REPORT

Seagrass metabolism and carbon dynamics in a tropical coastal embayment

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Abstract Net ecosystem metabolism and subsequent changes in environmental variables were studied seasonally in the seagrass-dominated Palk Bay, located along the southeast coast of India. The results showed that although the water column was typically net heterotrophic, the ecosystem as a whole displayed autotrophic characteristics. The mean net community production from the seagrass meadows was $99.31 \pm 45.13 \text{ mM C m}^{-2} \text{ d}^{-1}$, while the *P/R* ratio varied between 1.49 and 1.56. Oxygen produced through in situ photosynthesis, exhibited higher dependence over dissolved CO_2 and available light. Apportionment of carbon stores in biomass indicated that nearly three-fourths were available belowground compared to aboveground. However, the sediment horizon accumulated nearly 40 times more carbon than live biomass. The carbon storage capacities of the sediments and seagrass biomass were comparable with the global mean for seagrass meadows. The results of this study highlight the major role of seagrass meadows in modification of seawater chemistry. Though the seagrass meadows of Palk Bay are increasingly subject to human impacts, with coupled regulatory and management efforts focused on improved water quality and habitat conservation, these key coastal ecosystems will continue to be valuable for climate change mitigation, considering their vital role in C dynamics and interactions with the overlying water column.

Keywords Aragonite saturation · Carbon uptake · NCP · Palk Bay · Seagrass meadows

INTRODUCTION

Seagrass meadows represent one of the most ecologically rich and productive marine ecosystems, occupying <0.2% of the world's oceans (Fourqurean et al. 2012). They have been widely studied across the globe, with community carbon budgets, community metabolism measurements, and estimates of carbon storage capacity; all indicating their net autotrophic nature and carbon sequestration potential (Duarte et al. 2010; Greiner et al. 2013; Lavery et al. 2013; Watanabe and Tomohiro 2015; Olivé et al. 2016). Seagrass meadows act as net CO_2 sinks (Tokoro et al. 2014) with the capacity to accumulate large carbon pools in the sediment profile and store it over millenary time scales (Kennedy et al. 2010; Fourqurean et al. 2012; Greiner et al. 2013). In addition to the significant carbon sequestration potential, they represent important nursery habitats for a wide range of fish and other aquatic species, providing habitat and harboring significant biodiversity (Gladstone 2009; Unsworth and Cullen 2010). Seagrass meadows actively regulate dissolved oxygen and inorganic carbon content (Larkum et al. 2006), the two key variables in marine biogeochemistry. The rate of change in the pH of seawater is faster now (dropping 0.5 units by 2100) than at any time during the past 50 million years, and associated changes in carbonate chemistry is unprecedented (Marsh 2005). This may lead to significant negative consequences for marine taxa, particularly those that build skeletons, shells, and tests made of biogenic calcium carbonate (Guinotte and Fabry 2008). Additionally, seagrass meadows are among the few ecosystems with the capacity to

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enhance their photosynthetic activities under the increasing levels of CO₂ in seawater (Russell et al. 2013; Hendriks et al. 2014).

Although extensive studies focusing on various biogeochemical aspects of seagrass ecosystems have been carried out globally (Duarte et al. 2010; Fourqurean et al. 2012; Greiner et al. 2013; Lavery et al. 2013; Unsworth et al. 2015; Watanabe and Tomohiro 2015; Olivé et al. 2016; Lamb et al. 2017), research pertaining to the factors regulating the variability of carbon metabolism and sink capacity among seagrass meadows is particularly sparse. Further, these are one of the least studied ecosystems in Southeast Asia, not only with regard to spatial distribution, but also to productivity potential (Singh et al. 2015). Recent estimates suggest that 471.25 km² of seagrass meadows are distributed along the mainland coast of India and the Andaman and Nicobar Islands (Geevarghese et al. 2016). Often, these seagrass meadows coexist with coral reef ecosystems. Over 50% of these seagrass meadows (330 km²) are present in Palk Bay, located in southeastern India. Although a few classical studies on seagrass ecosystem productivity exist (Qasim and Bhattathiri 1971; Balasubramanian and Wafar 1975; Kaladharan and Raj 1989), they do not differentiate phytoplankton productivity from that of seagrass. The present study is the first attempt to quantify and partition net community productivity of the dense seagrass meadows of Palk Bay. Additionally, we hypothesize that seagrass ecosystem metabolism strongly modifies the carbonate chemistry of the shallow coastal waters and has the potential to influence other associated ecosystems. Associated carbon stock in the different compartments of seagrass meadows (i.e., biomass and sub-surface sediments) was also estimated in the study area to understand carbon storage partitioning.

MATERIALS AND METHODS

Study area

Palk Bay, located along the southeast coast of India, extends to a length of ~260 km from Point Calimere in the north to Pamban in the south, and comprises the largest seagrass ecosystem in India (Fig. 1). Seagrass meadows extend 2–3 km from the coastline in up to 7 m of water, however, the most productive and dominant beds are located in shallow waters with an average depth of 2 m (Manikandan et al. 2011). Tides in this region are semi-diurnal in nature, with spring tidal range of ~0.6 m and neap tidal range of ~0.16 m (Gowthaman et al. 2013). Coral reef patches are located adjacent to the seagrass meadows on the seaward side at depths of 3–4 m. Distribution of seagrass meadows in the Palk Bay area varies

along the coast (Fig. S1) and is estimated to be ~330 km² (Geevarghese et al. 2016).

Palk Bay annually experiences two major seasons: wet (October–January) and dry (February–September). The northeast monsoon comprises the wet season, contributing to a higher amount of annual rainfall in contrast to the southwest monsoon, which dominates the dry season. Furthermore, the region receives seasonal inputs of freshwater from land-based sources. The Bay exhibits stable climatic conditions with extremes of air and water temperature during dry and wet seasons (Sridhar et al. 2008).

In India, highest seagrass species diversity has been reported from the Palk Bay (14 species), of which *Cymodocea serrulata* and *Syringodium isoetifolium* are the most dominant (Govindasamy and Arulpriya 2011). In addition, small beds of *Cymodocea nodosa*, *Thalassia hemprichii*, *Enhalus acoroides*, *Cymodocea rotundata*, and scattered distribution of *Halodule uninervis*, *Halodule wrightii*, *Halodule pinifolia*, *Thalassodendron ciliatum*, *Halophila ovalis*, *Halophila minor*, *Halophila stipulacea*, and *Halophila decipiens* are also reported in various parts of the Bay (Manikandan et al. 2011). Highest seagrass biodiversity and density were reported near-shore compared to offshore waters. Healthy live coral patches (66 species of corals belonging to 23 genera) have been reported adjacent to this seagrass meadow (Kumaraguru et al. 2003; Manikandan et al. 2014). Despite the fact that the region harbors healthy seagrass ecosystems, (Manikandan et al. 2011) it is among the least studied ecosystems in India.

Field sampling

Two sampling locations, Mandapam (Station 1: 9°17'28.79"N; 79°7'43.48"E) and Devipattinam (Station 2: 9°29'4.97"N; 78°54'3.68"E; ~35 km north of Mandapam), with dense seagrass cover (water column depth ~2 m), were chosen to study the hydrogeochemical dynamics and net community metabolism (Fig. 1). These two sampling locations were selected from 54 sites, previously studied as part of an extensive spatial reconnaissance survey and assessment of seagrass cover, water column depth, and water quality of the entire stretch of Palk Bay, and chosen to best represent the major seagrass cover in the area for the determination of diel periodicity.

Station 1 is seasonally influenced by monsoonal discharge from River Vaigai, whereas Station 2 is influenced by human activities, especially by surrounding aquaculture operations and religious tourism at Navagraha temple (which includes bathing and release of untreated wastewater). Station 1 is dominated by a high abundance of *Cymodocea serrulata*, whereas dense cover of two mixed

Fig. 1 Map of Palk Bay in south-eastern India with locations of sampling stations

seagrass species [*Cymodocea serrulata* (70%) and *Syringodium isoetifolium* (30%)] is present at Station 2. Healthy coral patches, which account for only 26.7% of the corals present in the region with the balance as dead corals colonized by macro/turf algae, have been observed adjacent to seagrass meadows at Station 1 (Manikandan et al. 2014).

Field surveys were carried out April 30, 2014, during the dry season, and November 28, 2014, during the wet season. Simultaneous sampling at both stations 1 and 2 was carried out using separate boats and crews anchored at fixed locations. Water samples were collected hourly over one complete diel cycle, with 24 samples collected in 5 l Niskin bottles (Hydro-Bios, Germany) at approximately 0.1 m above the top of the seagrass beds.

One liter sub-samples were filtered through pre-weighed 0.45 μm cellulose acetate membrane (Millipore) filters and stored in suitable holders for the estimation of suspended particulate matter (SPM) in the laboratory. Triplicate sub-samples (100 ml each) were immediately filtered through pre-combusted 47 mm Whatman GF/F filters and stored in pre-washed HDPE bottles for dissolved inorganic nutrient analysis (NO_3^- , NO_2^- , NH_4^+ , P, and Si). Filtered water samples were frozen and stored during sampling, and then transferred to the laboratory for immediate analysis. Similarly, replicate samples for total alkalinity (TA) were collected in 100 ml air tight amber color glass bottles and

preserved with 0.05 ml of 50% HgCl_2 to avoid biological alteration, and then stored in the dark at 4°C. Chlorophyll *a* was measured in situ with triplicate replication using conventional methods (i.e., spectrophotometrically using an acetone extract passed through 47 mm GF/F Whatman filters).

Two sediment cores of 60 cm depth were collected from each station using a 7 cm diameter stainless steel corer. The cores were taken carefully to avoid compression of the sediments, which was recorded just prior to extraction, and were sectioned at 5 cm interval in situ. A compaction correction factor (i.e., the length of sample recovery divided by the length of core penetration) was used to compensate for observed compaction during sampling (Howard et al. 2014). The 5 cm core intervals were stored in zip-lock[®] plastic bags on ice, and transported to the laboratory where they were freeze-dried and stored at 4°C until further analysis.

In situ measurements of seagrass water quality

Air temperature, wind velocity, and relative humidity were measured at 15-min intervals using automatic weather monitor stations (i.e., DAVIS 7440) mounted on the top of the boats used during sampling. Water quality parameters viz. pH (NBS), electrical conductivity, dissolved oxygen (DO), turbidity, PAR, and chlorophyll *a* were measured

0.1 m above the seagrass canopy at 15-min intervals using pre-calibrated multiparametric Hydrolab[®] sonde. The sonde used an optical probe to measure DO at 5-min intervals 0.4 m and 0.1 m above the seagrass beds, and then integrated the data over a 24-h period. Oxygen optodes were used as they performed best under well-mixed conditions and did not require temperature corrections. Additionally, the luminescence quenching principle used in the oxygen optodes offered several advantages such as non-stirring sensitivity, high long-term stability, no pressure hysteresis, faster response time, etc., and the ability to measure absolute oxygen concentration without repeated calibrations. The precision of DO measurements using the oxygen optodes was $<0.1 \mu\text{mol kg}^{-1}$ under ambient conditions, whereas accuracy with respect to the measured DO from Winkler titration was $\pm 3.0 \mu\text{mol kg}^{-1}$.

Photosynthetically Active Radiation (PAR, $\mu\text{E m}^{-2} \text{s}^{-1}$) was measured at 5-min intervals underwater at seagrass canopy level using a LiCor Li-1700 quantum radiometer, and daily PAR was calculated by summation of the integrated hourly data. Discrete gross water column primary production and community respiration rates were measured in situ using light and dark bottle method (Strickland and Parsons 1972). For measurement of discrete water column productivity, 300 ml Biological Oxygen Demand (BOD) bottles were filled with ambient water samples (light and dark bottles). Triplicate samples were incubated for 24 h in situ at two different depths (0.4 m and overlying the seagrass canopy). Changes in oxygen were converted to carbon assimilated/respired assuming a photosynthetic quotient of 1.2 and respiratory quotient of 1.0. Results obtained for the two different depths were used to integrate water column gross primary productivity and community respiration for both seasons.

In situ measurement of seagrass productivity and respiration

The community metabolic status was quantified by determining the net community production (NCP), which corresponds to the difference between gross primary productivity (GPP) and community respiration (CR, the sum of autotrophic and heterotrophic respiration) in both the pelagic and benthic compartments (Odum 1956; Champenois and Borges 2012) as follows:

$$\text{NCP} = \text{GPP} - \text{CR}.$$

Community metabolic rates (GPP, CR, and NCP) were calculated on a daily basis using the integrative open water mass balance approach for dissolved oxygen (Odum 1956). Oxygen saturation levels and temperature profiles were logged at hourly intervals to accommodate the typical duration of deployments. Dissolved oxygen concentrations

were computed from oxygen saturation level, seawater temperature, and salinity using the algorithm given by Benson and Krause (1984). Since the study area is in general vertically isothermal, integrated O_2 content of the whole water column ($\sim 2 \text{ m}$) was used for the computations of productivity. The datasets were integrated to provide the vertical integrated gradient of O_2 (Q_{O_2} in mmol m^{-2}) on an hourly basis. Computations were made by considering a 24-h cycle starting at sunrise of any given day.

Contribution of biological activity (photosynthesis + respiration) on concentration of DO during daylight hours (at an hourly basis) was computed after adjusting the air-sea fluxes from the measured DO values between two successive hours.

$$\left(\frac{\Delta \text{O}_2}{\Delta t}\right)_{\text{bio}} = \left(\frac{\Delta \text{O}_2}{\Delta t}\right)_{\text{measured}} + \left(\frac{\Delta \text{O}_2}{\Delta t}\right)_{\text{air-water}}.$$

Laboratory analysis

Dissolved nutrient (inorganic nitrogen (DIN), inorganic phosphorous (DIP), and inorganic silicate (DISi)) samples were analysed (Grasshoff et al. 1999) using an automated continuous flow nutrient analyzer system (Skalar San++[®]). TA of the water samples was measured using Autotitrator (Mettler Toledo-Compact Titrator G20). The dissolved inorganic carbon (DIC; sum of CO_3^{2-} , HCO_3^- , and aqueous CO_2 concentration), pCO_2 , and aragonite saturation state were computed with the CO2SYS program (version 14) using in situ pH (NBS), TA, salinity, temperature, and nutrients (phosphate and silicate) data (Lewis and Wallace 1998). The CO_2 dissociation constants given by Millero et al. (2006) for the 0 to 40 salinity range were used for this computation.

Sediment inorganic N (in duplicate) was analyzed using KCl extraction method (Ganguly et al. 2009). Available sediment phosphorus was extracted using MgCl_2 solution and the extract analyzed using an automated continuous flow nutrient analyzer system (Skalar San++) to determine available phosphorus. Elemental Analyzer (Thermo Finnigan, Flash EA1112) was used to quantify organic carbon (%) of sediments after treatment with HCl to remove inorganic carbon.

Estimation of seagrass biomass

For the estimation of seagrass above- and belowground biomass during the dry season, ten quadrates of $0.25 \text{ m} \times 0.25 \text{ m}$ were deployed randomly around each of the sampling stations, and samples were collected for estimation of dry biomass. All seagrass plant materials

were separated into roots, rhizomes, and leaves and were washed with fresh water over a 1.5 mm mesh sieve to remove sediments without losing plant material. These samples were stored in labeled plastic bags in a refrigerator ($<4^{\circ}\text{C}$) until further processing. The stored seagrass samples were then oven dried to a constant weight at 75°C . During the wet season, biomass samples were collected from six common locations around each of the sampling stations. However, no significant seasonal variations in seagrass biomass were observed ($p > 0.05$) for either sampling station.

Statistical analysis

One Way ANOVA test was used to evaluate the significance of the spatio-temporal variability of the various water quality parameters. Prior to the ANOVA, the water quality data were tested using the Kolmogorov–Smirnov test to confirm normal distribution and Levene's test to confirm the homogeneity of variances without transformation. Principal component analysis (varimax rotated) was used to determine the dominance of environmental factors (using 11 parameters and 48 observations for each season) and the processes regulating the hydrogeochemistry in the seagrass system. All statistical analyses were carried out using IBM SPSS software version 19.0 (Wagner 2016). Bivariate Correlation Analysis was performed to evaluate the relationship between DO and DIC in the seagrass meadows. Dependence of 'biologically produced O_2 ' on the water quality parameters was assessed using stepwise Multiple Regression Analysis to determine the degree of biogeochemical interactions in the seagrass meadows. Water temperature, pH, nutrients, pCO_2 , and hourly PAR were considered independent variables, and biologically produced O_2 (during the daytime $[(\Delta\text{O}_2/\Delta t)_{\text{bio}}]$) was the dependent variable.

RESULTS

Hydrogeochemical controls and carbon chemistry in seagrass meadows

The hydrogeochemical characteristics for both dry and wet seasons of Station 1 and 2 are provided in Table 1. The tidal amplitude was low ($<0.6\text{ m}$) at both the stations, irrespective of seasonal differences. Water temperature, salinity, and pH were relatively higher during the dry season compared to the wet season at both the stations indicating the influence of freshwater input from land-based sources during the wet season. Additionally, higher solar radiation during the dry season may have also contributed to increased temperature, salinity, and primary

production, which induced higher pH. Wind speed was higher during the day (6.56 and 2.53 m s^{-1} in dry and wet seasons, respectively) compared to night (2.93 and 1.75 m s^{-1} in dry and wet seasons, respectively), resulting in the typical diel pattern of turbidity due to wind-driven re-suspension of sediment and particulate matter.

Surface water temperature and pH showed consistent periodicity in relation to the diurnal tidal cycle. pH values were in general, higher at both Station 1 and 2 during the day (Table 1), with largest diel variation of 0.24 at Station 1, which is dominated by *Cymodocea* sp. Salinity and SPM showed insignificant spatial variation ($p > 0.05$), whereas the seasonal differences were significant ($p < 0.001$). Daily irradiance was high in the dry season ($41.78\text{ E m}^{-2}\text{ d}^{-1}$) as compared to the wet season ($33.74\text{ E m}^{-2}\text{ d}^{-1}$), indicating a 19% reduction in solar radiation during wet season. Active photosynthesis and respiration processes at both the stations were also reflected by the significant diel fluctuation in DO concentrations ($p < 0.05$).

Diel variations of pH, DO, DIC, and aragonite saturation during dry and wet seasons at Palk Bay are given in Fig. 2a–d. Dissolved oxygen concentrations during the day increased from 0.47 to $0.65\text{ mg l}^{-1}\text{ h}^{-1}$, whereas the rate of decrease at night was between 0.39 and $0.46\text{ mg l}^{-1}\text{ h}^{-1}$. DIC concentrations showed a maximum diel variation of $\sim 12\%$ during the dry season at Station 2 (Fig. 2c). These variations were significant for both stations (Station 1, $p < 0.01$; Station 2, $p < 0.05$) during the dry season, but only for Station 2 during the wet season ($p < 0.05$). Chlorophyll *a*, representing the water column producers (phytoplankton), showed higher concentrations during the wet season compared to the dry season (Fig. 3).

Varimax-rotated factor analysis revealed that 27% of the variability in the dataset during the dry season (Factor 1) and 21% during the wet season (Factor 2) were controlled by ecosystem metabolism (i.e., photosynthesis-respiration) with strong association with surface water temperature, pH, DO, and DIC (Table 2a). In addition, during the wet season, Factor 1 accounted for 30% of the variation and reflected the influence of the fresh water in the systems (e.g., rainfall), which is evident in the cluster of turbidity, salinity, TDS, DIN (positive loading), and DIP (negative loading; Table 2b). Similar inverse loading between turbidity and DIP during the dry season was also recorded (Factor 2), perhaps indicating the significance of fresh water on the release of phosphorus from suspended sediments (Jordan et al. 2008). However, this phenomenon needs further strengthening through additional experimental observations.

Net community metabolism in seagrass meadows

In the seagrass meadows, DO and DIC were strongly correlated ($R^2 = 0.71$) as indicated by the consumption of

Table 1 Mean ($\pm$ S.D.) water quality parameters at the two sampling stations during dry and wet seasons (range is given in parenthesis)

Parameters	Station 1		Station 2	
	Dry	Wet	Dry	Wet
Wind speed (m s^{-1})	3.47 ± 1.54 (0.8–6.2)	2.68 ± 0.95 (0.6–4.2)	3.83 ± 1.83 (0.4–6.4)	2.64 ± 0.59 (0.8–3.8)
Water temp. ($^{\circ}\text{C}$)	32.44 ± 0.93 (31.0–33.9)	27.09 ± 0.94 (26.2–28.4)	32.17 ± 1.52 (29.8–34.15)	28.51 ± 1.23 (27.1–30.23)
PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	451 ± 245	355 ± 177	457 ± 255	364 ± 219
pH	8.21 ± 0.07 (8.10–8.35)	8.08 ± 0.14 (7.898–8.21)	8.26 ± 0.12 (8.05–8.38)	8.14 ± 0.11 (7.98–8.25)
Salinity	34.96 ± 0.15 (34.7–38.15)	31.08 ± 0.6 (30.5–32.9)	34.61 ± 0.38 (34.1–35.01)	32.1 ± 0.50 (31.2–32.8)
SPM (mg l^{-1})	158.97 ± 7.05 (145–171)	63.76 ± 5.33 (51–67)	161.71 ± 4.66 (156–176)	57.3 ± 8.00 (47–69)
DO (μM)	212.96 ± 47.3 (135–304)	235.8 ± 56.3 (151–290)	201.39 ± 43.3 (105–277)	213.4 ± 41.2 (138–297)
Chl a ($\mu\text{g l}^{-1}$)	0.68 ± 0.5 (0.38–1.41)	2.15 ± 0.6 (1.38–3.25)	0.57 ± 0.3 (1.7–3.16)	2.30 ± 0.5 (0.2–1.12)
DIN (μM)	3.09 ± 0.45 (2.2–5.59)	19.80 ± 3.61 (14.1–21.5)	3.81 ± 1.05 (2.2–6.74)	14.30 ± 2.00 (10.6–16.4)
DIP (μM)	1.33 ± 0.53 (0.8–1.9)	0.8 ± 0.25 (0.4–1.2)	1.85 ± 0.47 (1.4–2.27)	1.1 ± 0.30 (0.6–1.48)
Silicate (μM)	4.02 ± 1.04 (2.9–5.9)	13.64 ± 5.61 (10.2–22.1)	7.00 ± 1.50 (5.9–9.6)	11.59 ± 1.85 (9.8–15.6)
N:P	2.93 ± 1.76	26.48 ± 8.01	2.23 ± 0.87	14.6 ± 5.40
DIC ($\mu\text{M kg}^{-1}$)	2057 ± 107.0 (1804–2177)	1931 ± 47.6 (1764–2157)	1987 ± 64.7 (1664–2115)	1880 ± 149.0 (1701–2093)
pCO ₂ (μatm)	374 ± 81.7 (218–429)	481 ± 115.7 (344–714)	313 ± 95.5 (201–424)	369 ± 84.2 (245–486)
Ω_{Ar}	4.90 ± 0.58 (4.22–5.77)	3.52 ± 0.70 (2.6–5.19)	5.06 ± 0.64 (3.9–5.42)	3.68 ± 0.64 (2.8–4.74)
$([\text{DIC}]:[\text{H}^+]^{-1}) \times 10^3$	249.48 ± 28.29	213.34 ± 52.34	265.89 ± 40.04	218.1 ± 34.12

0.90 mol of DIC for the production of 1 mol of DO. The results suggested that oxygen production (by photosynthesis during the day) directly influenced the carbonate system in the meadow (Fig. 4). Combined metabolic activities (photosynthesis and respiration) of both the benthic (seagrass) as well as water column producers (phytoplankton) mostly contributed to the net community productivity (NCP) at both the stations. In the mixed seagrass meadow (Station 2), NCP, GPP and CR were higher during both seasons compared to the *Cymodocea* sp.-dominated meadow at Station 1 (Fig. 5). It was observed that during the dry season, water column metabolism (by phytoplankton) followed a reverse trend to that of the net community metabolism (Fig. 6). Notable increase in the ratio of water column production to ecosystem production

was recorded during wet season following the seasonal increase in DIN and DISi concentrations.

Carbon storage in Seagrass meadows (biomass and sediments)

Mean aboveground biomass (AGB) values of seagrasses were 278 ± 30 and 259 ± 19 g dwt m^{-2} at Stations 1 and 2, respectively, during the dry season. Mean belowground biomass (BGB) values at Stations 1 and 2 were 717 ± 89 and 830 ± 75 g dwt m^{-2} , respectively, and were ~ 3.2 times higher than mean AGB. Sediment organic carbon underlying the seagrass meadow showed a marginally elevated concentration of $1.01 \pm 0.25\%$ during the dry season compared to the wet season ($0.93 \pm 0.29\%$), with

Fig. 2 Diurnal variations of **a** pH, **b** dissolved oxygen, **c** DIC, and **d** aragonite saturation during dry and wet seasons in Palk Bay, India

Fig. 3 Diurnal variations of chlorophyll *a* in the water column of Palk Bay, India

an average dry bulk density of $1.36 \pm 0.15 \text{ g ml}^{-1}$ (Table 3). A decrease in C_{org} with depth was observed at the rate of -0.012 cm^{-1} (Fig. S2). Total organic carbon stock was calculated as $1.396 \times 10^{-2} \text{ Mg } C_{\text{org}} \text{ m}^{-3}$, assuming that the mean sediment DBD and mean C_{org} content represented the central tendency of the top one meter of the seagrass sediments. The net organic carbon

reservoir of the Palk Bay seagrass ecosystem (area $\sim 330 \text{ km}^2$) was extrapolated as $4.6 \times 10^6 \text{ Mg}$ (or 4.6 Tg) in the top 1 m of the sediments (Fig. 7).

DISCUSSION

Bioregulatory mechanisms in seagrass meadows

The hydrogeochemistry of surface waters in the Palk Bay region was highly seasonal. Higher concentrations of DIN and DISi during the wet season resulted in a threefold increase in water column chlorophyll *a*, indicating a significant increase in the phytoplankton population. On the contrary, limitation in DIN (w.r.t DIP) during the dry season was attributed to the combined effect of rapid biological removal and reduced supply (Wu et al. 2016). Varimax-rotated factor analysis indicated that 21% of the variations in water quality during wet season (as against 14% of variation during dry season) were associated with water column chlorophyll *a* concentrations. Nutrient enrichment (DIN, DISi) in wet season resulted in a significant increase in phytoplankton

Table 2 VARIMAX-rotated factor-loading matrix (with Kaiser normalization) of water parameters during (a) dry season and (b) wet season

Variables	Factor 1	Factor 2	Factor 3	Factor 4
a. Rotated component matrix				
Water temp.	0.830	0.421	−0.235	0.017
pH	0.919	−0.183	0.086	−0.165
Salinity	−0.149	0.056	0.946	0.222
TDS	−0.015	0.099	0.949	0.213
Turbidity	−0.018	0.848	0.227	0.073
DO in μM	0.777	0.151	−0.350	0.202
DIN	0.188	0.265	−0.228	−0.670
DIP	−0.025	−0.871	0.001	−0.167
Silicate	0.069	−0.282	−0.249	−0.642
DIC	−0.840	0.174	−0.144	0.368
Chl a	0.053	0.275	0.012	0.732
Loading (%)	27	20	19	14
Variables	Factor 1	Factor 2	Factor 3	Factor 4
b. Rotated component matrix				
Water temp.	−0.393	0.590		0.579
pH	−0.041	0.816		0.359
Salinity	0.538	0.266		−0.451
TDS	0.791	0.050		−0.093
Turbidity	0.948	−0.120		−0.003
DO	0.286	0.841		−0.020
DIN	0.840	−0.005		−0.004
DIP	−0.691	−0.257		−0.152
Silicate	−0.323	0.024		−0.690
DIC	0.601	−0.658		0.174
Chl a	−0.260	0.128		0.877
Loading (%)	30	21		21

Factor loadings >0.5 were considered statistically significant and were highlighted in bold

Fig. 4 Variation of DO versus DIC in the water column of Palk Bay, India **Fig. 5** Net ecosystem fluxes of carbon ($\text{mmol C m}^{-2} \text{d}^{-1}$) in the seagrass meadows of Palk Bay, India

productivity (also the enhanced phytoplankton to ecosystem production ratios) which enhanced the relative contributions of these water column producers in regulating water quality.

Similar observations on the impact of nutrient enrichment over ecosystem metabolism were reported by Onuf (1996) and Ziegler and Benner (1999) from the sub-tropical

Fig. 6 Biological fluxes of carbon ($\text{mmol C m}^{-2} \text{d}^{-1}$) in the water column of Palk Bay, India

Table 3 Sediment characteristics of the Palk Bay seagrass ecosystem

	Dry	Wet
SOC (% dry soil)	1.01 ± 0.25	0.93 ± 0.29
Sediment N (mg g^{-1} of dry soil)	44.74 ± 6.5	37.65 ± 5.21
Sediment P (mg g^{-1} of dry soil)	7.89 ± 1.56	4.23 ± 0.91
Sediment N/P molar ratio	15.72	21.35
Bulk density (g ml^{-1})	1.36 ± 0.15	

seagrass meadows of Laguna Madre along the Texas coasts. Further increase in dissolved nutrient concentrations in this shallow coastal ecosystem may lead to a rapid upsurge in phytoplankton population and enhanced interspecies competition for light and nutrients (Lee et al. 2007). Factor loadings between chlorophyll *a* and DISi (diatom growth) in

both the seasons, and with DIN only during dry season implies that under conditions of limited freshwater and nutrients (dry season) supply, DIN and chlorophyll *a* in the water column have a higher capacity of spatial discrimination between the two stations. Further, dominance of single seagrass species (*Cymodocea serrulata*) at Station 1, and a more diverse and productive community at Station 2, explains the spatial differences in nutrient fluxes, in addition to other natural and anthropogenic interactions (Coll et al. 2011).

The combined inputs of DIC from the water column and benthic seagrass respiration indicated heterotrophic respiration at night, consuming 0.97 mol of CO_2 per mol of O_2 consumed. During the day, the water remained mostly undersaturated with respect to atmospheric equilibrium, with the lowest pCO_2 value of 201 μatm during dry seasons. However, during the wet season, Station 1 had higher saturation of pCO_2 ($481 \pm 115.7 \mu\text{atm}$) compared to Station 2 ($369 \pm 84.2 \mu\text{atm}$). This increase in saturation level may be attributed to the import of land-derived seasonal runoff through various canals that were inactive during the dry season. Dufault et al. (2012) suggested that calcifying organisms are positively influenced by the ecologically mediated diel oscillation of pCO_2 in sea water. Aragonite saturation values (Ω_{arag}), calculated from pCO_2 , are often indicative of enhanced calcification rates (Chou et al. 2013). In this study, Ω_{arag} values were always higher than the critical value of 1.7 (Barton et al. 2012) indicating the biogeochemical regulation of water chemistry by the seagrass meadows. Day Ω_{arag} values were high, with an average diel variation of $\sim 15\%$ recorded for Ω_{arag} at the seagrass beds of this study. During the wet

Fig. 7 Carbon pools and fluxes in Palk Bay, India

season, mean Ω_{arag} values were $\sim 27\%$ lower than those observed during the dry season. Overall, higher Ω_{arag} (aragonite saturation) was observed during periods of increased seagrass productivity, especially during the dry season as well as during the day. Accretion rates of the calcifying organisms can be explained by the $[\text{DIC}]:[\text{H}^+]$ ratio, which is a measure of relative availability of inorganic carbon in relation to the concentration of inhibitory calcification waste product (H^+) in the bulk water surrounding the calcifier (e.g., corals; Jokiel 2013). The $[\text{DIC}]:[\text{H}^+]$ ratio for this study varied between $213.34 \pm 52.34 \times 10^3$ (wet season) and $265.89 \pm 40.04 \times 10^3$ (dry season). Highest diel variation in $[\text{DIC}]:[\text{H}^+]$ ratios was observed at Station 1 of up to 26% during the wet season, whereas Station 2 was up 15% for the same time period. High diel variation at Station 1 during the wet season may be attributed to increased land-based inputs (watershed runoff) as discussed earlier. A linear relationship ($r^2 = 0.88$) was observed between in situ $[\text{DIC}] \times [\text{H}^+]^{-1} \times 10^3$ and measured Ω_{arag} during the study, which can be represented through the following equation:

$$[\text{DIC}] \times [\text{H}^+]^{-1} \times 10^3 = 41.199 \Omega_{\text{arag}} + 57.638.$$

These results demonstrate the role of seagrass metabolism in modifying the carbonate chemistry of the shallow coastal waters, and that these changes can strongly affect the conditions of the associated ecosystems. However, biologically mediated calcification involving different organisms (corals, calcifying algae, seagrasses, and other calcifying fauna) is a complex process that requires detailed study to understand the interactions between biogeochemical processes (i.e., calcification and photosynthesis) and various organisms involved.

Carbon metabolism in seagrass

Discrete GPP and R measurements of phytoplankton clearly indicated that water column productivity changed from net heterotrophic during the dry season to net autotrophic during the wet season ($P:R = 0.57\text{--}1.36$). This increase in the $P:R$ ratio from dry to wet seasons is in response to higher nutrient inputs during the wet season from land-based sources. On the contrary, the seagrass meadows of the Palk Bay remained highly productive (net autotrophic), where net community GPP exceeded R, throughout the study period (annual $P:R = 1.49\text{--}1.56$). The net increase in DO in association with the net decrease of DIC specially during the dry season (when pelagic $P:R < 1$) indicates that DIC consumption through photosynthesis activity by the benthic primary producers (mostly seagrasses) dominated over the DIC production through respiration by both benthic and pelagic organisms.

Seagrass productivity and growth has been linked with available sediment and nutrient resources by several

researchers (Duarte 1990; Lee et al. 2007; Cabaco et al. 2013; Ow et al. 2016). In the present study, a considerable reduction in the relative abundance of soil P with respect to N was observed during the wet season, presumably due to the limited binding strength of phosphate to the sediments. Consequently, a large proportion of dissolved nutrients became available to phytoplankton as well as to the benthic seagrasses that may promote higher productivity rates. Further, additional nutrient inputs due to various human activities (e.g., religious tourism and aquaculture) at a close proximity to the stations, particularly to Station 2, may have stimulated primary productivity relative to Station 1. These activities immensely support the immobilization of dissolved nutrients as phytoplankton and seagrass biomass in the surrounding coastal waters near Station 2 (Shrinithiviahshini et al. 2014).

These results indicate that while water column productivity was seasonal, NCP of seagrass meadows was at least ten times higher than that of phytoplankton. This is largely due to the dependence of phytoplankton to extraneous nutrient sources, whereas seagrasses draw nutrients from underlying sediments. Plus et al. (2015) quantified the relative NCP of the seagrass *Zostera noltii* to range from 56 to 81%, and that of phytoplankton from 17 to 39% in Arcachon Bay, France. Observations from the seagrass meadows of Palk Bay indicate that water column phytoplankton productivity was always limited to 13% of the net ecosystem productivity, suggesting greater dominance of seagrasses in community metabolism.

It was observed from stepwise multiple regression analysis that variability of NCP (biologically produced O_2) in the seagrass meadows during day can significantly be explained by the dominance of pCO_2 (24.4%) and PAR (26.8%), compared to other environmental variables (Table 4).

$$\left(\frac{\Delta \text{O}_2}{\Delta t}\right)_{\text{bio}} = -32 - 2.81T_w + 4.0\text{pH} + 0.519\text{SPM} \\ + 0.278\text{DIN} + 18.4\text{DIP} + 0.0622\text{pCO}_2 \\ + 0.0180\text{PAR}.$$

The above results are in agreement with Russell et al. (2013) that reported enhanced seagrass growth rates under

Table 4 Multiple regression analysis with a stepwise variable selection. Dependent variables: $(\Delta \text{O}_2/\Delta t)_{\text{bio}}$, independent variables: WT ($^{\circ}\text{C}$), SPM (mg l^{-1}), DIN (μM), DIP (μM), pCO_2 (μatm), and PAR ($\mu\text{E m}^{-2} \text{s}^{-1}$)

	r^2 (%)	df	p	f
Water temp.	1.6	35	0.442	0.6
pH	8.7	35	0.218	0.89
SPM	21.1	35	0.010	4.84
DIN	21.2	35	0.018	3.55
DIP	30.1	35	0.005	4.11
pCO_2	54.5	35	<0.001	9.19
PAR	81.3	35	<0.001	17.45

Fig. 8 Comparison of net community production between various seagrass ecosystems in the world

elevated dissolved CO₂ conditions followed by burial as belowground biomass in seagrass meadows. Further, we compared the NCPs of various seagrass meadows globally (Fig. 8) and observed that the calculated mean NCP values from seagrass meadows of Palk Bay ($99.31 \pm 45.13 \text{ mM C m}^{-2} \text{ d}^{-1}$) was at least three times above the global mean NCP ($27.17 \text{ mM C m}^{-2} \text{ d}^{-1}$; Duarte et al. 2010).

Carbon storage in seagrass meadows

Two distinct types of carbon stores in seagrass meadows are discussed: (i) carbon resulting from in situ production of AGB and BGB, and (ii) carbon transported from other areas and deposited. The average AGB of seagrass (Stations 1 and 2) measured in this study was 268 g dwt m^{-2} , which was at least three times higher than reported by Manikandan et al. (2011) of $70.77 \text{ g dwt m}^{-2}$ at the near-shore region of Palk Bay. Duarte et al. (2010) suggested that seagrass meadows with an average AGB in excess of 41 g dwt m^{-2} can be considered autotrophic and may act as net CO₂ sinks. This study indicates that the seagrass meadows of Palk Bay have AGB more than twofold higher than the autotrophic threshold of 41 g dwt m^{-2} . Assuming dry seagrass biomass has an average carbon content of 35% (Duarte 1990; Fourqurean et al. 2012), the total carbon stored as seagrass biomass is $0.94 \text{ Mg C}_{\text{org}} \text{ ha}^{-1}$ (94 g m^{-2}). The average BGB (Stations 1 and 2) measured in this study was 773 g dwt m^{-2} , which is nearly three times higher than AGB. This indicates the efficient transfer of photosynthetically fixed carbon to the rhizomes and roots. Extrapolating the data for seagrass meadows of Palk Bay (330 km^2), we observed that over three-fourth of the biomass carbon (0.14 Tg C) was stored as BGB (Fig. 7), indicating the significance of seagrass rhizomes in carbon sequestration. Sediments act

as an ultimate sink for storing sequestered carbon for millennia in the seagrass meadows (Russell et al. 2013; Duarte and Jensen 2017). In Palk Bay, although the dry bulk density (DBD) of seagrass sediments was significantly higher than the global mean ($1.03 \pm 0.02 \text{ g ml}^{-1}$), the C_{org} was at least two times lower (1.03%) than the global mean (2.5%; Fourqurean et al. 2012). Low concentrations of organic carbon observed in the sediment column could be attributed to the shallow, oxic water column, and a sandy–silty sediment substrate of the Palk Bay region. This study measured a total organic carbon content of $139.6 \text{ Mg C}_{\text{org}} \text{ ha}^{-1}$ in the top 1 m of seagrass sediments in Palk Bay, which is comparable with the global mean of $165.6 \text{ Mg C}_{\text{org}} \text{ ha}^{-1}$. Apportionment of carbon stores in the Palk Bay seagrass meadows indicates an accumulation of ~40 times in the sediment horizon compared to live biomass.

CONCLUSION

Here we present the first study of net ecosystem metabolism and carbon storage capacity of seagrass meadows of Palk Bay in southeastern India. The dominant regulators of biological carbon fixation by the seagrass of Palk Bay are pCO₂ and PAR. Strong dependence of dissolved nutrient availability governed phytoplankton productivity, which was always lower than seagrass productivity throughout the study period. High NCP values during the dry season lead to a higher degree of aragonite saturation with high mean Ω_{arag} values, which improved water quality for calcifying organisms present adjacent to the seagrass meadows. Thus, not only is the carbon uptake capacity of seagrass meadows high, but they also act as a buffer to the associated ecosystems by altering the water chemistry. Seagrass ecosystems of the Palk Bay region have often been neglected and subject to physical damage due to trawler boat operations and trap net fishing in the near-shore area. Further, increased anthropogenic nutrient inputs may lead to substantial proliferation of fast growing algae that poses additional threats to the slow growing seagrass species. The conservation and protection of these ecosystems is very much essential as degradation may cause the release of stored carbon to the atmosphere, accelerating global warming (Macreadie et al. 2014). However, Government of India has now brought seagrass ecosystems under the Coastal Regulation Zone Notification (2011), which encourages conservation and preservation of such key coastal ecosystems that are valuable in mitigation of climate change.

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REFERENCES

- Balasubramanian, T., and M.V.M. Wafar. 1975. Primary productivity of some seagrass beds in the Gulf of Mannar. *Mahasagar* 8: 87–91.
- Barton, A., B. Hales, G.G. Waldbusser, C. Langdon, and R.A. Feely. 2012. The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near-term ocean acidification effects. *Limnology and Oceanography* 57: 698–710.
- Benson, B.B., and D. Krause. 1984. The concentration and isotopic fractionation of oxygen dissolved in freshwater and seawater in equilibrium with the atmosphere. *Limnology and Oceanography* 29: 620–632.
- Cabaco, S., E.T. Apostolaki, P. García-Marín, R. Gruber, I. Hernández, B. Martínez-Crego, O. Mascaró, M. Pérez, et al. 2013. Effects of nutrient enrichment on seagrass population dynamics: Evidence and synthesis from the biomass–density relationships. *Journal of Ecology* 101: 1552–1562.
- Chou, W.C., G.C. Gong, C.C. Hung, and Y.H. Wu. 2013. Carbonate mineral saturation states in the East China Sea: Present conditions and future scenarios. *Biogeosciences* 10: 6453–6467.
- Champanois, W., and A.V. Borges. 2012. Seasonal and interannual variations of community metabolism rates of a *Posidonia oceanica* seagrass meadow. *Limnology and Oceanography* 57: 347–361.
- Coll, M., A. Schmidt, T. Romanuk, and H.K. Lotze. 2011. Food-web structure of seagrass communities across different spatial scales and human impacts. *PLoS ONE* 6: e22591. doi:10.1371/journal.pone.0022591.
- Duarte, C.M. 1990. Seagrass nutrient content. *Marine Ecology Progress Series* 67: 201–207.
- Duarte, C.M., M. Núria, G. Esperança, W.F. James, B. Jeff, B. Cristina, and T.A. Eugenia. 2010. Seagrass community metabolism: Assessing the carbon sink capacity of seagrass meadows. *Global Biogeochemical Cycles* 24: 1–8.
- Duarte, C.M., and D.K. Jensen. 2017. Export from seagrass meadows contributes to marine carbon sequestration. *Frontiers in Marine Science*. doi:10.3389/fmars.2017.00013.
- Dufault, A.M., V.R. Cumbo, F. Tung-Yung, and P.J. Edmunds. 2012. Effects of diurnally oscillating pCO₂ on the calcification and survival of coral recruits. *Proceedings of the Royal Society Biological Sciences* 279: 2951–2958.
- Fourqurean, J.W., C.M. Duarte, H. Kennedy, N. Marbà, M. Holmer, M.A. Mateo, E.T. Apostolaki, G.A. Kendrick, et al. 2012. Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* 5: 505–509.
- Ganguly, D., M. Dey, S. Sen, and T.K. Jana. 2009. Biosphere-atmosphere exchange of NO_x in the tropical mangrove forest. *Journal Geophysical Research*. doi:10.1029/2008JG000852.
- Geevarghese, G.A., A. Babu, G. Magesh, S. Raja, P. Krishnan, R. Purvaja and R. Ramesh. 2016. A comprehensive geospatial assessment of seagrass status in India Abstract No. 1.2, National conference on “Management and conservation of seagrass in India,” organized by Ministry of Environment, Forest and Climate Change, Govt of India, GIZ-GmbH, and IUCN. 12–13 July 2016, New Delhi.
- Greiner, J.T., K.J. McGlathery, J. Gunnell, and B.A. McKee. 2013. Seagrass restoration enhances “Blue Carbon” sequestration in coastal waters. *PLoS ONE* 8: e72469. doi:10.1371/journal.pone.0072469.
- Gladstone, W. 2009. Conservation and management of tropical coastal ecosystems. In *Ecological Connectivity among Tropical Coastal Ecosystems*, ed. I. Nagelkerken, 565–605. Dordrecht: Springer.
- Govindasamy, C., and M. Arulpriya. 2011. Seasonal variation in seagrass biomass in Northern Palk Bay, India. *Biodiversity* 12: 223–231.
- Gowthaman, R., V. Sanil Kumar, G.S. Dwarakish, S.S. Mohan, J. Singh, and K. Ashok Kumar. 2013. Waves in Gulf of Mannar and Palk Bay around Dhanushkodi, Tamil Nadu, India. *Current Science* 104: 1431–1435.
- Grasshoff, K., K. Kremling, and M. Ehrhardt. 1999. Analysis by electrochemical methods. In *Methods of Sea Water Analysis*, ed. K. Grasshoff, M. Ehrhardt, and K. Kremling, 159–226. Weinheim: Wiley.
- Guinotte, J.M., and V.J. Fabry. 2008. Ocean acidification and its potential effects on marine ecosystems. *Annals of the New York Academy of Sciences* 1134: 320–342.
- Hendriks, I., Y. Olsen, R.L. Basso, A. Stechbauer, T.S. Moore, J. Howard, and C.M. Duarte. 2014. Photosynthetic activity buffers ocean acidification in seagrass meadows. *Biogeosciences* 11: 333–346.
- Howard, J., S. Hoyt, K. Isensee, M. Telszewski, and E. Pidgeon, editors. 2014. *Coastal Blue Carbon: Methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses*. Arlington, Virginia: Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature.
- Jokiel, P.L. 2013. Coral reef calcification: Carbonate, bicarbonate and proton flux under conditions of increasing ocean acidification. *Proceedings of Royal Society B* 280: 20130031.
- Jordan, T.E., J.C. Cornwell, W.R. Boynton, and J.T. Anderson. 2008. Changes in phosphorus biogeochemistry along an estuarine salinity gradient: The iron conveyor belt. *Limnology and Oceanography* 53: 172–184.
- Kaladharan, P., and I.D. Raj. 1989. Primary production of seagrass *Cymodocea serrulata* and its contribution to the productivity of Amini Atoll, Lakshadweep Islands. *Indian Journal of Marine Sciences* 18: 215–216.
- Kennedy, H., J. Beggins, C.M. Duarte, J.W. Fourqurean, M. Holmer, N. Marbà, and J.J. Middelburg. 2010. Seagrass sediments as a global carbon sink: Isotopic constraints. *Global Biogeochemical Cycles*. doi:10.1029/2010GB003848.
- Kumaraguru, A.K., K. Jayakumar, and C.M. Ramakritinan. 2003. Coral bleaching 2002 in the Palk Bay. Southeast coast of India. *Current Science* 85: 1787–1793.
- Lamb, J.B., J.A.J.M. van de Water, D.G. Bourne, C. Altier, M.Y. Hein, E.A. Fiorenza, N. Abu, J. Jompa, et al. 2017. Seagrass ecosystems reduce exposure to bacterial pathogens of humans, fishes, and invertebrates. *Science* 355: 731–733.
- Larkum, A.W.D., R.J. Orth, and C.M. Duarte. 2006. *Seagrasses: Biology, Ecology and Conservation*, 136. Dordrecht: Springer.
- Lavery, P.S., M.-A. Mateo, O. Serrano, and M. Rozaimi. 2013. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS ONE* 8: e73748.
- Lee, K.S., S.R. Park, and Y.K. Kim. 2007. Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *Journal of Experimental Marine Biology and Ecology* 350: 144–175.
- Lewis, E. and D.W.R. Wallace. 1998. CO₂SYS—Program developed for the CO₂ system calculations Report ORNL/CDIAC-105 (Oak Ridge, TN: Carbon Dioxide Information Analysis Center, ORNL).
- Macreadie, P.I., M.E. Baird, S.M. Trevathan-Tackett, A.W. Larkum, and P.J. Ralph. 2014. Quantifying and modelling the carbon sequestration capacity of seagrass meadows: A critical assessment. *Marine Pollution Bulletin* 83: 430–439.

- Manikandan, B., J. Ravindran, S. Shrinivaasu, N. Marimuthu, and K. Paramasivam. 2014. *Environmental Monitoring and Assessment* 186: 5989–6002.
- Manikandan, S., S. Ganesapandian, and K. Parthiban. 2011. Distribution and zonation of seagrasses in the Palk Bay. Southeastern India. *Journal of Fisheries and Aquatic Science* 6: 178–185.
- Marsh, G. 2005. *Seawater pH and anthropogenic carbon dioxide*, 15. Chicago: Argonne National Laboratory. University of Chicago.
- Millero, F.J., T.B. Graham, F. Huang, H. Bustos-Serrano, and D. Perrot. 2006. Dissociation constants of carbonic acid in seawater as a function of salinity and temperature. *Marine Chemistry* 100: 80–94.
- Odom, H.T. 1956. Primary production in flowing waters. *Limnology and Oceanography* 1: 102–117.
- Olivé, I., J. Silva, M.M. Costa, and R. Santos. 2016. *Estuaries and Coasts* 39: 138. doi:10.1007/s12237-015-9973-z.
- Onuf, C.P. 1996. Biomass patterns in seagrass meadows of the Laguna Madre, Texas. *Bulletin of Marine Science* 58: 404–420.
- Ow, Y.X., N. Vogel, C.J. Collier, J.A.M. Holtum, F. Flores, and S. Uthicke. 2016. Nitrate fertilisation does not enhance CO₂ responses in two tropical seagrass species. *Scientific Reports* 6: 23093.
- Plus, M., I. Auby, D. Maurer, G. Trut, Y. Del Amo, F. Dumas, and B. Thouvenin. 2015. Phytoplankton versus macrophyte contribution to primary production and biogeochemical cycles of a coastal mesotidal system. A modelling approach. *Estuarine, Coastal and Shelf Science* 165: 52–60.
- Qasim, S.Z., and P.M.A. Bhattathiri. 1971. Primary productivity of a seagrass bed on Kavaratti atoll (Laccadives). *Hydrobiologia* 38: 29–38.
- Russell, B.D., S.D. Connell, S. Uthicke, N. Muehllehner, K.E. Fabricius, and J.M. Hall-Spencer. 2013. Future seagrass beds: Can increased productivity lead to increased carbon storage? *Marine Pollution Bulletin* 73: 463–469.
- Singh, G., D. Ganguly, A. Paneer Selvam, K. Banerjee, R. Purvaja, and R. Ramesh. 2015. Seagrass ecosystem and climate change: An Indian perspective. *Journal of Climate Change* 1: 67–74. doi:10.3233/JCC-150005.
- Sridhar, R., T. Thangaradjou, and L. Kannan. 2008. Comparative investigation of physico-chemical properties of coral reef and seagrass ecosystems of Palk Bay. *Indian Journal of Marine Science* 37: 207–213.
- Shrinithiviahshini, N.D., V. Rajendhiran, S. Mariyaselvam, C. Rengaraj, M. Duraisamy, and R. Dharmaraj. 2014. An assessment of religious ceremonies and their impact on the physico-chemical and microbiological characterization of foremost seawater in Navagraha Temple, Devipattinam, Tamil Nadu, India. *Global Journal of Science Frontier Research: H Environment & Earth Science* 14: 71–80.
- Strickland, J.D.H. and T.R. Parsons. 1972. A practical handbook of seawater analysis, 2nd ed. Fisheries Research Board of Canada.
- Tokoro, T., S. Hosokawa, E. Miyoshi, K. Tada, K. Watanabe, S. Montani, H. Kayanne, and T.I. Kuwae. 2014. Net uptake of atmospheric CO₂ by coastal submerged aquatic vegetation. *Global Change Biology* 20: 1873–1884.
- Unsworth, R.K.F., and L.C. Cullen. 2010. Recognising the necessity for Indo-Pacific seagrass conservation. *Conservation Letters* 3: 63–73.
- Unsworth, R.K.F.C.J., M. Collier, L.J. Waycott, and L.Cullen-Unsworth Mckenzie. 2015. A framework for the resilience of seagrass ecosystems. *Marine Pollution Bulletin* 100: 34–46.
- Wagner, W.E.I.I. 2016. *Using IBM® SPSS® statistics for research methods and social science statistics*. Thousand Oaks: Sage.
- Watanabe, K., and K. Tomohiro. 2015. *Global Change Biology* 21: 2612–2623. doi:10.1111/gcb.12924.
- Wu, M.-L., Y.G. Hong, J.P. Yin, J.D. Dong, and Y.S. Wang. 2016. Evolution of the sink and source of dissolved inorganic nitrogen with salinity as a tracer during summer in the Pearl River Estuary. *Scientific Reports*. doi:10.1038/srep36638.
- Ziegler, S., and R. Benner. 1999. Nutrient cycling in the water column of a subtropical seagrass meadow. *Marine Ecology Progress Series* 188: 51–62.

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