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Decade of change in *Enhalus acoroides* seagrass meadows in Guam, Mariana Islands

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Abstract. Seagrasses provide important ecosystem services, including carbon sequestration. However, there are significant gaps in our estimates of seagrass coverage, particularly in the western tropical Pacific. In the present study we assessed the status and extent of seagrass meadows, dominated by *Enhalus acoroides*, around Guam, the largest and most populated island in the Marianas. The combined above- and belowground biomass of *E. acoroides* (~2300 g dry weight m^{-2}) is the highest reported for this species and among the highest for all seagrass species. Elemental analysis of C, N and P revealed variations across site and plant part (i.e. above- *v.* belowground); N : P ratios suggested N limitation. Between 2004 and 2015, seagrass meadows in Guam decreased in total size by 22%, although it is unclear whether this change was part of a long-term trend and whether it was caused by natural or human factors. The high standing stock of *E. acoroides* suggests that further examination of this species and this region will be needed to better estimate global seagrass carbon stocks.

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Introduction

Seagrasses and the meadows they create are important components of coastal marine ecosystems worldwide. Seagrass meadows provide a range of ecosystem services that support coastal protection, local economies and food security (Cullen-Unsworth and Unsworth 2013; Nordlund *et al.* 2016). There has been growing interest in mapping the extent and loss of seagrass meadows due to their provision of important ecosystem services, including carbon sequestration (Kennedy *et al.* 2010; Mcleod *et al.* 2011). According to Fourqurean *et al.* (2012), up to 10% of the ocean's organic carbon resides in seagrass meadows, with most of the C in the soils. Because of the anaerobic nature of these soils, the carbon can potentially be sequestered for thousands of years. However, seagrass meadows have been lost at an accelerating rate over the past several decades, often as a result of human activity (Orth *et al.* 2006; Waycott *et al.* 2009). Therefore, declines in seagrass meadow area represent a lost carbon sink, as well as the loss of other valuable services (Pendleton *et al.* 2012)

One of the challenges in fully accounting for the value of seagrasses has been estimating the extent and condition of seagrass meadows worldwide. In their reviews, Waycott *et al.* (2009) and Fourqurean *et al.* (2012) noted significant data gaps, particularly in the western tropical Pacific. Although the availability of satellite imagery has aided this effort (e.g. Mumby *et al.* 1997; Burdick 2005; Yang and Yang 2009; Misbari and Hashim 2016), the analysis of digital images is not straightforward and direct observation is needed to ground truth the status of the seagrass meadows (Roelfsema *et al.* 2013; Hossain *et al.* 2015).

In this study we assessed the status and extent of seagrass meadows around Guam, the largest (~540 km^2), southernmost and most populated island in the Marianas. Ten species of seagrasses are known to occur on Guam (Lobban and Tsuda 2003), with *Enhalus acoroides* (Linnaeus f.) Royle the most dominant (K. Kim and L. J. Raymundo, unpubl. obs.). Up to now, little beyond species distributions has been assessed in Guam or the surrounding region (Tsuda *et al.* 1977; Kock and Tsuda 1978; Tsuda and Kamura 1990). More than a decade ago, Burdick (2005) created detailed benthic maps of Guam, including the extent of the seagrass meadows, using a combination of satellite image analysis and ground truthing. Houk and van Woesik (2008) documented the loss of seagrass meadows in Saipan and attributed this loss to nutrient pollution. More recently, Pinkerton *et al.* (2015) used stable isotope analysis to show that sewage-derived nitrogen (N) was the dominant source of N in the coastal water, but that it did not appear to have a negative effect on growth rates of *E. acoroides.*

In this study we report above- and belowground biomass, organic carbon and nutrient content of *E. acoroides*. We also document decadal changes in the extent of seagrass meadows using a combination of satellite imagery analysis and on-the-ground measurements. These data will begin to fill an important data gap to increase our understanding of the significance of seagrass meadows in the provision of critical ecosystem services in the western tropical Pacific.

Materials and methods

Study site and sampling

Guam is the largest and southernmost of the Mariana Islands, with a land area of ~540 km^2. Guam has a tropical climate with a rainy season from July to November and a dry season from December to May. Samples of *E. acoroides* were collected from 10 sites around the island (Fig. 1) on 2 occasions, August 2015 and May 2016, using a polyvinyl chloride (PVC) push core (inner diameter 15.3 cm), driven down to the underlying carbonate platform, resulting in cores 30–50 cm deep. These sites were selected because they were located within large seagrass meadows and based on their accessibility from shore: <25 m from shore and in depths <1.5 m at high tide. At each site, three cores, each ~5 m apart, were taken from the central area of the seagrass meadow. The extracted cores were sieved onsite to remove sediment and soil, associated fauna and other non-seagrass matter before placing the remaining materials in plastic bags. The samples were placed in a −18°C freezer before they were transported to American University, where they were air dried for 3 days, then sorted to separate out aboveground (i.e. shoots) and belowground (i.e. roots and rhizomes) matter. Once separated, the samples were dried at ~65°C for 2 days and cooled in a desiccation chamber before weighing to determine dry weights. To determine ash-free dry weight, ~15 g was placed in a 500°C furnace for 3 h, then transferred to a desiccation chamber for 1 h before weighing. Ash-free dry weight was taken as the difference between the dry weight and the ashed weight. Nutrient analyses (i.e. C, N and P content) were performed to assess nutrient limitation and were performed by the Cornell Nutrient Analysis Laboratory (Ithaca, NY, USA; cnal.cals.cornell.edu, accessed 16 June 2016) for August 2015 samples only.

Seagrass meadow measurements

Seagrass meadows were first delineated by Burdick (2005) based on IKONOS-2 images (0.82-m resolution) taken between 2003 and 2004, and ground validation surveys. To quantify the extent of seagrass meadows, eight meadows were identified that constituted ~92% of the total by area from around the island (Fig. 1). To determine the extent of these seagrass beds in 2015, we analysed Worldview-2 images (0.46-m resolution). To ground truth these data, individuals with global positioning system (GPS)-equipped mobile telephones (Apple iPhone 6+, Cupertino, CA, USA) running the Trimble Outdoors Navigator application (ver. 6.0.0, Sunnyvale, CA, USA, see http://www.trimbleoutdoors.com) walked the perimeter of the following meadows in 2015: Leon Guerrero, Achang East, Piti and Agaña West. These meadows were selected because they were easily accessible from shore and shallow enough to allow walking of their perimeters. Any patch of seagrasses 1 m in diameter or larger that was non-contiguous with the main meadow was measured by walking out to that patch on a straight path from the main meadow, walking its perimeter and returning to the main meadow on the same path. Non-contiguous patches <1 m in diameter were not included. The GPS data were exported to ArcGIS (ver. 10.5, ESRI, Redlands, CA, USA) to determine meadow sizes.

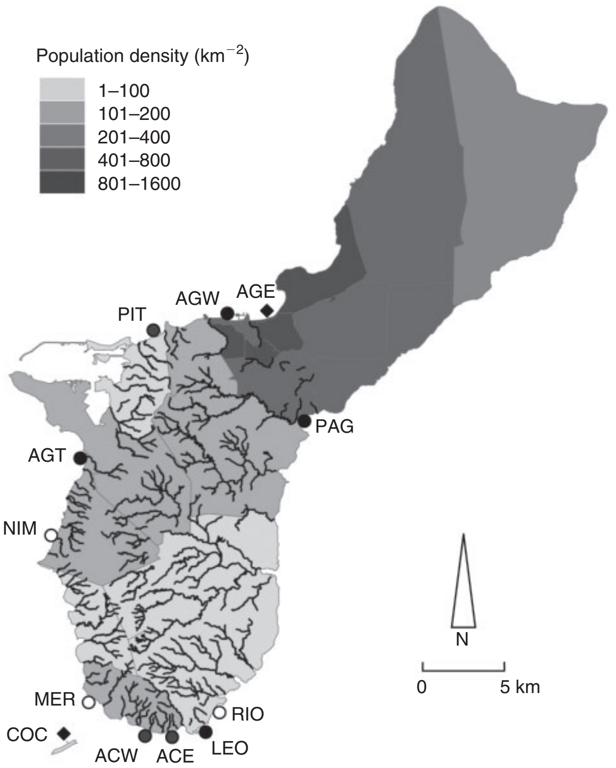

Fig. 1. Study site. The northern half of the island is a carbonate plateau with no rivers, whereas the southern half is volcanic and replete with rivers. Seagrass collection sites are noted by circles (either filled or open); filled circles indicate where meadow areal measurements were also made. Sites where meadow areal measurements were made but no samples were collected are noted by diamonds. Population densities of adjacent municipalities are based on the 2010 US Census (www.census.gov, accessed 22 June 2017). PAG, Pago; RIO, Rios; LEO, Leon Guerrero; ACE, Achang East; ACW, Achang West; COC, Cocos; MER, Merizo; NIM, Nimitz; AGT, Agat; PIT, Piti; AGW, Agaña West; AGE, Agaña East.

Statistical analyses

Dry weight (g m^{-2}), organic C (Mg ha^{-1}), %C, %N, %P and C : N, C : P and N : P ratios for below- and aboveground biomass were tested for normality using the Kolmogorov–Smirnov test and for homogeneity of variances using Levene's test. Because there were substantial differences in dry weights and organic C contents in biomass above and below ground, normality tests were performed for the above- and belowground data separately. Similarly, homogeneity of variance tests were performed for above- and belowground data separately using time as the grouping variable. The remainder (%C, %N, %P, C : N, C : P and N : P) were tested with the above- and belowground data combined. The following datasets were transformed using the

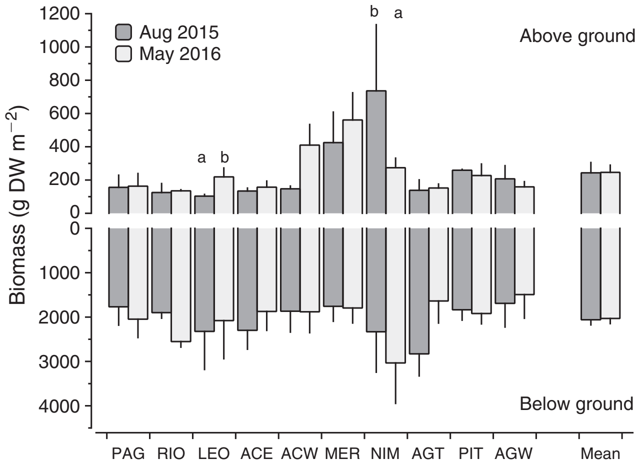

Fig. 2. Variation in above- and belowground biomass of *Enhalus acoroides* among sites and between sampling times. Data are the mean ± s.e.m. Significant effects of sampling time and site are indicated by letters. PAG, Pago; RIO, Rios; LEO, Leon Guerrero; ACE, Achang East; ACW, Achang West; COC, Cocos; MER, Merizo; NIM, Nimitz; AGT, Agat; PIT, Piti; AGW, Agaña West; AGE, Agaña East.

Box–Cox transformation: aboveground dry weight ($\lambda = -0.052$), aboveground organic C ($\lambda = -0.057$), %N ($\lambda = -0.023$), %P ($\lambda = -0.023$), C : P ($\lambda = -0.023$) and N : P ($\lambda = -0.023$). C : P and N : P could not be transformed to normality ($P = 0.045$ and 0.035 respectively), although they were homoscedastic after the transformation. For regression analyses (e.g. biomass above and below ground), we used site averages after testing for normality ($P > 0.05$ in all cases).

Because parametric tests are more sensitive to deviations from homoscedasticity than to non-normality, we used a two-way analysis of variance (ANOVA) with interactions to compare differences between above- and belowground biomass among sites and between times (August 2015 and May 2016). Because we treated above- and belowground data separately for dry weights and organic content, we used the Kruskal–Wallis test to test for differences. Finally, because we did not find significant variation between times, these data were combined for subsequent analyses.

For elemental analyses, because only August 2015 samples were analysed, a one-way ANOVA was used to test the effect of site on C, N and P content, as well as C : N, C : P and N : P ratios.

Where appropriate, data are given as the mean ± s.e.m.

Results

Biomass and nutrient content

The dry weight of *E. acoroides* was highly variable, ranging from 15 to 1528 g m^{-2} above ground, and from 607 to 3978 g dry weight (DW) m^{-2} below ground (Fig. 2). For both above- and belowground biomass, the variability was independent of sampling sites and times (Table 1). The biomass of *E. acoroides* in Guam (averaged across the two sampling times for a given site and then averaged across sites; i.e. $n = 10$) was 244 ± 45 and 2046 ± 97 g DW m^{-2} above and below ground respectively. Similarly, there was substantial variability in organic C content, which ranged from 0.07 to 4.76 Mg ha^{-1} above ground (mean 0.79 ± 0.12 Mg ha^{-1}) and from 1.77 to 13.9 Mg ha^{-1} below ground (mean 6.64 ± 0.34 Mg ha^{-1}); however, the variability was unrelated to site or time of sampling (Fig. 3; Table 1). We noted a significant interaction term (site × time) for aboveground biomass and C but not in any obvious pattern (Fig. 2, 3).

Table 1. Results of analysis of variance (ANOVA)

Above- and belowground biomass and organic C data were tested using separate analyses. Interactions were not included in the model for nutrient content because of missing data. Bold values indicate significant effects

Test and effects	d.f.	*F*	*P*-value
Biomass above ground			
Site	9	1.58	0.155
Time	1	1.67	0.204
Time × site	9	3.04	**0.007**
Biomass below ground			
Site	9	0.689	0.714
Time	1	0.021	0.885
Time × site	9	1.02	0.442
Organic C above ground			
Site	9	1.63	0.139
Time	1	1.81	0.187
Time × site	9	3.46	**0.003**
Organic C below ground			
Site	9	0.817	0.604
Time	1	0.0573	0.812
Time × site	9	1.04	0.43
Nutrient content and ratios			
%C above *v.* below	1	0.564	0.457
%C site	9	2.62	**0.018**
%N above *v.* below	1	278	**<0.001**
%N site	9	0.663	0.737
%P above *v.* below	1	2.83	0.1
%P site	9	1.34	0.25
Elemental ratios			
C : N above *v.* below	1	338	**<0.001**
C : N site	9	1.63	0.141
C : P above *v.* below	1	1.3	0.254
C : P site	9	1.3	0.271
N : P above *v.* below	1	10.3	**0.003**
N : P site	9	0.974	0.476

On average, there was more than an order of magnitude difference between below- and aboveground dry weight and organic C content (mean ratios below : above 13.5 ± 1.0 g m^{-2} (Fig. 2) and 13.5 ± 1.0 Mg ha^{-1} (Fig. 3; Table 1) respectively). Organic C content was strongly related to dry weight (August 2015 and May 2016 data combined) for both above- and belowground biomass ($r^2 = 0.998$ ($n = 20$; $P < 0.001$) and $r^2 = 0.964$ ($n = 20$; $P < 0.001$) respectively). Indeed, the relationship remained even when all the data were combined into a single analysis ($r^2 = 0.995$; $n = 40$; $P < 0.001$); however, above- and belowground biomass were not related to each other (data not shown).

Elemental analyses of the seagrass revealed varying effects of site and plant part (i.e. above *v.* below ground) on C, N and P content (Fig. 4). In the case of C, we noted a significant effect of site but not plant part, but for N there was a significant effect of

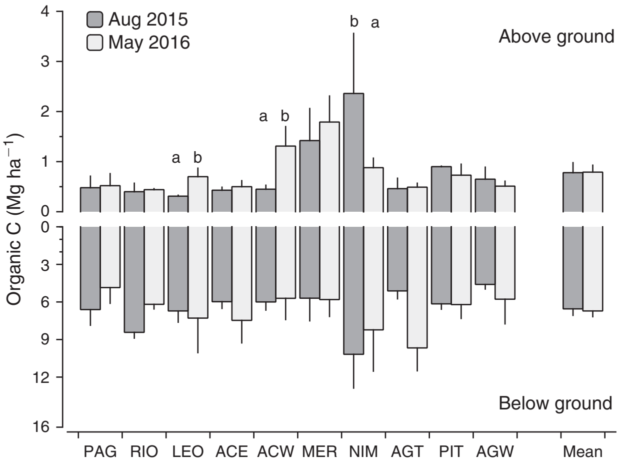

Fig. 3. Variation in above- and belowground organic C content of *Enhalus acoroides* among sites and between sampling times. Data are the mean ± s.e.m. Significant effects of sampling time and site are indicated by letters. PAG, Pago; RIO, Rios; LEO, Leon Guerrero; ACE, Achang East; ACW, Achang West; COC, Cocos; MER, Merizo; NIM, Nimitz; AGT, Agat; PIT, Piti; AGW, Agaña West; AGE, Agaña East.

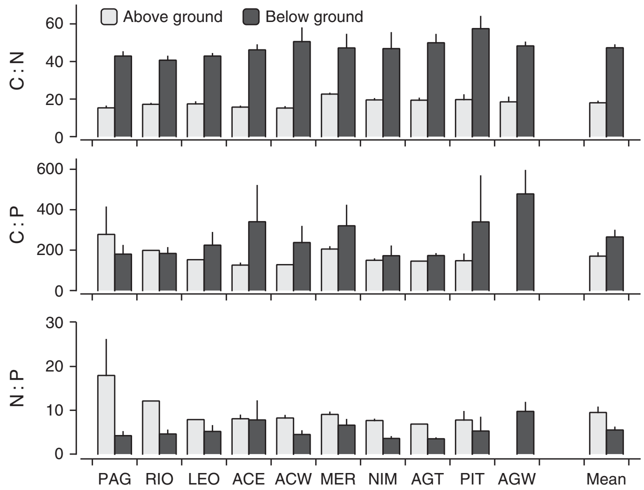

Fig. 5. Variation in nutrient ratios in above- and belowground tissues of *Enhalus acoroides* among sites. These data are for samples taken in August 2015 only. Data are the mean ± s.e.m. PAG, Pago; RIO, Rios; LEO, Leon Guerrero; ACE, Achang East; ACW, Achang West; COC, Cocos; MER, Merizo; NIM, Nimitz; AGT, Agat; PIT, Piti; AGW, Agaña West; AGE, Agaña East.

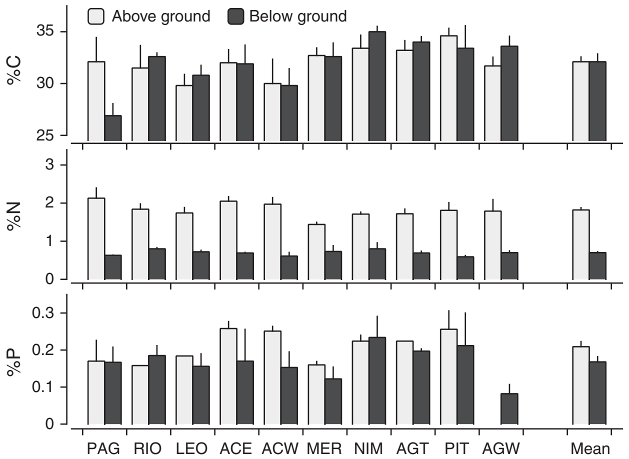

Fig. 4. Variation in nutrient content in above- and belowground tissues of *Enhalus acoroides* among sites. These data are for samples taken in August 2015 only. Data are the mean ± s.e.m. PAG, Pago; RIO, Rios; LEO, Leon Guerrero; ACE, Achang East; ACW, Achang West; COC, Cocos; MER, Merizo; NIM, Nimitz; AGT, Agat; PIT, Piti; AGW, Agaña West; AGE, Agaña East.

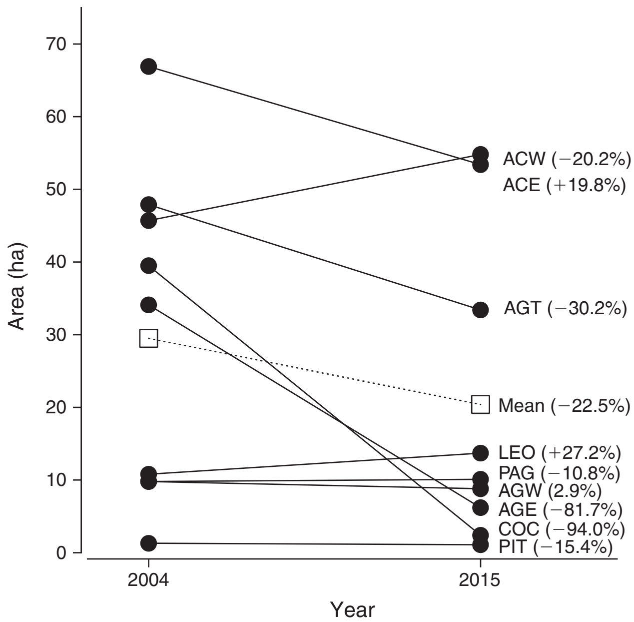

Fig. 6. Changes in the extent of seagrass meadows between 2004 and 2015. ACW, Achang West; ACE, Achang East; AGT, Agat; LEO, Leon Guerrero; PAG, Pago; AGW, Agaña West; AGE, Agaña East; COC, Cocos; PIT, Piti.

plant part (N higher in aboveground biomass) but not location. Neither site nor plant part had an effect on P content. The ratios of these elements remained constant across sampling sites (Table 1), but varied by plant parts for C : N (higher below ground) and N : P (higher above ground; Fig. 5).

Changes in seagrass meadows

Analysis of areal measurements using Worldview-2 images resulted in larger meadow size estimates than measurements made on the ground. On average, walking the perimeter of the meadows produced size estimates that were approximately 7.1 ± 2.6% lower than estimates produced by tracing perimeters on the Worldview-2 images. Thus, we corrected all areal estimates derived from satellite images for subsequent analyses.

The size of nine seagrass meadows examined ranged in size between 1.3 (Piti) and 67 ha (Achang West) in 2004; the same meadows measured 1.1 and 57 ha respectively in 2015 (Fig. 6). Over 11 years, these nine seagrass meadows decreased in size

Table 2. Biomass of *Enhalus acoroides*

Values shown are for meadows dominated (>50%) by *E. acoroides* and are the mean of replicated sites or sampling times within a study. Italic values are calculated from data presented in the studies. AG, above ground (leaves and sheath); BG, below ground (roots and rhizomes); DW, dry weight

Location	*Enhalus acoroides* biomass (g DW m^{-2})			BG : AG	References
	AG	BG	Total		
Australia	31.6	–	–	–	Rasheed *et al.* (2008)
Indonesia	83	157	*240*	1.89	Erftemeijer (1994)
Indonesia	–	–	224	–	Erftemeijer and Herman (1994)
Guam	244	2046	2290	13.5	Present study
Micronesia	–	–	171	–	Ogden (1992)
Philippines	–	152			Duarte *et al.* (1998)
Philippines	53	180	233	*3.4*	Vermaat *et al.* (1995)
Tanzania	83.5	–	–	–	Gullström *et al.* (2006)
Tanzania	92	–	–	–	Gullström *et al.* (2006)
Thailand	13	–	–	–	Nakaoka and Supanwanid (2000)
Thailand	56.8	140	197	2.46	Poovachiranon and Chansang (1994)
Thailand	255	589	844	2.31	Wirachwong and Holmer (2010)
Mean	101	543	600	3.69	
s.e.	31	338	319	1.34	
CV (%)	86.8	139	130	72.7	

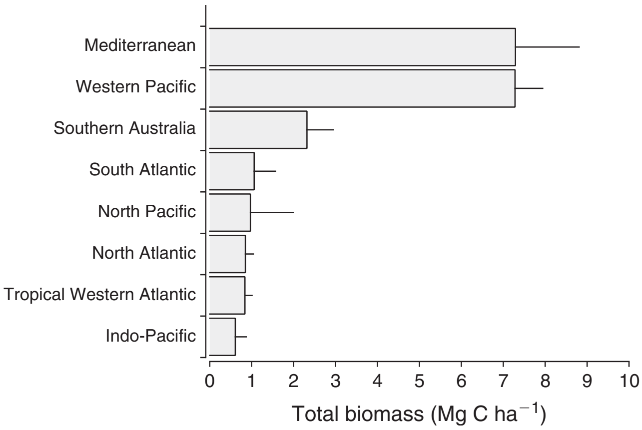

Fig. 7. Comparison of seagrass biomass from major oceanic regions. The Western Pacific is represented by the present study only; data for other regions have been summarised by Fourqurean *et al.* (2012).

from a total of 266 to 184 ha, a loss of 82 ha or 22%. Substantial declines were recorded at Cocos (loss of 37 ha, or a 94% decrease) and at Agaña East (loss of 28 ha, or an 82% decrease). Three meadows that increased in size (Leon Guerrero, Achang East and Agaña West) added a total of ~12 ha to Guam's seagrass meadows.

Discussion

Biomass: within-plant and temporal patterns

The combined above- and belowground biomass of *E. acoroides* (~2300 g DW m^{-2}) is the highest reported for this species (Table 2) and among the highest for all seagrass species (Fig. 7; Duarte and Chiscano 1999; Fourqurean, Duarte *et al.* 2012). Using turnover rates of 1.5 and 0.34% per day for above- and belowground biomass respectively (Duarte and Chiscano 1999), we estimated that biomass production of *E. acoroides* was ~10.6 g DW m^{-2} day^{-1}, making this species among the most productive of all seagrasses.

Nearly 90% of the biomass of *E. acoroides* in Guam is below ground (Fig. 2), which is substantially higher than reported for the species in other locations (Table 2). It is not clear why *E. acoroides*, in general, allocates so much of its biomass to belowground material; it may be a response to growing in nutrient-poor carbonate sediments, which requires greater surface area for nutrient absorption, or the need for frequent regrowth after aerial exposure or heavy grazing (Erftemeijer 1994; Erftemeijer and Herman 1994). In Guam, *Enhalus* meadows predominantly occur in carbonate sediments, typically at depths <50 cm, atop limestone pavement. Moreover, the meadows occur in the intertidal zone and are often completely exposed to air during low tides. Although grazing could also have been important in driving allocation patterns, it is no longer the case because of extensive overfishing of the nearshore waters (L. R. Raymundo, unpubl. obs.).

Both the biomass and organic C content remained unchanged between the two sampling times (Fig. 2, 3). This contrasts with several other studies of *E. acoroides* that found increases in biomass and density of shoots during the wet season, concomitant with terrestrial inputs of nutrients (Erftemeijer and Herman 1994; Rasheed *et al.* 2008; Wirachwong and Holmer 2010). The lack of variation in Guam may be due to the intertidal environment in which these seagrasses are found: even at high tide, they are rarely completely submerged. Thus, tidal height may constrain the upper limit on size, and is likely more important than nutrient availability in determining productivity (Estacion and Fortes 1988; Unsworth *et al.* 2012).

The high standing stock of *E. acoroides* reported here has implications for estimating global C sequestration by seagrass meadows. Previous work has shown species-specific differences in seagrass meadow carbon stocks (Lavery *et al.* 2013), and estimates of the global seagrass carbon sink have been

Table 3. Nutrient content and elemental ratios of *Enhalus acoroides*

Values reported here are for meadows dominated (>50%) by *E. acoroides* and are the mean of replicated sites or sampling times. Italic values are calculated from data presented in the studies

Location	%C	%N	%P	C : N	C : P	N : P	References
Above ground (leaves and sheath)							
Australia	37	*1.5*	*0.083*	*24.7*	*444*	*18*	Atkinson and Smith (1983)
Australia	–	1.57	0.22	–	–	7.14	Birch (1975)
Guam	32.1	1.82	0.21	18	170	9.51	Present study
Indonesia	31.6	2.71	0.34	*11.7*	*92.9*	*7.97*	Erftemeijer (1994)
Indonesia	28.9	1.82	0.2	*15.9*	*144*	*9.08*	Erftemeijer and Herman (1994)
Indonesia	31.8	1.6	–	*19.8*	–	–	Nienhuis *et al.* (1989)
Indonesia	35	–	–	–	–	–	Supriadi *et al.* (2014)
Philippines	–	1.8	–	–	–	–	Agawin *et al.* (1996)
Philippines	–	–	–	22	257	–	Cebrián and Duarte (1998)
Philippines	–	2.01	0.333	–	–	*6.7*	Terrados *et al.* (1999*a*)
Philippines	–	1.96	0.34	–	–	*5.76*	Terrados *et al.* (1999*b*)
Thailand	34.9	3.28	–	*10.6*	–	–	Holmer and Olsen (2002)
Thailand	32.1	2.33	0.128	*13.8*	*252*	*18.2*	Wirachwong and Holmer (2010)
Thailand	31.7	3.31	0.513	*9.56*	*61.7*	*6.45*	Yamamuro *et al.* (2004)
Mean	33.6	2.13	0.24	16.7	303	13.7	
s.e.	1.1	0.17	0.044	1.64	108	4.08	
CV (%)	10.3	28.6	59	31.1	101	94.2	
Below ground (roots and rhizomes)							
Australia	–	0.37	0.17	–	–	2.18	Birch (1975)
Guam	31.9	0.696	0.177	47.2	241	5.02	Present study
Indonesia	35.2	1.29	0.145	*27.4*	*243*	*8.86*	Erftemeijer (1994)
Indonesia	28.9	0.77	0.098	*37.6*	*297*	*7.9*	Erftemeijer and Herman (1994)
Indonesia	31	1.1	–	*28.2*	–	–	Nienhuis *et al.* (1989)
Indonesia	36.8	–	–	–	–	–	Supriadi *et al.* (2014)
Philippines	–	0.7	–	–	–	–	Agawin *et al.* (1996)
Thailand	29	0.37	–	*78.3*	–	–	Holmer and Olsen (2002)
Thailand	31.2	0.888	0.155	*35.1*	*202*	*5.74*	Yamamuro *et al.* (2004)
Mean	32.6	0.79	0.13	42.1	328	7.62	
s.e.	1.16	0.1	0.019	6.58	84	1.93	
CV (%)	10.1	39	35	41.3	57.2	62.1	

limited by over-reliance on measurements of *Posidonia oceanica*, a seagrass found in the Mediterranean (Duarte *et al.* 2013). The results of the present study show that *E. acoroides* can have a total biomass comparable to that of *P. oceanica*. Although we did not evaluate the sediment carbon in these *E. acoroides* meadows, the high standing stock suggests the potential for high C sequestration rates (Fourqurean *et al.* 2012; but see Howard *et al.* 2018). Additional research to determine C sequestration rates in *E. acoroides* meadows will be critical to understanding carbon storage in tropical seagrass meadows. Meadows in understudied areas such as the western Pacific are likely important components of the global seagrass carbon stock.

Nutrient content

In comparing the results from this study with previous measurements of *E. acoroides*, C content was the least variable feature, scaling very closely with biomass in a relationship that included data from both the above- and belowground materials. Indeed, C content appears to be a conserved feature of the species, varying by ~10% (i.e. coefficient of variation) despite the fact that the available data spanned several locations in the western tropical Pacific and ~40 years among studies (Table 3). In a review of a broad range of aquatic primary producers, Duarte (1992) found that C content in seagrasses was less variable than in the other groups.

N and P contents were much more variable than C, likely reflecting differences in the availability of these elements in the environments in which the seagrasses were growing. Overall N : P ratios for *E. acoroides* in Guam and elsewhere were all well below 30 : 1, indicating N limitation (Atkinson and Smith 1983; Duarte 1990).

Meadow loss

This study of seagrass meadows in Guam revealed a decrease in total size by 22% between 2004 and 2015 (Fig. 6). Globally, seagrass meadows have declined by 30% between 1879 and 2006 (Waycott *et al.* 2009); however, Waycott *et al.* (2009) noted that the rate of loss has been accelerating since 1990, and highlighted coastal development, dredging activities and declining water quality as drivers of this accelerating loss. In comparison, seagrasses in Guam have fared better than those elsewhere. This difference may reflect the level of human activity on the island, which has been increasing but is substantially lower than in those areas where large-scale losses have occurred, such as the north-east of the US, the Gulf of Mexico and the Mediterranean.

The loss of seagrass meadows in Guam has occurred without obvious links to human activity. Development on Guam has been concentrated on the north-western side of the island. Although we documented ~83% meadow loss at the nearby Agaña East meadow, the Agaña West meadow, ~2 km from Agaña East, remained largely unchanged (Fig. 6). Both sites share a well-developed coastline affected by sewage-derived N (Pinkerton *et al.* 2015). In contrast, the Cocos meadow, offshore to a reasonably unpopulated area of Guam (Fig. 1), declined by 94% during the study period. The nearby Cocos Island is a tourist attraction that is modest in size and does not support overnight stays. Although visitor data are unavailable, the effect of tourism around Cocos is likely to be far less than that of human activity around Agaña.

The loss of seagrass meadows in the Mariana Islands was first reported by Houk and van Woesik (2008), who noted that ~34% of mixed seagrass–macroalgae beds in Saipan, located ~200 km north of Guam, were replaced by sand over a 50-year period. The decline was largely due to the loss of *Halodule uninervis*, a seagrass species that is susceptible to overgrowth by macroalgae, which benefit from increased nutrient pollution associated with coastal development. In general, the negative effects of nutrient pollution appear to be indirect, namely in promoting the growth of epiphytes or algae and thereby leading to light attenuation and reductions in photosynthesis by seagrasses (Lapointe *et al.* 1994; Burkholder *et al.* 2007).

However, Houk and van Woesik (2008) also found that *E. acoroides* meadows increased in extent during the same 50-year period. Indeed, *E. acoroides* appears to be a stress-tolerant species that does well under low-tide conditions (Bridges and McMillan 1986), is resistant to fouling and siltation and does well when N availability increases (Agawin *et al.* 1996; Terrados *et al.* 1998, 1999*a*; Udy *et al.* 1999; van Katwijk *et al.* 2011; Pinkerton *et al.* 2015). Thus, it is difficult to attribute the loss of seagrass meadows in Guam, primarily made up of *E. acoroides*, to nutrient pollution. It is also possible that the decline in seagrass meadows in Guam is part of a natural cycle of gains and losses coincident with long-term climate variability and tidal exposure (Rasheed and Unsworth 2011; Unsworth *et al.* 2012). In the absence of data for the intervening years of our study, it is difficult to evaluate this hypothesis. However, in north-east Australia, the effect of climate variability and tidal exposure on *E. acoroides* meadows was only apparent as changes in biomass and not meadow size (Unsworth *et al.* 2012). Regardless of the cause, the loss has been substantial, with potential concomitant losses in ecosystem services such as C sequestration (Fourqurean *et al.* 2012; Alongi *et al.* 2016) and the support of subsistence fisheries (Nakamura and Sano 2004; Unsworth *et al.* 2007).

It is unclear why the Agaña East and Cocos meadows have not recovered. Given that the areas with declining meadows are not isolated and are in close proximity (<2 km) to other apparently healthy meadows, *E. acoroides* allocates substantial effort to sexual reproduction (Verheij and Erftemeijer 1993; Duarte *et al.* 1997; Rollón *et al.* 2003) and the species produces seeds that are buoyant for as long as 14 h (Lacap *et al.* 2002), there should be more than sufficient connectivity for recolonisation. Indeed, Nakajima *et al.* (2014) found little genetic differentiation among populations of *E. acoroides* between the north-east Philippines and southern Japan, a distance of ~1100 km, suggesting that dispersal by sexual propagules is a life history feature of this species. Thus, it appears that dispersal is not the bottleneck in the process.

Conversely, according to Rollón *et al.* (1998), *E. acoroides* is among the slowest of tropical seagrass species to recover from disturbance events, needing as long as 10 years to fully recolonise an area, due to a combination of low recruitment rates and slow vegetative growth rates. Given the noted declines in Agaña East and Cocos (Fig. 6), it is possible that the losses occurred recently and there has not been sufficient time for recovery.

The high productivity of the *E. acoroides* meadows in Guam suggests that they provide substantial ecosystem services to local communities and contribute to C sequestration. Given that this species is an important part of seagrass meadows in the Western Pacific, regional contributions to C sequestration may indeed be substantial, and this highlights the need for additional effort in the area. The availability of satellite imagery has vastly improved our ability to monitor environmental change at increasing resolutions and spatial scales. However, these digital data can be expensive, may lack the necessary temporal resolution (Hossain *et al.* 2015) and may be difficult to interpret (Roelfsema *et al.* 2013). We show that for features such as the *E. acoroides* meadows, on-the-ground measurements using readily available hand-held GPS devices can provide a viable, and perhaps more accurate, alternative for monitoring landscapes in a rapidly changing world.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

Agawin, N. S. R., Duarte, C. M., and Fortes, M. D. (1996). Nutrient limitation of Philippines seagrasses (Cape Boliano, NW Philippines): *in situ* experimental evidence. *Marine Ecology Progress Series* **138**, 233–243. doi:10.3354/MEPS138233

Alongi, D. M., Murdiyarso, D., Fourqurean, J. W., Kauffman, J. B., Hutahaean, A., Crooks, S., Lovelock, C. E., Howard, J., Herr, D., Fortes, M., Pidgeon, E., and Wagey, T. (2016). Indonesia's blue carbon: a globally significant and vulnerable sink for seagrass and mangrove carbon. *Wetlands Ecology and Management* **24**(1), 3–13. doi:10.1007/S11273-015-9446-Y

Atkinson, M. J., and Smith, S. V. (1983). C-N-P ratios of benthic marine plants. *Limnology and Oceanography* **28**(3), 568–574. doi:10.4319/LO.1983.28.3.0568

Birch, W. R. (1975). Some chemical and calorific properties of tropical marine angiosperms compared with those of other plants. *Journal of Applied Ecology* **12**, 201–212. doi:10.2307/2401729

Bridges, K. W., and McMillan, C. (1986). The distribution of seagrasses of Yap, Micronesia, with relation to low tide conditions. *Aquatic Botany* **24**(4), 403–407. doi:10.1016/0304-3770(86)90106-3

Burdick, D. (2005) Guam coastal atlas. University of Guam Marine Laboratory, Technical Report 114, Mangilao. Available at www.guammarinelab.org/coastal.atlas [Verified 08 Aug 2018].

Burkholder, J. M., Tomasko, D. A., and Touchette, B. W. (2007). Seagrasses and eutrophication. *Journal of Experimental Marine Biology and Ecology* **350**(1–2), 46–72. doi:10.1016/J.JEMBE.2007.06.024

Cebrián, J., and Duarte, C. M. (1998). Patterns in leaf herbivory on seagrasses. *Aquatic Botany* **60**(1), 67–82. doi:10.1016/S0304-3770(97)00070-3

Cullen-Unsworth, L., and Unsworth, R. (2013). Seagrass meadows, ecosystem services, and sustainability. *Environment* **55**(3), 14–27. doi:10.1080/00139157.2013.785864

Duarte, C. M. (1990). Seagrass nutrient content. *Marine Ecology Progress Series* **67**(2), 201–207. doi:10.3354/MEPS067201

Duarte, C. M. (1992). Nutrient concentration of aquatic plants – patterns across species. *Limnology and Oceanography* **37**(4), 882–889. doi:10.4319/LO.1992.37.4.0882

Duarte, C. M., and Chiscano, C. L. (1999). Seagrass biomass and production: a reassessment. *Aquatic Botany* **65**(1–4), 159–174. doi:10.1016/S0304-3770(99)00038-8

Duarte, C. M., Uri, J. S., Agawin, N. S. R., Fortes, M. D., Vermaat, J. E., and Marba, N. (1997). Flowering frequency of Philippine seagrasses. *Botanica Marina* **40**(6), 497–500.

Duarte, C. M., Merino, M., Agawin, N. S. R., Uri, J., Fortes, M. D., Gallegos, M. E., Marba, N., and Hemminga, M. A. (1998). Root production and belowground seagrass biomass. *Marine Ecology Progress Series* **171**, 97–108. doi:10.3354/MEPS171097

Duarte, C. M., Kennedy, H., Marba, N., and Hendriks, I. (2013). Assessing the capacity of seagrass meadows for carbon burial: current limitations and future strategies. *Ocean and Coastal Management* **83**, 32–38. doi:10.1016/J.OCECOAMAN.2011.09.001

Erftemeijer, P. L. A. (1994). Differences in nutrient concentrations and resources between seagrass communities on carbonate and terrigenous sediments in South Sulawesi, Indonesia. *Bulletin of Marine Science* **54**(2), 403–419.

Erftemeijer, P. L. A., and Herman, P. M. J. (1994). Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. *Oecologia* **99**(1–2), 45–59. doi:10.1007/BF00317082

Estacion, J. S., and Fortes, M. D. (1988). Growth rates and primary production of *Enhalus acoroides* (L.f.) Royle from Lag-It, North Bais Bay, the Philippines. *Aquatic Botany* **29**(4), 347–356. doi:10.1016/0304-3770(88)90078-2

Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marba, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience* **5**(7), 505–509. doi:10.1038/NGEO1477

Gullström, M., Lunden, B., Bodin, M., Kangwe, J., Ohman, M. C., Mtolera, M. S. P., and Bjork, M. (2006). Assessment of changes in the seagrass-dominated submerged vegetation of tropical Chwaka Bay (Zanzibar) using satellite remote sensing. *Estuarine, Coastal and Shelf Science* **67**(3), 399–408. doi:10.1016/J.ECSS.2005.11.020

Holmer, M., and Olsen, A. B. (2002). Role of decomposition of mangrove and seagrass detritus in sediment carbon and nitrogen cycling in a tropical mangrove forest. *Marine Ecology Progress Series* **230**, 87–101. doi:10.3354/MEPS230087

Hossain, M. S., Bujang, J. S., Zakaria, M. H., and Hashim, M. (2015). The application of remote sensing to seagrass ecosystems: an overview and future research prospects. *International Journal of Remote Sensing* **36**(1), 61–114. [Erratum published in *International Journal of Remote Sensing* 2015; **36**(1): 1–3].. doi:10.1080/01431161.2014.990649

Houk, P., and van Woesik, R. (2008). Dynamics of shallow-water assemblages in the Saipan Lagoon. *Marine Ecology Progress Series* **356**, 39–50. doi:10.3354/MEPS07252

Howard, J. L., Creed, J. C., Aguiar, M. V. P., and Fourqurean, J. W. (2018). CO_2 released by carbonate sediment production in some coastal areas may offset the benefits of seagrass 'Blue Carbon' storage. *Limnology and Oceanography* **63**(1), 160–172. doi:10.1002/LNO.10621

Kennedy, H., Beggins, J., Duarte, C. M., Fourqurean, J. W., Holmer, M., Marba, N., and Middelburg, J. J. (2010). Seagrass sediments as a global carbon sink: isotopic constraints. *Global Biogeochemical Cycles* **24**, GB4026. doi:10.1029/2010GB003848

Kock, R. L., and Tsuda, R. T. (1978). Seagrass assemblages of Yap, Micronesia. *Aquatic Botany* **5**, 245–249. doi:10.1016/0304-3770(78)90067-0

Lacap, C. D. A., Vermaat, J. E., Rollón, R. N., and Nacorda, H. M. (2002). Propagule dispersal of the SE Asian seagrasses *Enhalus acoroides* and *Thalassia hemprichii. Marine Ecology Progress Series* **235**, 75–80. doi:10.3354/MEPS235075

Lapointe, B. E., Tomasko, D. A., and Matzie, W. R. (1994). Eutrophication and trophic state classification of seagrass communities in the Florida Keys. *Bulletin of Marine Science* **54**, 696–717.

Lavery, P. S., Mateo, M. A., Serrano, O., and Rozaimi, M. (2013). Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLoS One* **8**(9), e73748. doi:10.1371/JOURNAL.PONE.0073748

Lobban, C. S., and Tsuda, R. T. (2003). Revised checklist of benthic marine macroalgae and seagrasses of Guam and Micronesia. *Micronesica* **35**, 54–99.

Mcleod, E., Chmura, G. L., Bouillon, S., Salm, R., Bjork, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R. (2011). A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. *Frontiers in Ecology and the Environment* **9**(10), 552–560. doi:10.1890/110004

Misbari, S., and Hashim, M. (2016). Change detection of submerged seagrass biomass in shallow coastal water. *Remote Sensing* **8**(3), 200. doi:10.3390/RS8030200

Mumby, P. J., Green, E. P., Edwards, A. J., and Clark, C. D. (1997). Measurement of seagrass standing crop using satellite and digital airborne remote sensing. *Marine Ecology Progress Series* **159**, 51–60. doi:10.3354/MEPS159051

Nakajima, Y., Matsuki, Y., Lian, C. L., Fortes, M. D., Uy, W. H., Campos, W. L., Nakaoka, M., and Nadaoka, K. (2014). The Kuroshio Current influences genetic diversity and population genetic structure of a tropical seagrass, *Enhalus acoroides. Molecular Ecology* **23**(24), 6029–6044. doi:10.1111/MEC.12996

Nakamura, Y., and Sano, M. (2004). Comparison between community structures of fishes in *Enhalus acoroides*- and *Thalassia hemprichii*-dominated seagrass beds on fringing coral reefs in the Ryukyu Islands, Japan. *Ichthyological Research* **51**(1), 38–45. doi:10.1007/S10228-003-0191-5

Nakaoka, M., and Supanwanid, C. (2000). Quantitative estimation of the distribution and biomass of seagrasses at Haad Chao Mai National Park, Trang province, Thailand. *Kasetsart University Fisheries Research Bulletin* **22**, 10–22.

Nienhuis, P. H., Coosen, J., and Kiswara, W. (1989). Community structure and biomass distribution of seagrasses and macrofauna in the Flores Sea, Indonesia. *Netherlands Journal of Sea Research* **23**(2), 197–214. doi:10.1016/0077-7579(89)90014-8

Nordlund, L. M., Koch, E. W., Barbier, E. B., and Creed, J. C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS One* **11**(10), e0163091. doi:10.1371/JOURNAL.PONE.0163091

Ogden, J. C. (1992). The impact of Hurricane Andrew on the ecosystems of south Florida. *Conservation Biology* **6**(4), 488–490. doi:10.1046/J.1523-1739.1992.06040488.X

Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Olyarnik, S., Short, F. T., Waycott, M., and Williams, S. L. (2006). A global crisis for seagrass ecosystems. *Bioscience* **56**(12), 987–996. doi:10.1641/0006-3568(2006)56[987:AGCFSE]2.0.CO;2

Pendleton, L., Donato, D. C., Murray, B. C., Crooks, S., Jenkins, W. A., Sifleet, S., Craft, C., Fourqurean, J. W., Kauffman, J. B., Marba, N., Megonigal, P., Pidgeon, E., Herr, D., Gordon, D., and Baldera, A. (2012). Estimating global 'blue carbon' emissions from conversion and degradation of vegetated coastal ecosystems. *PLoS One* **7**(9), e43542. doi:10.1371/JOURNAL.PONE.0043542

Pinkerton, K., Baker, D. M., Cuddy, M. R., Raymundo, L. J., Meyer, K. A., and Kim, K. (2015). Nitrogen dynamics on Guam as revealed by the seagrass *Enhalus acoroides. Marine Ecology Progress Series* **528**, 117–126. doi:10.3354/MEPS11270

Poovachiranon, S., and Chansang, H. (1994). Community structure and biomass of seagrass beds in the Andaman Sea. I. Mangrove-associated seagrass beds. *Research Bulletin – Phuket Marine Biological Center* **59**, 53–64.

Rasheed, M. A., and Unsworth, R. K. F. (2011). Long-term climate-associated dynamics of a tropical seagrass meadow: implications for the future. *Marine Ecology Progress Series* **422**, 93–103. doi:10.3354/MEPS08925

Rasheed, M. A., Dew, K. R., McKenzie, L. J., Coles, R. G., Kerville, S. P., and Campbell, S. J. (2008). Productivity, carbon assimilation and intra-annual change in tropical reef platform seagrass communities of the Torres Strait, north-eastern Australia. *Continental Shelf Research* **28**(16), 2292–2303. doi:10.1016/J.CSR.2008.03.026

Roelfsema, C., Kovacs, E. M., Saunders, M. I., Phinn, S., Lyons, M., and Maxwell, P. (2013). Challenges of remote sensing for quantifying changes in large complex seagrass environments. *Estuarine, Coastal and Shelf Science* **133**, 161–171. doi:10.1016/J.ECSS.2013.08.026

Rollón, R. N., van Steveninck, E. D. D., van Vierssen, W., and Fortes, M. D. (1998). Contrasting recolonization strategies in multi-species seagrass meadows. *Marine Pollution Bulletin* **37**(8–12), 450–459.

Rollón, R. N., van Steveninck, E. D. D., and van Vierssen, W. (2003). Spatio-temporal variation in sexual reproduction of the tropical seagrass *Enhalus acoroides* (L.f.) Royle in Cape Bolinao, NW Philippines. *Aquatic Botany* **76**(4), 339–354. doi:10.1016/S0304-3770(03)00070-6

Supriadi, S., Kaswadji, R. F., Bengen, D. G., and Hutomo, M. (2014). Carbon stock of seagrass community in Barranglompo Island, Makassar. *Ilmu Kelautan* **19**, 1–10. doi:10.14710/IK.IJMS.19.1.1-10

Terrados, J., Duarte, C. M., Fortes, M. D., Borum, J., Agawin, N. S. R., Bach, S., Thampanya, U., Kamp-Nielsen, L., Kenworthy, W. J., Geertz-Hansen, O., and Vermaat, J. (1998). Changes in community structure and biomass of seagrass communities along gradients of siltation in SE Asia. *Estuarine, Coastal and Shelf Science* **46**(5), 757–768. doi:10.1006/ECSS.1997.0304

Terrados, J., Agawin, N. S. R., Duarte, C. M., Fortes, M. D., Kamp-Nielsen, L., and Burum, J. (1999*a*). Nutrient limitation of the tropical seagrass *Enhalus acoroides* (L.) Royle in Cape Bolinao, NW Philippines. *Aquatic Botany* **65**(1–4), 123–139. doi:10.1016/S0304-3770(99)00036-4

Terrados, J., Borum, J., Duarte, C. M., Fortes, M. D., Kamp-Nielsen, L., Agawin, N. S. R., and Kenworthy, W. J. (1999*b*). Nutrient and mass allocation of South-east Asian seagrasses. *Aquatic Botany* **63**(3–4), 203–217. doi:10.1016/S0304-3770(99)00004-2

Tsuda, R. T., and Kamura, S. (1990). Comparative review on the floristics, phytogeography, seasonal aspects and assemblage patterns of the seagrass flora in Micronesia and the Ryukyu Islands. *Galaxea* **9**, 77–93.

Tsuda, R. T., Fosberg, F. R., and Sachet, M. H. (1977). Distribution of seagrasses in Micronesia. *Micronesica* **13**, 191–198.

Udy, J. W., Dennison, W. C., Long, W. J. L., and McKenzie, L. J. (1999). Responses of seagrass to nutrients in the Great Barrier Reef, Australia. *Marine Ecology Progress Series* **185**, 257–271. doi:10.3354/MEPS185257

Unsworth, R. K. F., Taylor, J. D., Powell, A., Bell, J. J., and Smith, D. J. (2007). The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. *Estuarine, Coastal and Shelf Science* **74**(1–2), 53–62. doi:10.1016/J.ECSS.2007.04.001

Unsworth, R. K. F., Rasheed, M. A., Chartrand, K. M., and Roelofs, A. J. (2012). Solar radiation and tidal exposure as environmental drivers of *Enhalus acoroides* dominated seagrass meadows. *PLoS One* **7**(3), e34133. doi:10.1371/JOURNAL.PONE.0034133

van Katwijk, M. M., van der Welle, M. E. W., Lucassen, E. C. H. E. T., Vonk, J. A., Christianen, M. J. A., Kiswara, W., al Hakim, I. I., Arifin, A., Bouma, T. J., Roelofs, J. G. M., and Lamers, L. P. M. (2011). Early warning indicators for river nutrient and sediment loads in tropical seagrass beds: a benchmark from a near-pristine archipelago in Indonesia. *Marine Pollution Bulletin* **62**(7), 1512–1520. doi:10.1016/J.MARPOLBUL.2011.04.007

Verheij, E., and Erftemeijer, P. L. A. (1993). Distribution of seagrasses and associated macroalgae in south Sulawesi, Indonesia. *Blumea* **38**(1), 45–64.

Vermaat, J. E., Agawin, N. S. R., Duarte, C. M., Fortes, M. D., Marba, N., and Uri, J. S. (1995). Meadow maintenance, growth and productivity of a mixed Philippine seagrass bed. *Marine Ecology Progress Series* **124**(1–3), 215–225. doi:10.3354/MEPS124215

Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., Calladine, A., Fourqurean, J. W., Heck, K. L., Hughes, A. R., Kendrick, G. A., Kenworthy, W. J., Short, F. T., and Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences of the United States of America* **106**(30), 12377–12381. doi:10.1073/PNAS.0905620106

Wirachwong, P., and Holmer, M. (2010). Nutrient dynamics in 3 morphological different tropical seagrasses and their sediments. *Aquatic Botany* **93**(3), 170–178. doi:10.1016/J.AQUABOT.2010.06.004

Yamamuro, M., Umezawa, Y., and Koike, I. (2004). Internal variations in nutrient concentrations and the C and N stable isotope ratios in leaves of the seagrass *Enhalus acoroides. Aquatic Botany* **79**(1), 95–102. doi:10.1016/J.AQUABOT.2004.01.007

Yang, D. T., and Yang, C. Y. (2009). Detection of seagrass distribution changes from 1991 to 2006 in Xincun Bay, Hainan, with satellite remote sensing. *Sensors* **9**(2), 830–844. doi:10.3390/S90200830

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