable across both seasons and sites (Table 1). The permeability at the bare site was 5.8×10^{-12} m^2, which is at the border above which pore-water advection rather than molecular diffusion dominates transport in the surface sediments (Huettel and Gust 1992). This increases the risk for flux methods that isolate a portion of the sediment (flux chambers or sediment core incubations) to underestimate the O_2 flux (Berg et al. 2013).

An increase in gross metabolism (GPP and R) with meadow age (time since seeding; Fig. 1A,D) was evident for the chronosequence in October (R, linear fit: $r^2 = 0.98$, $p = 0.07$; GPP, linear fit: $r^2 = 0.99$, $p = 0.04$, fit not shown) and August 2012 (R, linear fit: $r^2 = 0.99$, $p = 0.02$; GPP, linear fit: $r^2 = 0.99$, $p = 0.005$, fit not shown). NEM was only significantly different between sites in June (one-way ANOVA with Tukey post-hoc test, $F_9 = 20.5$, $p = 0.001$). At the bare site, there was no significant difference between sediment core and eddy correlation estimates of GPP, while R and NEM were significantly smaller in the sediment cores (Table 2).

The effect of meadow age on rates of R and GPP can also be seen when comparing fluxes over time at the 11 yr site (Fig. 2). Combining our August 2011 data with those measured by an earlier eddy correlation study (Hume et al. 2011) at the same site showed the following pattern: NEM shifted from balanced at the bare site (one-sample t-test, $p = 0.11$) to slight autotrophy (at the $\alpha = 0.1$ significance level $p = 0.09$) at 6 yr after seeding (as reported in Hume et al. 2011), to net heterotrophy at 10 yr since seeding (t-test, $t = -3.29$, df = 4, $p = 0.03$). The metabolism rates calculated at the bare site in Hume et al. (2011) were not significantly different from the rates reported during any sampling period in the present study (one-way ANOVA, R:

Table 1. Site characteristics for the bare, 5 yr, and 11 yr sites. Benthic chlorophyll (Chl) and phaeopigment (Phaeo) concentrations (mg m^{-3}) ± SE (n = 8) and seagrass shoot density (Density ± SE, shoots m^{-2}) are given for each site. The number of samples varied by season and is shown in parentheses. The bare and 5 yr sites were not sampled in August 2011.

Site	Aug 2011	Oct	Feb	Jun	Aug 2012
Bare					
Chl	—	23.2±3.8[a]	18.7±3.1[a]	23.8±3.3[a]	28.6±5.1[a]
Phaeo	—	34.9±5.0	30.6±5.5	34.5±5.1	38.5±3.7
5 yr					
Chl	—	38.2±3.9[a,b]	50.4±7.3[a,b]	31.7±4.2[a]	38.6±5.9[a,b]
Phaeo	—	42.1±5.4	48.1±4.3[1]	32.7±2.6	37.0±1.7
Density	—	26±2.5 (4)[α,3]	196±120.6 (8)[1]	407.3±78.4 (6)[α,2]	224±23.9 (8)[α,1]
11 yr					
Chl	54.7±6.9	43.8±4.9[b]	90.5±27.2[b]	50.7±4.7[b]	54.5±7.2[b]
Phaeo	15.5±3.6[1]	34.8±3.7[2]	32.9±5.5[2]	34.8±2.7[2]	38.4±4.3[2]
Density	516.4±49.8 (10)[1]	250.0±18.2 (4)[β,3]	158.2±64.2 (8)[3]	696±106.7 (6)[β,4]	490±19.3 (8)[β,1,2]

[a, b, α, β] indicates statistical difference at α = 0.05 using a one-way ANOVA and Tukey post-hoc means test across the three sites during a single sampling season.
[1,2,3,4] indicates statistical difference at α = 0.05 using a one-way ANOVA and Tukey post-hoc means test across sampling seasons at a single site.

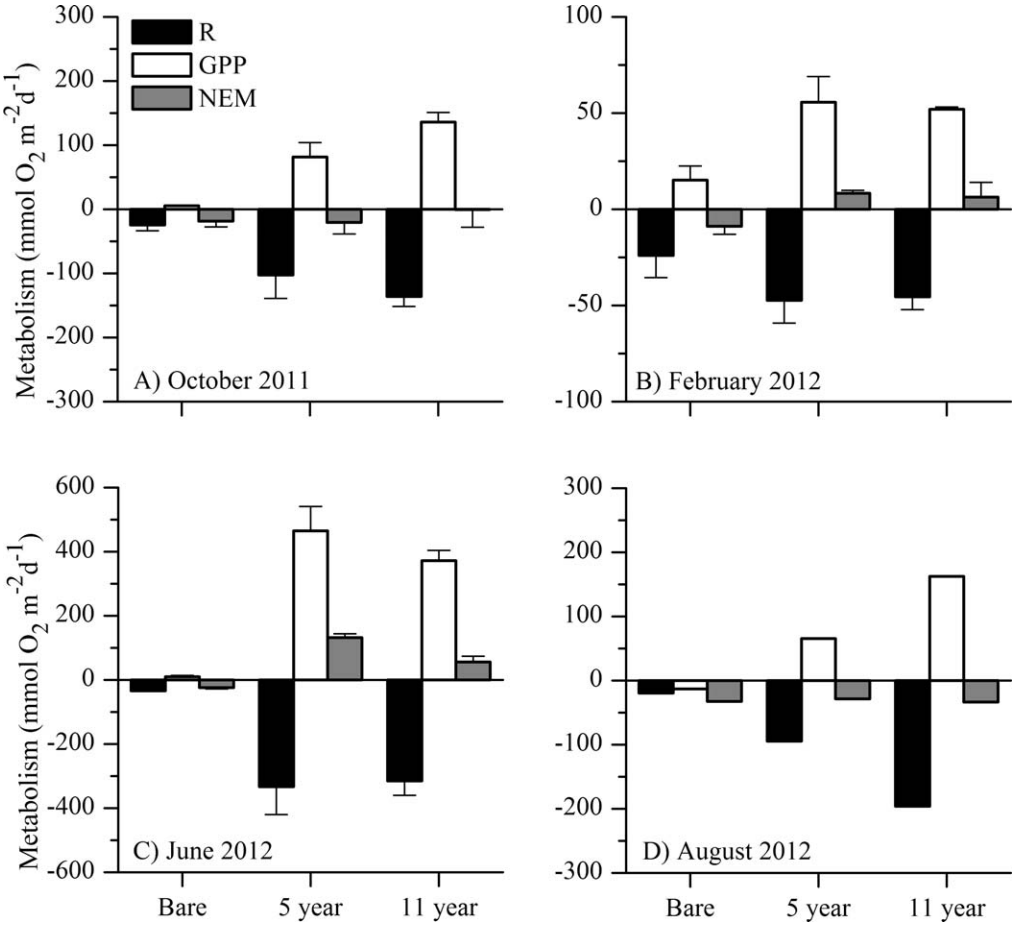

Fig. 1. (A–D) Average seasonal respiration (R), gross primary production (GPP), and net ecosystem metabolism (NEM) for October, February, June, and August, respectively. Note the different scales on the y-axis. Error bars are SE. Error bars are missing for August because average metabolic numbers for this season were obtained by combining all fluxes, each with several hourly fluxes missing, into one continuous 24 h record averaged by hour and then calculated as in Hume et al. (2011).

Table 2. Comparison of respiration (R), gross primary production (GPP), and net ecosystem metabolism (NEM) from sediment core and eddy correlation (EC) measurements in June 2012 (± SE, $n = 6$ and 3, respectively). The results of a two-sample *t*-test are given.

Method	R (mmol O_2 m^{-2} d^{-1})	GPP (mmol O_2 m^{-2} d^{-1})	NEM (mmol O_2 m^{-2} d^{-1})
Sediment cores	−19.2±1.9	10.4±1.9	−8.8±1.8
EC	−34.0±1.7	10.4±3.7	−23.6±4.1
df	7	7	7
p	0.002	0.991	0.006

$F_{12} = 0.585$, $p = 0.68$; GPP: $F_{12} = 0.990$, $p = 0.472$; NEM: $F_{12} = 1.019$, $p = 0.459$).

The seasonal average data from the August 2012 sampling at the 11 yr site (−196.1, 162.4, and −33.6 mmol O_2 m^{-2} d^{-1} for R, GPP, and NEM, respectively) fell within the 95% confidence interval of the mean from the 2011 sampling (−276.3 to −182.8, 142.8 to 221.2, and −87.8 to −7.4 mmol O_2 m^{-2} d^{-1} for R, GPP, and NEM, respectively).

Hourly fluxes from both the 5 and 11 yr sites were well-correlated to PAR during all seasons (Figs. 3, 4). Variability at the 5 yr site was much higher, and P–I relationships had a hyperbolic tangent relationship during all seasons (Fig. 3). However, during October, June, and August at the 11 yr site, linear P–I relationships were observed (Fig. 4A, C,D).

Using P–I relationships (Eq. 2) fitted to the hourly fluxes, the compensation irradiance (I_{comp})—the amount of light required for photosynthesis to balance respiration—was determined for each season at the 5 and 11 yr sites (Fig. 5). Between February and August, I_{comp} increased from 46 μmol photons m^{-2} s^{-1} to 257 μmol photons m^{-2} s^{-1} at the 5 yr site and from 63 μmol photons m^{-2} s^{-1} at to 472 μmol photons m^{-2} s^{-1} at the 11 yr site, corresponding to an average increase in temperature from 12.3°C to 27.9°C and 9.3°C to 30.5°C, respectively. A log-linear relationship between I_{comp} and temperature was observed at both sites (Fig. 5; 5 yr: $r^2 = 0.901$, $p = 0.051$ and 11 yr: $r^2 = 0.94$, $p = 0.030$).

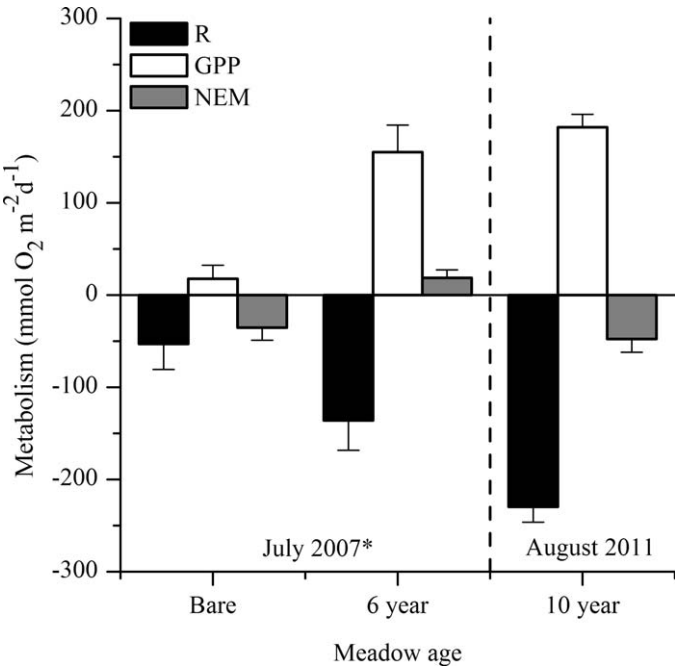

Fig. 2. Summer metabolism at the 11 yr site 6 and 10 yr after seeding and an adjacent bare site. The asterisk indicates bare and 6 yr data from Hume et al. (2011). Metabolism rates at the bare site measured by Hume et al. (2011) were not significantly different from those measured in the present study (*see* text for details). Error bars are SE.

Photosynthetically active radiation at the surface of the canopy (PAR_{canopy}) was related to meteorological PAR ($PAR_{incident}$) at the 11 yr site in October, February, and June (Fig. 6). A first-order exponential relationship between $PAR_{incident}$ and PAR_{canopy} ($PAR_{canopy} = 910.96e^{(PARincident/-9371.51)} - 915.21$; Fig. 6, $r^2 = 0.82$) was used to calculate available light at the canopy throughout the year (November 2011 to October 2012). It is possible that the scatter in this relationship would be less if a more complex function was used that also accounted for light attenuation from changing water depth due to tidal cycling and strong turbidity events from storms or high wind. However, we did not have the data to support such a refined model. Because the distributions of light at the canopy were not significantly different between the 5 and 11 yr sites during the sampling seasons (two-sample Kolmogorov–Smirnov test, $p = 0.530$, 0.833, and 0.287 for October, February, and June, respectively), we used the same exponential relationship for both sites.

Interpolating daily NEM—Using the P–I curves (Figs. 3, 4) with PAR_{canopy} predicted by the exponential relationship (Fig. 6), hourly fluxes and daily NEM were interpolated throughout the year for the 5 and 11 yr sites (Fig. 7). Total daily PAR_{canopy} ranged from ~ 200 mol photons m^{-2} d^{-1} during winter to 650 mol photons m^{-2} d^{-1} during summer (Fig. 7A). Daily NEM varied from −200 to 250 mmol O_2 m^{-2} d^{-1} at the 5 yr site (Fig. 7B) and −200 to 50 mmol O_2 m^{-2} d^{-1} at the 11 yr site (Fig. 7C). At the 5 yr site, seasonal differences in NEM were found where in early spring the system was net autotrophic for most days and in other seasons net heterotrophic for most days. At the 11 yr site, NEM was generally more consistent and clearly heterotrophic during late summer when temperatures were high.

Accumulation of daily NEM over the year, to estimate annual NEM, showed clear differences between the 5 and 11 yr sites (Fig. 8). Annual NEM estimates at the bare, 5 yr, and 11 yr sites were −7.6, 8.6, and −7.0 mol O_2 m^{-2} yr^{-1}, respectively.

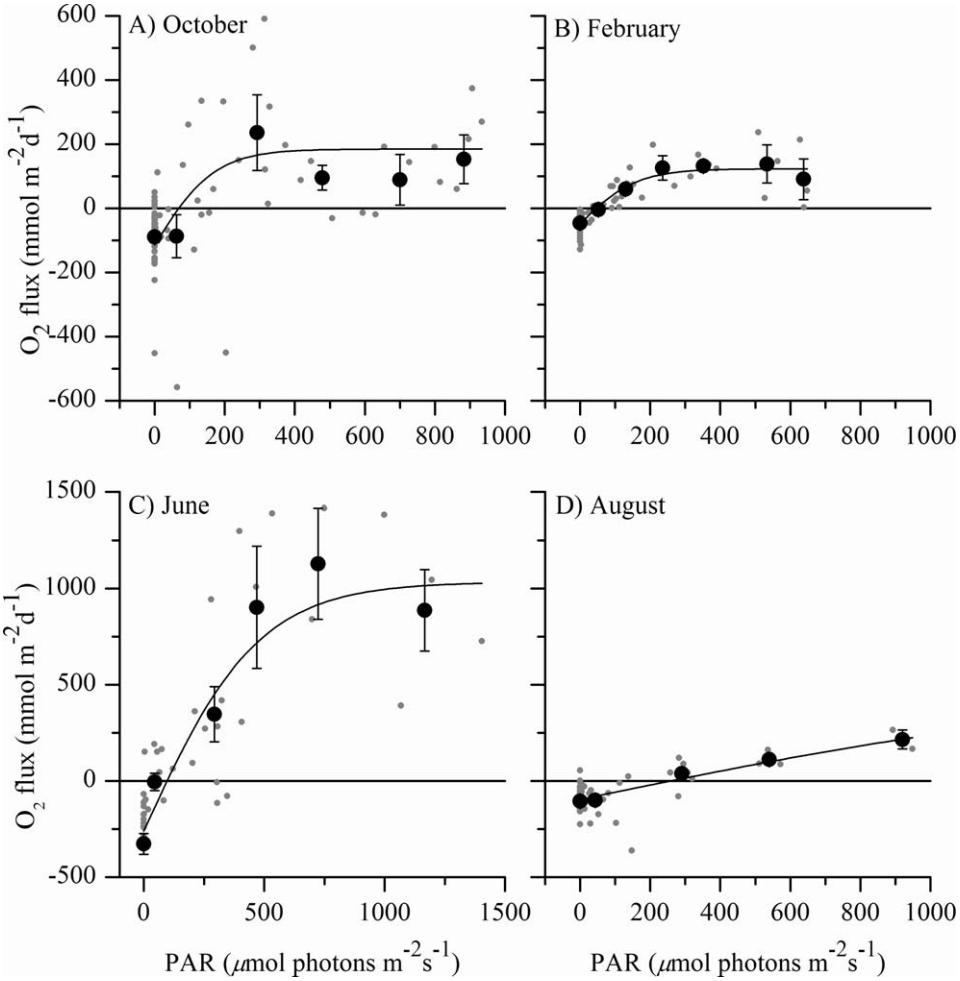

Fig. 3. (A–D) Photosynthesis–irradiance curves from the 5 yr site in October, February, June, and August, respectively. Note the different scales on the y-axis. Small dots are hourly oxygen fluxes and large dots are binned data to only illustrate relationships. Hyperbolic tangent functions (Eq. 2) modified from Jassby and Platt (1976) were fitted to the unbinned data.

Discussion

Production and respiration—This study, which applies the eddy correlation technique in seagrass meadows, provides new and important insights into the impacts of seagrass restoration on ecosystem metabolism. Here, we report that a successful large-scale *Z. marina* restoration project increased gross metabolism by up to 25-fold, but after 11 yr since seeding, did not alter the overall balance of ecosystem metabolism, because NEM was similar between the bare and 11 yr sites. The eddy correlation technique has been validated in several previous studies (Berg et al. 2003, 2013; Glud et al. 2010) and although we do not present a direct comparison of our seagrass measurements to an additional methodology, we show strong evidence to support the validity of our data. The reproducibility of our results (Fig. 1), the good agreement with a previous eddy correlation study at our 10–11 yr seagrass meadow (Fig. 2), the summertime heterotrophy of our measurements found at the bare site using both sediment core incubations and the eddy correlation technique (Table 2), and the good agreement with traditional paradigms on the drivers of metabolism (Figs. 3–5), combined, all provide a strong validation of our results.

Two lines of evidence show that seagrass restoration increased metabolism relative to bare sites and that the magnitude of this effect was related to meadow age. First, GPP and R increased 25- and 5-fold in October and 10- and 13-fold in August, respectively, with time since seeding (Fig. 1A, D). Second, the same pattern of increased GPP and R with meadow age is seen comparing the August 2011 flux data at the 11 yr site (10 yr after seeding) with the data from Hume et al. (2011) at the same location in 2007, 6 yr after seeding (Fig. 2). Interestingly, the rates Hume et al. (2011) measured in July for the site at 6 yr since seeding fall between the rates we measured for 5 yr in June and August (Fig. 1). This likely reflects the phenology of *Z. marina* at this site, with the maximum growth occurring in June and maximum biomass in July, followed by temperature stress in August. The increase in metabolism is linked to increasing shoot density with age as a proxy for seagrass biomass (Table 1). Rheuban et al. (2014) found a strong

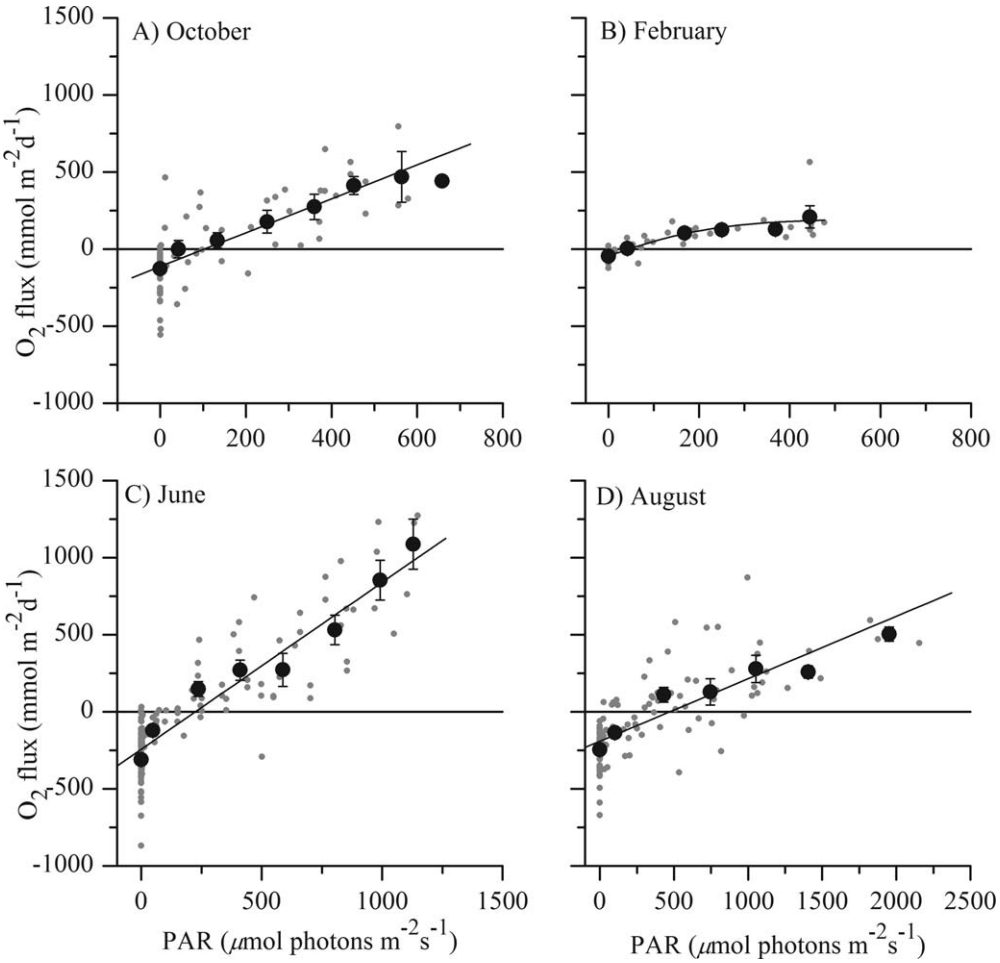

Fig. 4. (A–D) Photosynthesis–irradiance curves from the 11 yr site in October, February, June, and August, respectively. Small dots are hourly oxygen fluxes and large dots are binned data to only illustrate relationships. Hyperbolic tangent functions (Eq. 2) modified from Jassby and Platt (1976) or linear functions were fitted to the unbinned data (*see* text for details).

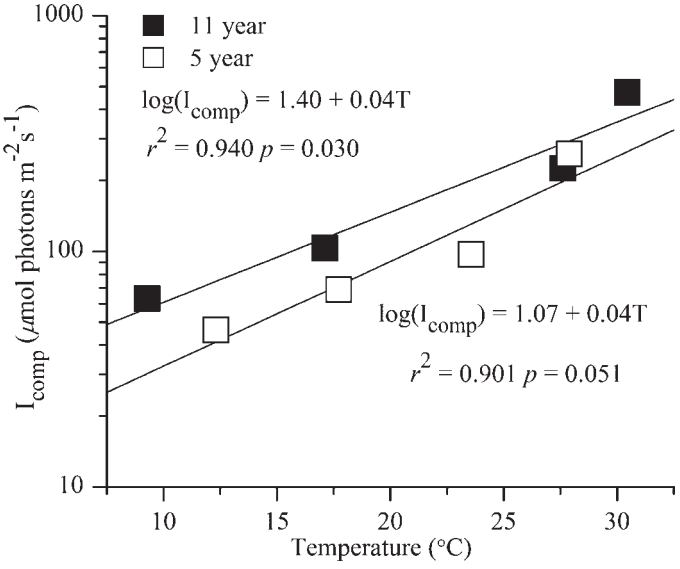

Fig. 5. Compensation irradiance (I_{comp}) vs. temperature (T) calculated from seasonal photosynthesis–irradiance (Eq. 2) relationships from 5 and 11 yr sites (Figs. 3 and 4).

correlation between rates of GPP and R with shoot density and attributed this relationship to several co-varying factors. GPP is influenced by shoot density directly through increased aboveground biomass and indirectly through increased efficiency of light absorption and thus photosynthesis with higher leaf area (Binzer et al. 2006; Sand-Jensen et al. 2007). Shoot density also influences respiration through increased belowground biomass or through indirect processes such as increased exudation of labile dissolved organic matter (Penhale and Smith 1977; Wetzel and Penhale 1979) and O_2 (Frederiksen and Glud 2006) from leaves, roots, and rhizomes. Older and more dense meadows also likely have higher biodiversity and populations of heterotrophic organisms relative to unvegetated sites (Hemminga and Duarte 2000), which further increases O_2 demand. The phenology of *Z. marina* at our sites and an interaction between shoot density and temperature may explain why GPP and R at the 5 and 11 yr sites were different from the bare site during February and June, but not from each other. In February, low temperatures and low shoot density reduced O_2 metabolism at both seagrass sites, while during June, high temperatures and high growth

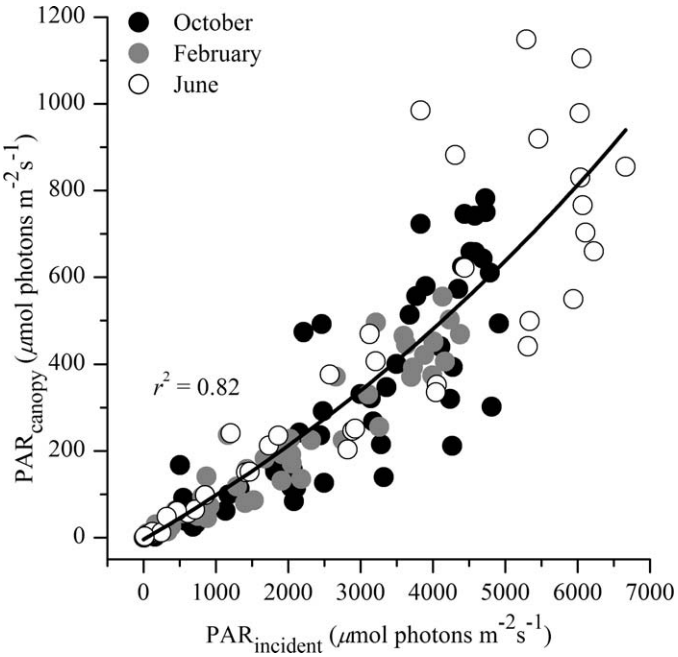

Fig. 6. Hourly photosynthetically active radiation (PAR) reaching the canopy (PAR_{canopy}) vs. hourly meteorological PAR ($PAR_{incident}$) for October, February, and June.

rates resulted in high shoot densities and larger production at both sites.

The average R, GPP, and NEM from August 2012 for the 11 yr site (−196.1, 162.4, −33.6 mmol m^{-2} d^{-1}; Fig. 1D) fell within the variability observed in the daily sampling from August 2011 (−276.3 to −182.8, 142.8 to 221.2, and −87.8 to −7.4 mmol O_2 m^{-2} d^{-1} for R, GPP, and NEM, respectively), suggesting that inter-annual variability may be small after 10 yr from seeding; however, more seasons of sampling would be necessary to confirm this perception.

Compared with vegetated sediments, the bare site was always either slightly net heterotrophic (June, August) or balanced (October, February; Fig. 1). This differs from results of previous core incubation studies in the VCR lagoons that have shown unvegetated sediments were net autotrophic during at least part of the year (McGlathery et al. 2001; Tyler et al. 2003; Giordano et al. 2012), but agrees well with the results found by Hume et al. (2011) using the eddy correlation technique (*see* Fig. 2). Concurrent core incubations and eddy correlation measurements in June (Table 2) both showed net heterotrophy, with NEM rates some three-fold lower in cores (−8.8 ± 1.8 vs. −23.6 ± 4.1 mmol O_2 $m^{-2}d^{-1}$), and also lower R in cores (−19.2 ± 1.9 vs. −34.0 ± 1.7 mmol O_2 m^{-2} d^{-1}). These differences are likely the result of the methods used, because core incubations generally do not replicate in situ hydrodynamic conditions well (Cook et al. 2007; Glud 2008). The sediment permeability of the bare site (5.8×10^{-12} m^2) was at the border above which current flow and wave action can drive advective exchange between the sediment and water column (Huettel and Gust 1992). Therefore, eddy correlation measurements are likely to more directly reflect the true in situ metabolism and thus produce higher rates.

The lack of light saturation in P–I relationships at the 11 yr site (Fig. 4) represents the first direct, in situ, field measurements of benthic macrophyte community scale P–I responses that confirm what has been proposed in theoretical studies (Binzer et al. 2006; Ralph et al. 2007; Sand-Jensen et al. 2007). When shoot density is high, although the upper parts of the leaves may be light-saturated, the understory may not be saturated even at high light levels because of self-shading (Short 1980; Binzer et al. 2006). Thus, ecosystem-scale measurements may be very different from P–I relationships determined by isolating a part of the plant such as a leaf segment (Binzer et al. 2006; Sand-Jensen et al. 2007). This non-saturating response was not evident in the 5 yr site, which instead showed a hyperbolic tangent relationship between photosynthesis and irradiance (Fig. 3) that was likely due to the smaller photosynthetic leaf area and less self-shading. Using leaf measurements from an annual survey in July 2012, the leaf area index (LAI) was nearly three-fold lower at the 5 yr site compared with the 11 yr site (1.17 ± 0.25 vs. 3.08 ± 0.53 m^2 m^{-2}, SE, $n = 5$ and 3; K. J. McGlathery unpubl.). Kentula and McIntire (1986) found shoot density can be a proxy for LAI up to a certain threshold value that lies much higher than the shoot densities measured in this study. In addition, previous work at the 11 yr site has shown no difference in aboveground biomass per shoot regardless of meadow age or shoot density (McGlathery et al. 2012), and further justifies the use of shoot density as a proxy for LAI. Thus, when LAI was higher at the 11 yr site than the 5 yr site (October, June, and August), differences in both the shape and the slope of the P–I relationship were seen (Figs. 3; 4A,C,D; Table 1). This ecosystem-scale response is important to include in P–I relationships that are used to predict production in seagrass communities in order to avoid underestimation. For example, using photosynthesis characteristics from Dennison (1987), who used *Z. marina* leaf incubations at 20°C to determine P–I relationships, maximum net production using the LAI from the 11 yr site would be 208.5 mmol O_2 m^{-2} d^{-1}, compared with a maximum net community production nearly five-fold larger (hourly flux measured in June, 1086.9 mmol O_2 m^{-2} d^{-1}) measured here by eddy correlation at similar temperatures.

The amount of light required for production to exceed respiration (I_{comp}) is an important parameter to consider when planning seagrass restoration or assessing the capacity of a seagrass meadow to survive under limited-light conditions. Plants cannot maintain a positive carbon balance if light reaching the canopy is not greater then I_{comp} for the majority of the day (Gacia et al. 2005; Ralph et al. 2007; Moore et al. 2012). Light compensation irradiance increased 10-fold with increasing temperature at both the 5 and 11 yr sites (Fig. 5) over the course of the year, a pattern remarkably similar to that found by Moore et al. (1997) from chamber incubations. This is likely due to increased sediment heterotrophic respiration (Murray and Wetzel 1987, Moore et al. 1997) and *Z. marina* respiratory requirements with higher temperatures (Marsh et al. 1986), as well as to the seasonal variation in plant biomass

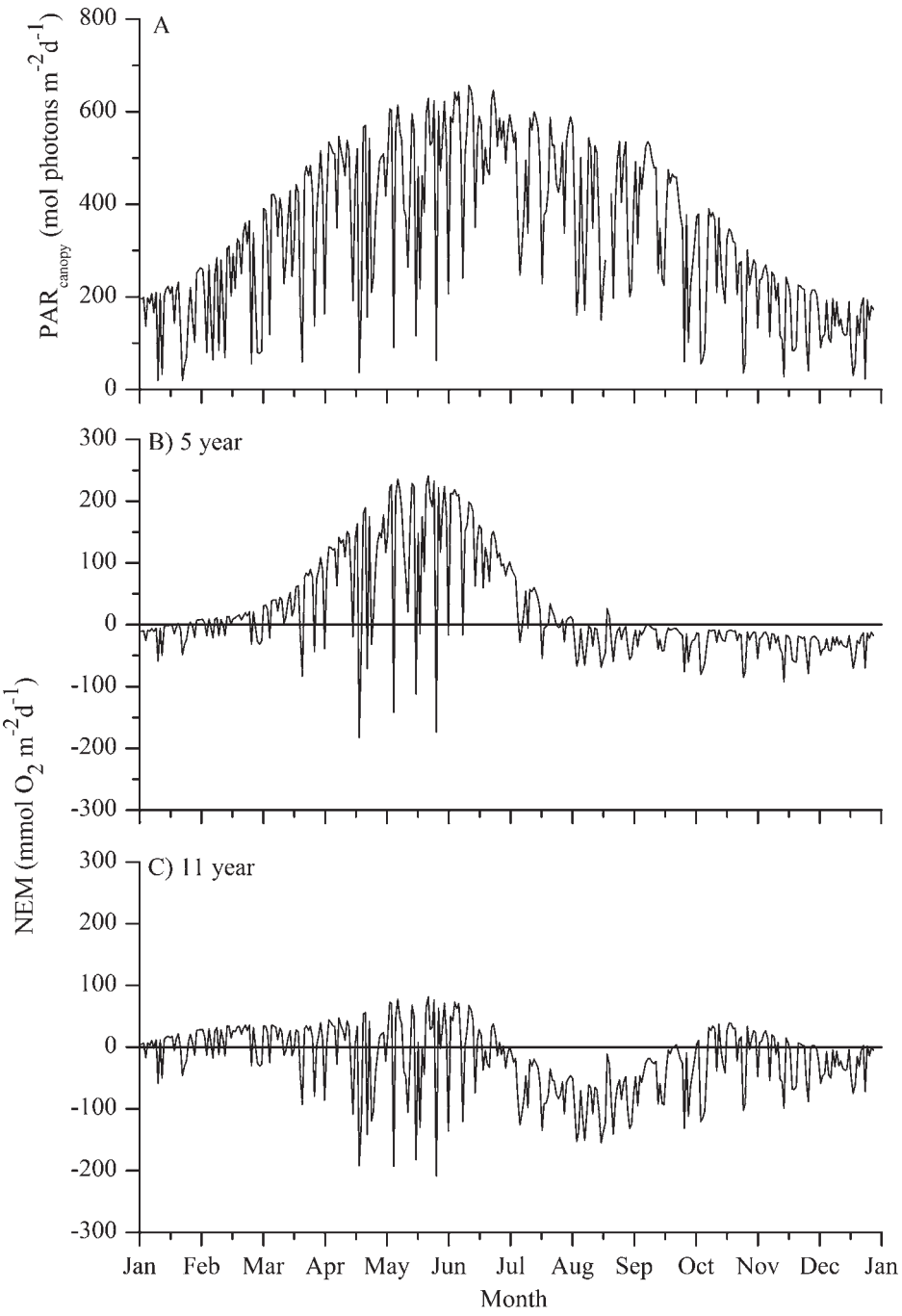

Fig. 7. (A) Daily photosynthetically active radiation (PAR_{canopy}). (B–C) Modeled daily net ecosystem metabolism (NEM) for the (B) 5 yr and (C) 11 yr sites.

(Table 1) and detritus. Although the two relationships were similar (Fig. 5), the I_{comp} tended to be higher at the 11 yr site, which may be because higher *Z. marina* belowground biomass (in July 2011, 36.0 ± 14.2 vs. 84.6 ± 20.6 g m^{-2}, SE, $n = 3$; K. J. McGlathery unpubl.) increases respiratory O_2 demand and the light requirement for photosynthesis to exceed respiration. Additionally, there may have been higher numbers of heterotrophic organisms within the older seagrass meadow (Hemminga and Duarte 2000) or sediments (Jones et al. 2003), which would further increase sediment heterotrophic O_2 demand with temperature. Interestingly, at both sites, the I_{comp} was above the regression line at the highest temperature, suggesting a disproportionate or non-linear effect of increasing temperature on ecosystem respiration compared with photosynthesis (Fig. 5; Marsh et al. 1986).

Interpolating net ecosystem metabolism—Light is the major driver of the O_2 flux, so in situ P–I relationships (Figs. 3, 4) that account implicitly for seasonal variability

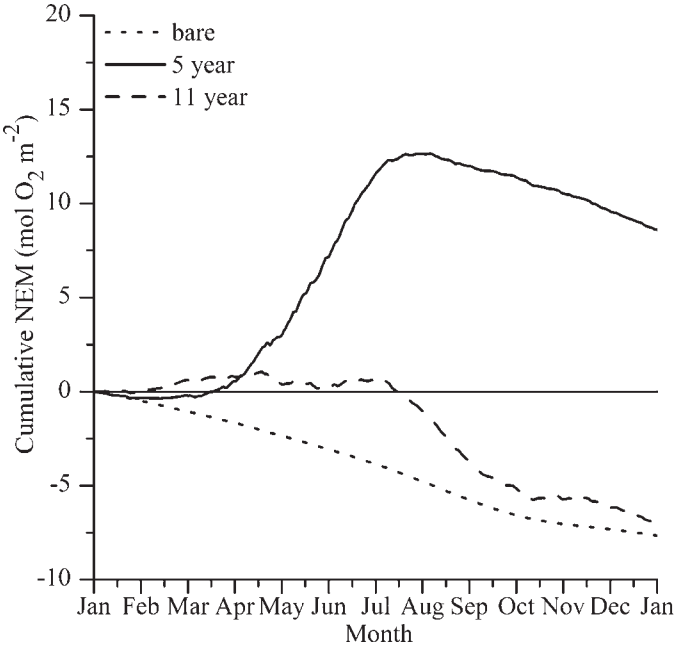

Fig. 8. Cumulative modeled net ecosystem metabolism (NEM) for the bare, 5 yr, and 11 yr sites. Annual NEM rates at the three sites were −7.6, 8.6, and −7.0 mol O_2 m^{-2} yr^{-1}, respectively.

in other drivers of metabolism can be used with a continuous record of available light to estimate NEM throughout the year (Fig. 7). One apparent limitation of this interpolation is that finer time-scale processes such as intermittent flow stimulation of respiration (Hume et al. 2011; Rheuban et al. 2014) are not directly included. However, the in situ P–I curves integrate over a wide range of flow conditions and thus account implicitly for daily and seasonal variation in flow.

The variation in daily NEM (Fig. 7B,C) was markedly different for the 5 and 11 yr sites and was likely related to different seagrass growth dynamics with time since seeding. The strong daily net autotrophy at the 5 yr site during the peak growth period (April–June) may be an indication of rapid seagrass expansion and significant increases in both below and aboveground biomass. This agrees well with measurements of shoot density and total biomass from McGlathery et al. (2012), who found a rapid increase in shoot density and biomass after an initial 4 yr lag. In contrast, the 11 yr site was less autotrophic and much more frequently heterotrophic during this peak growth period when exposed to the same conditions, likely due to the same mechanisms that would result in higher I_{comp} (Fig. 5)–higher belowground biomass that would result in higher seagrass respiratory O_2 demand and greater heterotrophic activity. In addition, O_2 demand can also be stimulated by the oxidation of reduced metabolites from anaerobic processes such as nitrogen fixation, which increases with seagrass colonization and organic matter at these sites (Cole and McGlathery 2012). Finally, rates of sulfate and iron reduction may also be higher at the 11 yr site.

Seasonal loss in biomass due to temperature stress during August is typical near the southern geographic limit of *Z. marina*. Previous studies at this limit have shown either partial (Wetzel and Penhale 1979; Orth and Moore 1986; Moore et al. 1997) or complete loss (Meling-López and Ibarra-Obando 1999) of aboveground biomass during summer in response to high temperatures. This seasonal temperature stress can also be seen in the daily NEM at both the 5 and 11 yr sites (Figs. 7B,C). Daily NEM dropped significantly during late summer from ~ 200 to nearly 0 mmol O_2 m^{-2} d^{-1} at the 5 yr site and about 50 to −100 mmol O_2 m^{-2} d^{-1} at the 11 yr site. This agrees well with large losses in shoot density from June to August at both sites (Table 1) and with temperature stress found in other studies at similar latitudes (Orth and Moore 1986; Moore et al. 1997).

Cumulative daily NEM throughout the year (Fig. 8) provides a refined estimate of annual NEM that accounts for significant daily and seasonal variability in environmental parameters. The net heterotrophy found at the 11 yr site differs from a previous study using in situ enclosures in a *Z. marina* bed in the nearby Chesapeake Bay that showed net autotrophy on an annual basis (Murray and Wetzel 1987). However, that study likely overestimated annual GPP by only measuring during peak sunlight hours and not accounting for daily variability in irradiance, which we show can switch a system between net autotrophy and heterotrophy on a daily basis (Fig. 7). A recent meta-analysis of seagrass community metabolism from Duarte et al. (2010) report highly variable estimates of NEM in *Z. marina* communities, with the annual average approximately balanced and our results fall well within the range of values reported (this study: −7.0 mol O_2 m^{-2} yr^{-1}, Duarte et al. 2010: −41 to 67 mol O_2 m^{-2} yr^{-1}).

The change between annual net heterotrophy at the bare site to net autotrophy after 5 yr and back to net heterotrophy after 11 yr suggests that there are two age thresholds where net metabolism shifts. One threshold exists between the unvegetated initial state and 5 yr, where there is a shift from net heterotrophy to autotrophy. This shift is supported by measurements of shoot density observed at this site (McGlathery et al. 2012). The other threshold exists between 5 and 11 yr, where net metabolism shifts from autotrophy back to heterotrophy and may indicate an age where *Z. marina* living biomass reaches steady-state. This agrees well with summertime (July) shoot density at the 11 yr site, which has been consistent since 9 yr from seeding (2010–2012, McGlathery et al. 2012; K. J. McGlathery unpubl.). In contrast, shoot density at the 5 yr site has almost doubled from 249.2 ± 35.1 (SE, n = 10) shoots m^{-2} in 2010 to 438.8 ± 24.9 in 2012 (SE, n = 10, McGlathery et al. 2012; K. J. McGlathery unpubl.).

The very close agreement between annual NEM at the bare and 11 yr sites suggests that the return of seagrass to this coastal system strongly affects the magnitude of metabolic rates, but not their overall balance. Maximum rates of GPP and R increased by up to 25- and 10-fold, indicating that seagrass meadows are locations of high heterotrophic and autotrophic activity. This result agrees

well with the findings of Eyre et al. (2011) and Hume et al. (2011). Despite this increase in both GPP and R with the state change from bare sediments to 11 yr old *Z. marina* meadows, the rates of NEM were similar and slightly net heterotrophic. This net heterotrophy found at the 11 yr site, combined with evidence of significant sediment carbon burial at the same location (Greiner et al. 2013), suggests that external sources of C are needed to close an overall C mass balance for the seagrass meadow. It also suggests that expected net export of seagrass detritus (Heck et al. 2008) is compensated for by import of external C. Most C budgets for seagrass communities have been determined for meadows that are much older than those studied here (Duarte and Cebrián 1996). In this newly restored ecosystem, 11 yr may be sufficient for the seagrass component of this ecosystem (live seagrass biomass) to reach steady state; however, we do not know how long it will be before net burial rates reach steady state. Continuing studies at our sites will further address the capacity of temperate seagrass meadows to sequester C.

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