

Megan I. Saunders*, Elisa Bayraktarov, Chris M. Roelfsema, Javier X. Leon^a,
Jimena Samper-Villarreal, Stuart R. Phinn, Catherine E. Lovelock and Peter J. Mumby

Spatial and temporal variability of seagrass at Lizard Island, Great Barrier Reef

Abstract: Increasing threats to natural ecosystems from local and global stressors are reinforcing the need for baseline data on the distribution and abundance of organisms. We quantified spatial and/or temporal patterns of seagrass distribution, shoot density, leaf area index, biomass, productivity, and sediment carbon content in shallow water (0–5 m) at Lizard Island, Great Barrier Reef, Australia, in field surveys conducted in December 2011 and October 2012. Seagrass meadows were mapped using satellite imagery and field validation. A total of 18.3 ha of seagrass, composed primarily of *Thalassia hemprichii* and *Halodule uninervis*, was mapped in shallow water. This was 46% less than the area of seagrass in the same region reported in 1995, although variations in mapping methods may have influenced the magnitude of change detected. There was inter-annual variability in shoot density and length, with values for both higher in 2011 than in 2012.

Seagrass properties and sediment carbon content were representative of shallow-water seagrass meadows on a mid-shelf Great Barrier Reef island. The data can be used to evaluate change, to parameterize models of the impact of anthropogenic or environmental variability on seagrass distribution and abundance, and to assess the success of management actions.

Keywords: benthic habitat mapping; *Halodule uninervis*; remote sensing; seagrass change analysis; *Thalassia hemprichii*.

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Introduction

Seagrass meadows provide high-value ecosystem services (Costanza et al. 1997, Barbier et al. 2011a,b, Costanza et al. 2014), such as habitat provision, stabilization of marine sediments, production and storage of organic carbon, and coastal protection (Duarte 2000, Hemminga and Duarte 2000, Barbier et al. 2011a). Seagrasses function as ecological engineers by actively changing the physical structure of the environment, mainly by attenuating water flow and promoting sediment deposition (Gutiérrez et al. 2011). Seagrass meadows serve as globally significant “blue carbon” stores (Fourqurean et al. 2012) owing to their ability to accumulate significant amounts of organic carbon as biomass and within associated sediments (Hemminga and Duarte 2000). The average global value for the ecosystem services provided by seagrass meadows was estimated at US \$28,916 ha⁻¹ year⁻¹ in 2011 (2007 dollars) (Costanza et al. 2014).

There is growing concern regarding the accelerating loss of seagrass meadows globally (Orth et al. 2006, Waycott et al. 2009), with an estimated area of 3370 km² lost from a maximum area of 11,592 km² during previous decades (Waycott et al. 2009). Seagrass meadows are impacted by stressors occurring both locally (e.g.,

^aPresent address: School of Science and Engineering, University of the Sunshine Coast, Maroochydore DC, Qld 4558, Australia.

*Corresponding author: **Megan I. Saunders**, The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia, e-mail: m.saunders1@uq.edu.au

Elisa Bayraktarov: The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia

Chris M. Roelfsema: School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Qld 4072, Australia

Javier X. Leon and Stuart R. Phinn: The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Qld 4072, Australia

Jimena Samper-Villarreal: Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia

Catherine E. Lovelock: The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and The School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia

Peter J. Mumby: The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia

increased sediment loading, eutrophication, and pollution) and globally (e.g., warming sea surface temperature, sea-level rise, increased frequency, and intensity of storms; Orth et al. 2006, Saunders et al. 2013a, 2014). Interactions between multiple stressors may further exacerbate declines (Brown et al. 2013, 2014). In the face of rapidly declining seagrass habitat area on a global scale, current baseline data are essential to document changes in distribution, abundance, and function. Mapping seagrass meadow extent, composition, and structure (e.g., cover or biomass) is a prerequisite for understanding the changes in seagrass communities due to natural and anthropogenic impacts (Ferguson et al. 1993, Kirkman 1996, Mumby et al. 1997, Roelfsema et al. 2013). Knowledge of current ecological conditions that can serve as baseline data is important to enable the identification of both the negative effects of stressors and the positive effects of conservation actions.

Tropical seagrass meadows occur in shallow sunlit and wave-sheltered environments, on muddy or sandy substrates, in estuaries, or along the coastal margins of tropical and subtropical regions (Hemminga and Duarte 2000). One of the largest tropical seagrass ecosystems in the world exists in the Great Barrier Reef World Heritage Area (GBRWHA), in Queensland, Australia. In this region, shallow inter-reef and lagoonal areas including seagrass habitats extend across 58% of the 347,800 km² seabed area (Coles et al. 2015). In the GBRWHA, seagrasses may be found in four main environments, including estuarine, coastal, deep-water, or reef environments (Carruthers et al. 2002). There has been considerably less focus on the soft sediment habitats of the GBRWHA than on the more charismatic coral reef environments, suggesting that there is a need to characterize the extent of existing seagrass meadows in the region (Coles et al. 2015).

Lizard Island, Great Barrier Reef (GBR), Australia, is a group of six high granitic islands located between the coast and the outer barrier reef, and is fringed by seagrass meadows, mangroves, sandy beaches, and corals. The majority of the land area comprises a national park, with the only coastal development being the Lizard Island Research Station operated by the Australian Museum, and a small luxury resort. Marine waters are protected by Marine National Park, Conservation and Scientific Research zones. Seagrass meadows at Lizard Island are therefore exposed to relatively few anthropogenic stressors. However, the distribution and abundance of seagrass at Lizard Island are thought to vary due to environmental (A. Hoggett and L. Vail, Lizard Island Research Station Directors, personal communication) and limited anthropogenic factors (e.g., anchoring; McKenzie et al. 1997). Furthermore, tropical Indo-Pacific seagrasses are predicted to be threatened by

climate change (Waycott et al. 2007, Collier and Waycott 2009, Saunders et al. 2014). Therefore, a quantitative assessment of seagrass at this site was timely.

Seagrasses in the region were previously mapped in the mid-1990s using spot checks and manual delineation of aerial photographs (McKenzie et al. 1997); however, spatial patterns in distribution have not been assessed since. In 1995, seagrasses were largely distributed along the western margin of the island and in the lagoon, and included the species *Thalassia hemprichii* (Ehrenberg) Ascherson, *Halodule uninervis* (Forsskål) Ascherson, *Halophila ovalis* (Brown) Hooker, *Halophila spinulosa* (Brown) Ascherson, and *Cymodocea* spp. König (Figure 1). To date, seagrass photosynthetic data have been reported from across a range of depths (Campbell et al. 2007), and information on seagrass recruitment, seasonality, and senescence has been documented for deep-water (>10 m) habitats (McCormack et al. 2013). However, detailed ecological information (e.g., shoot density, biomass, productivity, and sediment carbon content) has not been previously reported for shallow-water environments. Here, we report baseline data for seagrass at Lizard Island in 2011 and 2012. The aims of this study were (i) to quantify the spatial patterns of seagrass species distribution and abundance in shallow water (<5 m) in 2011, and to compare results with seagrass habitat maps produced in 1995 (McKenzie et al. 1997); and (ii) to quantify the spatial (one to four sites) and temporal (1–2 years) variabilities in percent cover, shoot density, shoot length, leaf area index (LAI), biomass, sediment organic carbon content, leaf production, and vertical and horizontal rhizome elongation, in 2011 and 2012. The results can be used to assess changes in seagrass distribution and abundance (e.g., Roelfsema et al. 2013), to contribute to global syntheses of seagrass ecosystems (e.g., Duarte and Chiscano 1999, Fourqurean et al. 2012), and to parameterize predictive models of ecological change (e.g., Saunders et al. 2013a, 2014).

Materials and methods

Study site

The study was conducted at Lizard Island, GBR (145°27'145" E; 14°40'12" S), located 250 km northeast of Cairns, northern Queensland, Australia (Figure 2A). The Lizard Island group comprises late Permian granite islands that are part of a unique set of north-south trending continental high islands in the northern GBR. The Holocene fringing

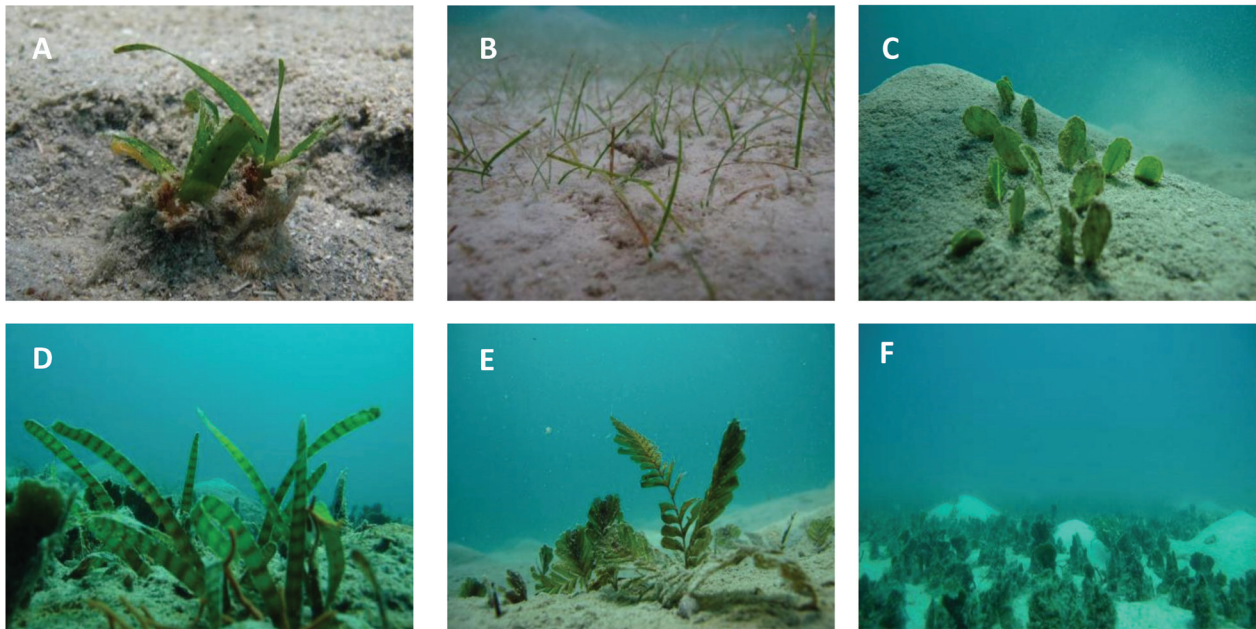


Figure 1 Marine plants of Lizard Island, Great Barrier Reef.

(A–E) Commonly observed seagrass species: (A) *Thalassia hemprichii*, (B) *Halodule uninervis*, (C) *Halophila ovalis*, (D) *Cymodocea serrulata*, and (E) *Halophila spinulosa*. (F) Macroalgae (typically *Udotea* and *Halimeda* spp.) observed at 9–12 m water depth shown for comparison.

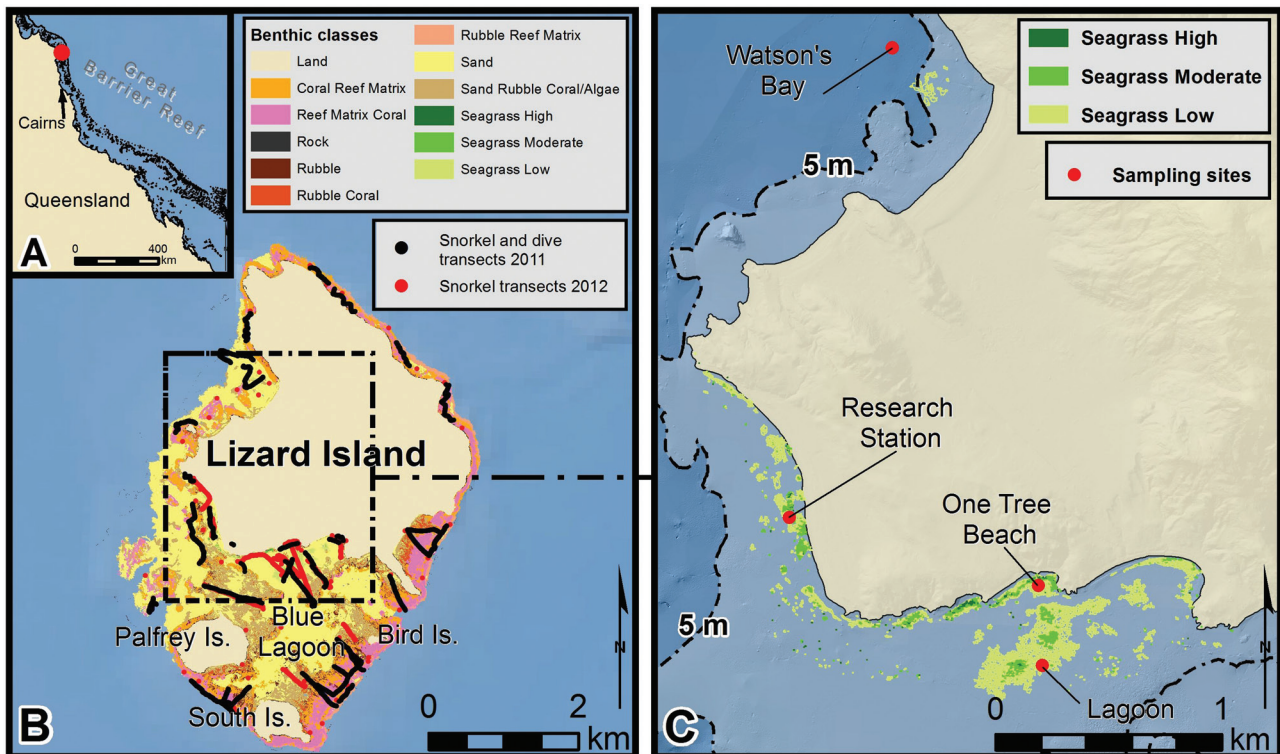


Figure 2 Study sites.

(A) Study location at Lizard Island, Great Barrier Reef, north-eastern Australia, indicated by red dot. (B) Map of benthic habitats at Lizard Island. Dive and snorkel transects conducted in 2011 and 2012 used to generate the map indicated by red and black lines, respectively (Saunders et al. 2014). (C) Inset of the Lizard Island study region with mapped seagrass habitats (low, medium, and high percent coverage) indicated in green. Four sampling stations are indicated by red dots. The site in Watson’s Bay was deeper (7 m) than the mapped extent of seagrass (<5 m).

reef rises steeply from approximately 30 m and encloses a relatively deep “Blue Lagoon” (~10 m) between the main Lizard Island and Palfrey, South and Bird Islands (Figure 2B; Leon et al. 2013). The islands have a tropical climate with an austral summer-wet season (December to April) and a winter-dry season (Brodie et al. 2007), and are exposed to predominantly south-easterly winds. The tidal range is approximately 3 m. In the present study, data were collected in two field trips of 10 days’ duration in 2 years (December 2011 and September/October 2012).

Mapping of seagrass species distribution in 2011 and comparison to maps from 1995

A seagrass species and percent cover map for 2011 was created using Object Based Image Analysis (OBIA) applied to a high spatial resolution satellite image, with geo-referenced field photo transects used for validation and calibration (Roelfsema and Phinn 2010, Phinn et al. 2012, Saunders et al. 2014). The seagrass presence/absence maps were presented in Saunders et al. (2014), with seagrass percent cover and species maps contributed in the present study. A high spatial resolution satellite (WorldView 2) image (2×2 m pixel size) was captured in October 2011, geo-referenced, and corrected for atmospheric distortions (Hamylton et al. 2014). In December 2011, geo-referenced field photographs were captured at 2–4 m intervals along transects by snorkeling or SCUBA, while towing a Global Positioning System. A total of 5735 photographs in 2011 and 1268 photographs in 2012 along 44 transects of 200–900 m length were obtained (Figure 2B). See Roelfsema and Phinn (2010) for further details. The snorkel surveys conducted in October 2012 were intended to fill in data gaps in the area of the shallow lagoon and reef flat.

Photographs were manually assigned a “benthic community” category using Coral Point Count Excel (CPCe) v4.0 software (Kohler and Gill 2006) informed by a classification scheme (Phinn et al. 2012). The OBIA classification consisted of an iterative process of image segmentation over three hierarchical levels, followed by class assignment based on membership rules associated with the individual levels: “reef,” “geomorphic zone,” and “benthic community.” Benthic community categories included seagrass, coral, soft coral, dead coral, macroalgae, cyanobacteria, and bare substrate, with the seagrass category refined to species level. *Cymodocea* was observed infrequently in photographs and was grouped together with *Thalassia*. Data are available online at www.pangaea.de (Saunders et al. 2013b,c). The benthic community level

map was transformed into a seagrass species map by assigning a dominant species to the segments based on the neighboring field data. The seagrass percent cover was classified as low ($\leq 30\%$), moderate (40–70%), and high ($\geq 70\%$).

To assess changes in seagrass species and distribution between years, a comparison was conducted between the seagrass species map created in the present study and a map from 1995 (McKenzie et al. 1997). Briefly, in 1995, seagrass species were mapped using aerial photography overlaid with field data. Quantitative comparison between the two maps was conducted using the software ArcGIS. Data for comparison between the two survey years (1995 and 2011) were limited to regions where both maps contained information (i.e., where data existed in the 1995 map but not in the 2011 map, or vice versa, those data were omitted from the analysis). It was assumed that, although methods to create the maps were different, they both represented the location of seagrass species at the time of each survey.

Spatial and temporal (2011 and 2012) variability of seagrass properties

Seagrass surveys overview

Surveys were conducted in 2011 and 2012 to quantify the properties of the seagrass meadows. Percent cover was determined using geo-referenced photo transects located throughout the study area, as described above. Four specific sites were surveyed in detail: Lagoon, Watson’s Bay, Research Station, and One Tree Beach (Figure 2C). Shoot density, leaf length, LAI, biomass, seagrass leaf elongation and biomass production, plastochrone interval, rhizome elongation, and sediment organic carbon content were quantified at the sites. Surveys were conducted using snorkel or SCUBA at 1–2 m depth (Lagoon, Research Station, and One Tree Beach) and at 7 m depth in Watson’s Bay, where shallower seagrass was absent.

Percent cover

Percent cover of seagrass in 2011 and 2012 was assessed using field data from the benthic photo transects used to inform the habitat maps (Figure 2B). Data are presented as histograms of the frequency of occurrence of particular percent cover categories for all seagrass species combined, and for *Halodule uninervis*, *Halophila ovalis*/*Halophila spinulosa*, and *Thalassia hemprichii*/*Cymodocea* spp. Data

were grouped into these categories on the basis of relative abundance and ability to distinguish species in the benthic photographs (*T. hemprichii* and *Cymodocea* spp. were not distinguishable from one another during photo analysis). Only data from photographs containing seagrass are presented.

Shoot density and length

At each site, seagrass was surveyed in 20 quadrats (0.25 m²) placed systematically at 1 m intervals along a 20 m transect. Transects were placed haphazardly in the center of a seagrass patch identified in the satellite images and verified by field surveys. In each quadrat, the total number of shoots of each species present was counted, and the lengths of a subset of 10 shoots located in a predetermined corner of the quadrat were measured.

Seagrass LAI, biomass, and sediment organic carbon content

Seagrass biomass and sediment organic carbon content at each of the four sites were determined from cores obtained in 2012. Samples (n=6 per site) were obtained at 1 m intervals parallel to the transect used to determine shoot density and length. Biomass samples were collected using a PVC corer with 9-cm diameter to a sediment depth of 15 cm. Biomass samples were sieved underwater using 1 mm mesh and frozen within 1 h of sampling at -20°C until analysis. Samples were rinsed with fresh water and allowed to thaw before processing.

Seagrass biomass [g dry weight (dw) m⁻²] was determined according to Duarte and Kirkman (2001), and the number of seagrass shoots per sample was quantified for each species. Material was separated into aboveground biomass (leaves), belowground biomass (rhizomes, roots), and detritus. The leaves of three seagrass shoots per sample were photographed, and the seagrass leaf area was determined using ImageJ (Rasband 2012). The LAI (Enríquez and Pantoja-Reyes 2005) was calculated by multiplying the mean one-sided leaf area for each species by shoot density per benthic surface area sampled and is reported as m² leaf m⁻² benthic surface area. When multiple species were present, LAI was determined as the sum of LAI of each species. Calcareous epiphytes were removed before drying by immersion in 10% HCl. Samples were dried at 60°C to constant weight (24–48 h), and dry weight was determined with an analytical balance (precision 0.0001 g).

Sediment samples were collected adjacent to sampling sites for seagrass biomass (<30 cm distance) using 60-ml

modified syringes (3 cm diameter and 6 cm length). The bulk density of each sample was determined as sediment dry weight per sample volume (g cm⁻³). Sediment samples were dried and stored in the dark until further analysis. After manual homogenization using mortar and pestle, organic carbon and carbonate content were estimated by the loss-on-ignition method (Heiri et al. 2001). Improved estimates could have been obtained using elemental analysis, but at a substantially higher cost. Subsamples of pulverized sediment (0.8–1.8 g) were placed into pre-weighed, dry ceramic crucibles and subsequently combusted at 550°C (4 h) and 950°C (2 h) in a muffle furnace. Organic and inorganic matter contents were calculated according to Heiri et al. (2001) and Kauffman and Donato (2012). Organic carbon was calculated assuming that 43% of the ignited organic matter was organic carbon (Fourqurean et al. 2012). Values of material lost after combustion at 950°C were multiplied by the factor 1.36 to account for carbonate content (Heiri et al. 2001).

Seagrass leaf elongation, production, and plastochrone interval

Growth and production of *Thalassia hemprichii* (at Lagoon) and *Halodule uninervis* (at One Tree Beach) were measured in 2012 according to a modified needle punch method (Short and Duarte 2001). Seagrass shoots at 1–2 m depth were marked using small plastic ties. A hole was made in each marked shoot *in situ* through the upper section of the leaf sheath near the leaf/sheath junction. Shoots were left to grow for 7 days, collected, and kept frozen at -20°C until further analysis. Of each species, 100 shoots were marked, with as many marked shoots recovered after 7 days as possible (*T. hemprichii*: n=45; *H. uninervis*: n=16).

Leaf elongation was measured using ImageJ (Rasband 2012) and is reported as mm shoot⁻¹ day⁻¹. The dry weight of new growth was determined by drying the newly produced leaf sections at 60°C until constant weight, and is reported as g dw shoot⁻¹ day⁻¹. Areal productivity was calculated by multiplying the values (in g dw shoot⁻¹ day⁻¹) by the shoot density and is expressed as g dw m⁻² day⁻¹. Leaf plastochrone interval was calculated on the basis of the number of marked *T. hemprichii* and *H. uninervis* shoots containing a newly produced leaf during the measurement period (Marbà and Walker 1999). Seagrass biomass and density on the northern GBR is of intermediate abundance in October (McCormack et al. 2013); therefore, the plastochrone interval reported in the present study is likely to be representative of mean annual values.

Rhizome elongation

Horizontal rhizomes of *Thalassia hemprichii* were sampled from a depth of 1–2 m at Lagoon and kept frozen at -20°C until analysis. The number of leaf scars plus the number of standing leaves per shoot for each shoot on the rhizome were counted to obtain a shoot age estimate in days, and the number of scars per shoot was multiplied by the leaf plastochrone interval (time to produce a new leaf; Duarte et al. 1994). Vertical rhizome elongation rate was estimated by measuring the length of the fourth internode back from the meristem (representing a mature plant part) of each seagrass vertical shoot and then dividing by the leaf plastochrone interval (Short and Duarte 2001). Horizontal rhizome elongation rate was calculated by dividing the length of the rhizome between two consecutive vertical shoots by the difference in the ages of the two shoots (Duarte et al. 1994). All measurements were performed on photographs of seagrass samples using ImageJ (Rasband 2012).

Statistical analyses

The effect of year (two levels: 2011 and 2012) on shoot density and length was tested using a linear mixed-effects model (LMM) with site as a random factor. Statistical analyses were not conducted for percent cover, as different transects were sampled in the two study years, or for the metrics that were only sampled in one year. Statistical comparisons among sites were not deemed meaningful given the varying species composition among sites. Statistical analyses were computed using the *lme4* and *multcomp* packages in R 3.0.3 (R Core Development Team 2012). Unless otherwise indicated, results are reported as mean±SD.

Results

Seagrass species distribution in 2011 and 1995

A total of 18.3 ha of seagrass was mapped in 2011 at Lizard Island, comprising primarily *Thalassia hemprichii* and *Halodule uninervis* (Figures 2C and 3, Table 1). Of this, 0.3 ha was high percent cover (<2% of the study area), 2.8 ha was moderate cover (15%), and 15.2 ha was low cover (83%).

A total of eight species of seagrass were observed in the 2011/2012 photo transect surveys used to inform the habitat maps, including *Halodule uninervis*, *Thalassia hemprichii*, *Halophila ovalis*, *Halophila spinulosa*, *Cymodocea rotundata* Ascherson and Schweinfurth,

Cymodocea serrulata (Brown) Ascherson and Magnus, *Syringodium isoetifolium* (Ascherson) Dandy, and *Zostera muelleri* Irmisch ex Ascherson. The latter four species were observed only rarely. Consequently, species polygons for the 2011 map were classified as *H. uninervis*/*T. hemprichii*, *H. uninervis*/*Halophila* spp., *T. hemprichii*, *H. uninervis*, or “Other species” (Table 1, Figure 3). The distribution of seagrass species varied spatially, with 3.8 ha of mixed species including *H. uninervis*/*T. hemprichii* near the shoreline at One Tree Beach, 0.5 ha of *H. uninervis*/*Halophila* spp. in Watson’s Bay, 10.2 ha of *T. hemprichii* in the shallow Lagoon, and 3.7 ha of *H. uninervis* along the shoreline at Research Station (Figure 3, Table 1). Seagrass deeper than 5 m was not mapped because of limitations of the remote sensing techniques. However, observations from a photo transect in 9–12 m water depth in Watson’s Bay indicated only very sparse seagrass, with much higher abundances of benthic macroalgae (mainly *Udotea* spp. Lamouroux and *Halimeda* spp. Lamouroux; Figure 1F).

A 46% decrease in area of seagrass in 0–5 m water was observed in 2011 compared with 1995 (1995: 34 ha; 2011: 18.3 ha; Table 1). Overall, the spatial pattern in species composition was similar to that observed in the 1990s (McKenzie et al. 1997). However, *H. uninervis* was mapped along the shoreline at Research Station in 2011 where it was absent in 1995. Furthermore, in 2011, the deeper water regions (>5 m) of Watson’s Bay consisted primarily of benthic macroalgae such as *Udotea* spp. and *Halimeda* spp., whereas in the 1990s, those locations were mapped as seagrass (data not shown).

Spatial variability of seagrass properties (2011 and 2012)

Percent cover

In both 2011 and 2012, there were peaks in frequency of occurrence of seagrass percent cover at the low ($\leq 30\%$) and high ($\geq 70\%$) percent cover levels (Figure 4A,B). This general pattern was also observed for *Halodule uninervis* (Figure 4C,D). For *Halophila* spp. and *Thalassia hemprichii*, there was higher frequency of occurrence for the lower percentage cover categories with few observations of high percentage cover (Figure 4E–H).

Seagrass shoot density, leaf length, and LAI

Shoot density was higher in 2011 than in 2012 (data pooled across all sites and species; $p < 0.001$, LMM;

1995

2011

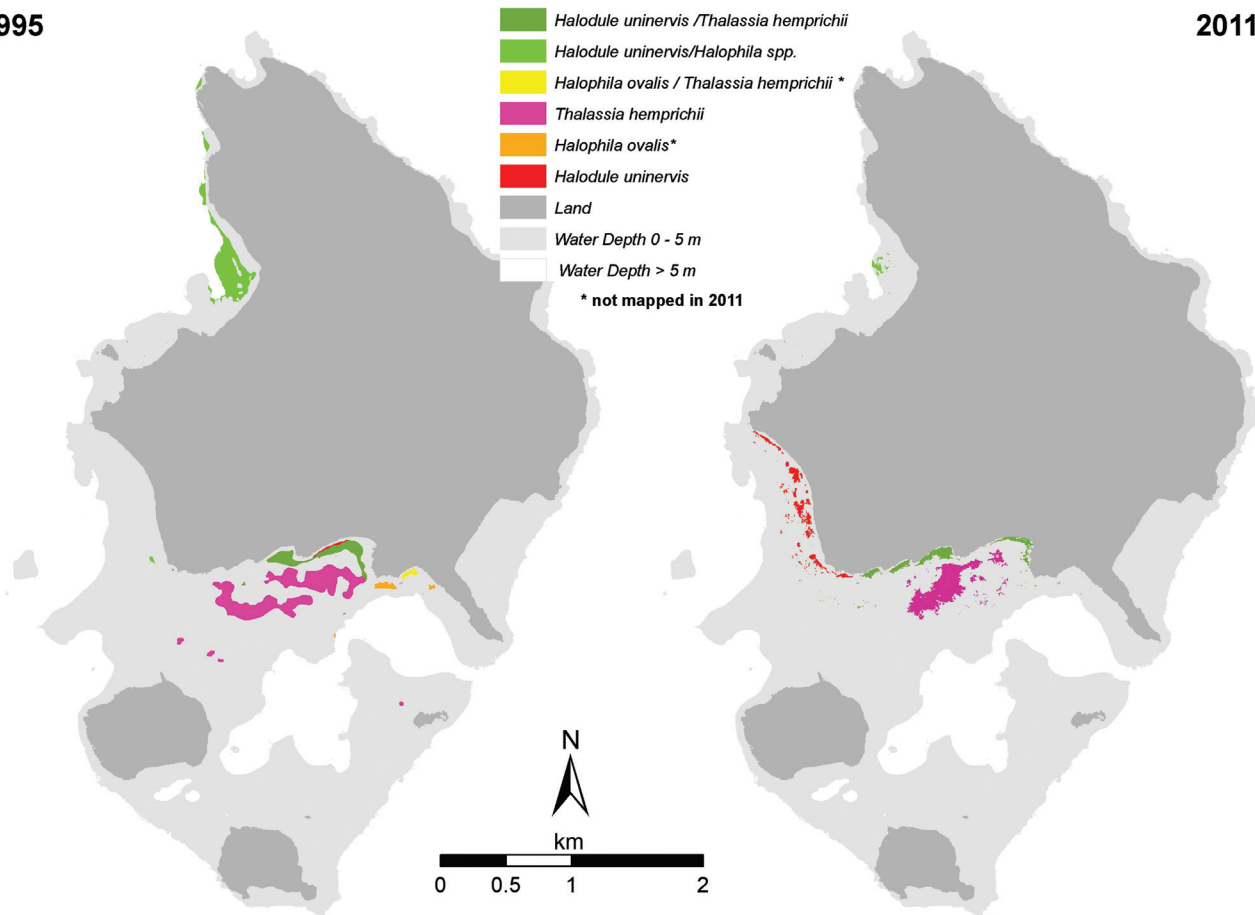


Figure 3 Seagrass species maps for 0–5 m depth at Lizard Island, Great Barrier Reef, Australia for 1995 (from McKenzie et al. 1997) and 2011.

Table 2). However, shoot density varied among species, with the highest total values for *Halodule uninervis* (Table 2). Across all sites and species, shoot lengths were significantly greater in 2011 (mean 5.5 cm) than in 2012 (mean 5.2 cm; $p < 0.001$, LMM), although there was considerable variability among sites and species (Table 2). The LAI was < 1 for all species (Table 2). The greatest mean leaf area per shoot was for *Thalassia hemprichii* at

Lagoon and the lowest for *H. uninervis* at One Tree Beach (Table 2).

Seagrass biomass

Biomass of all three seagrass components (aboveground, belowground, and detrital) was highest at Lagoon, where

Table 1 Comparison of seagrass area (per species and total) at Lizard Island, Great Barrier Reef, Australia, in 1995 (McKenzie et al. 1997) and 2011 (present study).

	Seagrass area in 1995 (ha) (McKenzie et al. 1997)	Seagrass area in 2011 (ha) (present study)	Change in area between 1995 and 2011 (ha)	Change in area between 1995 and 2011 (%)
<i>Halodule uninervis/Thalassia hemprichii</i>	4.8	3.8	-1	-21%
<i>Halodule uninervis/Halophila spp.</i>	9.6	0.5	-9.1	-95%
<i>Thalassia hemprichii</i>	18	10.2	-7.8	-43%
<i>Halodule uninervis</i>	0.3	3.7	3.4	1065%
Other species	1.3	0.1	-1.2	-92%
Total	34	18.3	-15.7	-46%

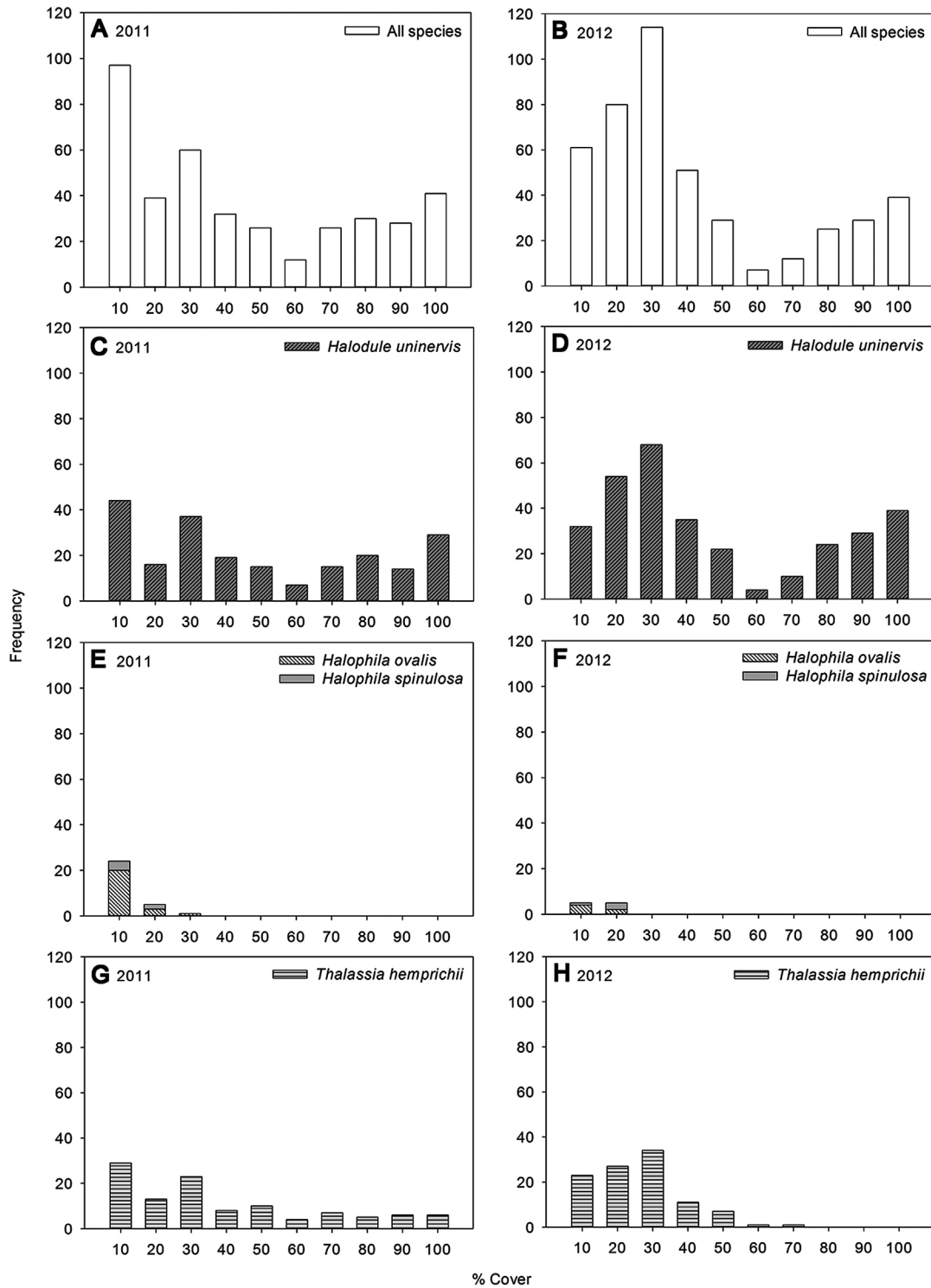


Figure 4 Frequency of occurrence of seagrass percent cover from photo transects at Lizard Island, Great Barrier Reef, in 2011 and 2012. Data were only used from photographs containing seagrass. (A, B) Overall seagrass cover in 2011 and 2012; (C, D) *Halodule uninervis* in 2011 and 2012; (E, F) *Halophila* mixed species (*H. ovalis* and *H. spinulosa*) in 2011 and 2012; (G, H) *Thalassia hemprichii* (with minor quantities of *Cymodocea* spp.) in 2011 and 2012.

seagrass was composed primarily of *Thalassia hemprichii* (Table 2). The biomass of each component was lowest at Watson's Bay, where seagrass was composed

of *Halodule uninervis* and *Halophila ovalis* (Table 2). At Research Station and One Tree Beach, biomass was composed primarily of *H. uninervis* (Table 2).

Leaf elongation and biomass production

At Lagoon, 49% of *Thalassia hemprichii* shoots produced a new leaf during the 7-day study period, which corresponded to a leaf plastochrone interval of 14.3 days (Table 2). The total leaf elongation (summed elongation of all leaves on a shoot, averaged across shoots) of *T. hemprichii* measured at Lagoon in 2012 was 3.8 mm shoot⁻¹ day⁻¹. The newly produced biomass per shoot during the 7-day study was 5.85 mg dw shoot⁻¹ day⁻¹. By multiplying the biomass production per shoot by the number of shoots counted at Lagoon in each year (2011: 2182 shoots m⁻²; 2012: 567 shoots m⁻²), the biomass production of *T. hemprichii* per square meter was estimated to be 12.8 g dw m⁻² day⁻¹ in 2011 and 3.32 g dw m⁻² day⁻¹ in 2012.

At One Tree Beach, 63% of *Halodule uninervis* shoots produced a new leaf during the 7-day study period, which corresponded to a leaf plastochrone interval of 11.2 days (Table 2). The total leaf elongation of *H. uninervis* measured in 2012 was 2.3 mm shoot⁻¹ day⁻¹, and biomass production per shoot was 0.74 mg dw shoot⁻¹ day⁻¹. With a shoot density of 4614 shoots m⁻² at One Tree Beach in 2011 and 1723 shoots m⁻² in 2012, the biomass production of *H. uninervis* per square meter was estimated to be 3.41 g dw m⁻² day⁻¹ in 2011 and 1.28 g dw m⁻² day⁻¹ in 2012, respectively.

Vertical and horizontal rhizome elongation

The vertical rhizome elongation of *Thalassia hemprichii* was 2.7 cm year⁻¹ (Table 2). The horizontal rhizome elongation estimated from rhizome fragments, each containing two adjacent shoots with attached leaves, of *T. hemprichii* was 33.1 cm year⁻¹ (Table 2).

Sediment organic carbon

The sediment organic carbon content in the study sites ranged from 7.3 to 16.8 mg g⁻¹ (corresponding to 0.7–1.7% sediment dw, as averaged per location) and was lowest at One Tree Beach and highest at Lagoon (Table 2). The sediment carbonate content was 20–25% of sediment dry weight at Lagoon, Watson's Bay, and Research Station, but only 4.8% at One Tree Beach (Table 2).

Discussion

The baseline data for the extent, composition, structural properties, and function of ecosystems provide key

information for the assessment of the impacts of environmental or anthropogenic disturbance and the effectiveness of management actions. Seagrass meadows provide a range of ecosystem services, yet are globally threatened and experiencing rates of loss of up to 7% year⁻¹ (Orth et al. 2006, Waycott et al. 2009). Here, we provide detailed spatial and temporal data of the species composition, percent cover, shoot density, biomass, leaf length, LAI, productivity, and sediment organic carbon and carbonate content of seagrass at Lizard Island, GBR, Australia.

Seagrass species distribution in 2011 and comparison to patterns in 1995

Seagrass area declined by 46% in 2011 compared to 1995, a surprising result given that Lizard Island is relatively unimpacted by human activities. However, a similar magnitude of decline in seagrass abundance was reported for reef platform seagrass communities at other sites in the GBR between 2004 and 2012 (Coles et al. 2015). The losses reported by Coles et al. (2015) were proposed to have been caused by a string of severe cyclones and floods on the Queensland coast. Decreases in seagrass distribution in the overall GBR region have been primarily attributed to anthropogenic activities such as agricultural, urban and industrial runoff, and urban and port developments, particularly in inshore areas (Grech et al. 2011). If the loss observed between 1995 and 2011 is accurate, and it occurred consistently during the 16-year time interval, the rate of loss would have been 2.9% year⁻¹, 60% less than the rate reported for seagrass globally (7% year⁻¹; Waycott et al. 2009). The lower rates of loss at Lizard Island are likely because of its remote location, minimal coastal development and port activities, and well-established marine protected areas.

It is feasible that the decrease in seagrass area reported in the present study was caused by anthropogenic or environmental factors; however, differences in mapping methods may also have influenced the results (see, e.g., Roelfsema et al. 2013). The methods used to create the maps for the surveys in 1995 and 2011 were different, with seagrass mapped in 1995 by manually digitizing seagrass on the basis of information from spot checks and aerial photographs, and seagrass mapped in 2011 by automatically assigning a seagrass class to each high spatial resolution satellite pixel, using an object-based classification routine and photo transects for calibration. The former method is likely to overestimate seagrass cover, whereas the latter method is likely to underestimate low (<10%) percent cover seagrass. Nonetheless, we

Table 2 Seagrass properties at four sites at Lizard Island, Great Barrier Reef, Australia, in 2011 and 2012.

Metric	Species	n	Lagoon		Watson's Bay		Research Station		Site and year	
			2011	2012	2011	2012	2011	2012	2011	2012
Shoot density (shoots m ⁻²)	All species	20	2182.4±590.6	584.0±166.2	128.8±242.2	224.0±295.4	10,812.8±2860.1	1566.4±376.4	4662.4±1619.1	1723.2±604.5
	<i>H. ovalis</i>	20		106.0±239.6		58.4±152.7				
Shoot length (cm)	<i>H. spinulosa</i>	20		9.2±33.6						
	<i>H. uninervis</i>	20		1.6±4.9	1.6±5.6	165.6±186.2	10,812.8±2860.1	1566.4±376.4	4614.4±1588.2	1723.2±604.5
	<i>T. hemprichii</i>	20	2182.4±590.6	567.2±179.1	12.0±19.8					
	<i>Z. muelleri</i>	20		15.2±40.7						48.0±118.7
Leaf area index (m ² leaf m ⁻² benthic area)	All species	6	6.4±1.9 (201)	5.3±1.2 (207)	4.7±2.3 (116)	4.3±1.8 (103)	5.5±1.8 (200)	5.7±2.0 (201)	5.1±1.8 (200)	5.0±1.9 (201)
	<i>H. ovalis</i>			3.2±1.2 (53)		1.8±0.5 (20)				
Leaf area per shoot (cm ²)	<i>H. spinulosa</i>			4.8±2.5 (19)						
	<i>H. uninervis</i>			4.0±1.4 (2)	6.3±2.4 (6)	4.9±1.4 (83)	5.5±1.8 (200)	5.7±2.0 (201)	5.1±1.8 (200)	5.0±1.9 (201)
Biomass AG (g dw m ⁻²)	<i>T. hemprichii</i>	6	6.4±1.9 (201)	5.3±1.2 (191)	6.5±2.0 (38)					
	<i>Z. muelleri</i>			5.7±1.6 (14)						
Biomass BG (g dw m ⁻²)	All species	6	0.284±0.105	3.72±1.19,		0.118±0.119		0.250±0.074		0.169±0.045
	Various species	6		<i>T. hemprichii</i>		1.49±0.42,		0.46±0.09,		0.35±0.16,
Shoot density from biomass cores (shoots m ⁻²)	All species	6		10.0±3.5		<i>H. uninervis, H. ovalis</i>		9.5±2.2		6.8±2.7
	Various species	6		401.3±144.0		2.7±2.8		227.1±121.7		132.6±45.9
Sediment organic carbon (mg g ⁻¹)	All species	6	20.2±13.7	734±81,		6.5±3.8		11.0±6.4		4.3±4.3
	Various species	6		<i>T. hemprichii</i>		3.5±3.3		5554±1602,		5318±1267,
Sediment organic carbon (% sediment dw)	All species	6	16.8±18.4			<i>H. uninervis, H. ovalis</i>		8.5±5.3		7.3±7.3
	Various species	6		1.7±1.8		10.4±2.6		0.8±0.5		0.7±0.7
Sediment carbonate (% sediment dw)	All species	6	20.0±0.9	14.3		1.0±0.3		20.5±1.6		4.8±0.5
	Various species	6		3.8±1.7		24.3±1.0				
Leaf plastochrone interval (days)	<i>T. hemprichii</i>	45								11.2
	<i>H. uninervis</i>	16								
Total (summed) leaf elongation rate (mm shoot ⁻¹ day ⁻¹)	<i>T. hemprichii</i>	45								
	Various species	45								
Biomass production AG (mg dw shoot ⁻¹ day ⁻¹)	<i>H. uninervis</i>	16								2.3±1.5
	<i>T. hemprichii</i>	45		5.85±2.93						
Aerial biomass production AG (g dw m ⁻² day ⁻¹)	<i>H. uninervis</i>	16								0.74±0.63
	<i>T. hemprichii</i>	45	12.8	3.32						
Vertical rhizome elongation (cm year ⁻¹)	<i>H. uninervis</i>	16								3.41
	<i>T. hemprichii</i>	10		2.7±1.0						1.28
Horizontal rhizome elongation (cm year ⁻¹)	<i>T. hemprichii</i>	6		33.1±21.2						
	Various species	6								

Abbreviations: *H. ovalis*, *Halophila ovalis*; *H. spinulosa*, *Halophila spinulosa*; *H. uninervis*, *Halodule uninervis*; *T. hemprichii*, *Thalassia hemprichii*; *Z. muelleri*, *Zostera muelleri*; AG, aboveground biomass; BG, belowground biomass. Values are reported as mean±SD. Sample size (n) is indicated in brackets where not otherwise specified.

speculate that the differences in mapping methodology would have made only a relatively minor contribution to the overall loss reported, although the exact contribution cannot be estimated. The remote sensing techniques used to map seagrass were only effective for water of <5 m depth, so that quantitative comparison with the distribution of deeper-water seagrass (e.g., McKenzie et al. 1997, McCormack et al. 2013) was precluded. Because data are only available for two points in time, it is not possible to discern whether the reported decline is a persistent trend or more reflective of seasonal or inter-annual variability.

Spatial variability of seagrass properties in 2011 and 2012

Percent cover

The histogram of seagrass percent cover was bimodal, with higher occurrence of low and high percentage cover levels, compared to moderate cover levels, driven by the abundant species *Halodule uninervis*. Conversely, histograms for *Thalassia hemprichii* and *Halophila* spp. were right skewed, with higher frequency of occurrence of lower percentage cover levels. The low coverage of *Halophila ovalis* and *H. spinulosa* was potentially a consequence of the shallow depth of survey (<5 m), as these species are often found in deeper water (Coles et al. 2009). In particular, *H. spinulosa* is known to occur in lower light environments, and has been found at up to 61 m water depth in the GBR lagoon (Coles et al. 2009).

Shoot density, shoot length, and LAI

Shoot density was lower in 2012 than in 2011. Seagrass distribution and abundance in 2011 was reported to be unusually high compared to previous years (A. Hoggett, personal communication). In that case, lower shoot densities in 2012 would reflect a pattern of decline to more representative values. Increased nutrient concentration resulting from large flood events on the Queensland Coast in 2011 may have influenced seagrass abundance in that year, as seagrass communities in reef settings respond positively to nutrient enhancement (Udy et al. 1999), although in this instance causative links remain to be tested. For Green Island, GBR, Udy et al. (1999) reported increases in *Halodule uninervis* shoot density from 4450 to 8000 shoots m⁻² (similar to the shoot density values of 10,813 shoots m⁻² in 2011 reported in the present study) after phosphorus and nitrogen enrichment. *Halodule*

uninervis is a pioneer species that grows rapidly and survives well in unstable environments (Coles et al. 2003). Alternatively, inter-annual variability may actually indicate seasonal variability in shoot density, with higher density in December (2011) than in October (2012). Ideally, seagrass shoot density would have been assessed in the same month in both years, or over multiple months in each year; however, logistical constraints on sampling at a remote location precluded such measurements.

We measured average shoot counts for *Halophila ovalis* of 106 shoots m⁻² in December 2011 and 58.4 shoots m⁻² in October 2012 at 7 m depth in Watson's Bay. In comparison, during the peak in abundance in November 2012, *H. ovalis* shoot density in 15 m water depth was 167.7 shoots m⁻² (McCormack et al. 2013). The values reported for Lizard Island were considerably lower than those reported for other regions (e.g., 13,806 shoots m⁻² for *H. ovalis* at Escape River, Queensland; Lee Long et al. 1993).

The LAI is a descriptor of the degree of leaf packing within the canopy (Watson 1947), where values <1 represent monolayered and LAIs >1 describe multilayered canopies (Enríquez and Pantoja-Reyes 2005). The LAI was <1 for all species, which classifies the leaf packing within the seagrass canopy as monolayered (Enríquez and Pantoja-Reyes 2005). Low LAI is indicative of species with the capacity to reduce self-shading, and potentially represents an adaptation strategy to low light environments (Coles et al. 1996, Collier et al. 2012). However, light was likely not limiting in shallow water in the mid-shelf GBR.

Biomass and production

The mean aboveground biomass at each site ranged from 2.7 to 10.0 g dw m⁻². These values are at the low end of the range of observations for seagrass biomass standing stock globally (Duarte and Chiscano 1999). In comparison to other studies on Australian seagrass, the values reported here are lower than for a *Halodule uninervis* meadow at Green Island, GBR, sampled in 1994 (16.6 g dw m⁻²; Coles et al. 2003). Biomass of *Halophila ovalis* was substantially lower than for a site at peak seasonal abundance in Western Australia (120 g dw m⁻²; Hillman et al. 1995).

The average aboveground production rate of *Thalassia hemprichii* from a meta-analysis of published literature was 0.5 g m⁻² day⁻¹ (Duarte and Chiscano 1999). The aboveground production rate in the present study was therefore above average in both years (12.8 and 3.3 g dw m⁻² day⁻¹ in 2011 and 2012, respectively), with

inter-annual variability caused by higher shoot density in 2011. Above-average values for production rate may have been observed because sampling occurred at the seasonal onset of peak seagrass abundance in November (McCormack et al. 2013).

Leaf production was assessed using the pinhole method; however, not all previously marked shoots could be recovered after the 7-day growth period. The recovery rates may have been influenced by lost tags, shoot breakage, or surveyor error. The recovery rate was particularly poor for *Halodule uninervis*, likely due to the very small size of leaves.

Rhizome elongation

The vertical rhizome elongation of *Thalassia hemprichii* shoots (2.7 cm year⁻¹) at Lizard Island was similar to estimates from other studies (3 cm year⁻¹; Vermaat et al. 1995, Marbà and Duarte 1998). The rate of horizontal rhizome elongation of *T. hemprichii* (33.1 cm year⁻¹) was within the range of estimates reported in the literature (mean 54, range 21–88 cm year⁻¹; Marbà and Duarte 1998). The plastochrone interval was estimated from the number of new leaves produced on marked shoots within a given timeframe, and then used to estimate rhizome production rates. Seasonal or spatial variation in plastochrone interval, which was not assessed in the present study, may have influenced the estimated elongation rates.

Sediment carbon content

Sediment organic carbon content ranged from 7.3 to 16.8 mg g⁻¹: (averaged per location) exceeding values reported for other sediments without seagrass, such as typical oxygenated marine sediments (<5 mg g⁻¹; Bordenave 1993, Jørgensen 1996), those within a coral reef lagoon in the GBR (3.4–4.7 mg g⁻¹; Moriarty 1982), and in upwelling-influenced coral reefs (1.9–2.5 mg g⁻¹; Bayraktarov and Wild 2014). This indicates accumulation of organic material, as is expected in seagrass habitats. Organic carbon content was higher than the average value reported for Australian seagrass meadows (5.26 mg C cm⁻³; Lavery et al. 2013). However, values for sediment organic carbon as dw percentage of 0.7–1.7% are at the lower end of values reported globally for seagrass habitats (Fourqurean et al. 2012). Scaling up to the 18.3 ha of seagrass mapped in water 0–5 m deep at Lizard Island, the organic carbon stock in seagrass sediments standardized to a sediment depth of 15 cm was estimated to be 200–460 Mg (based

on lowest and highest average sediment organic carbon content values in mg g⁻¹).

Sediments had generally low carbonate content (20–25%) in comparison with other reef locations (85–99% for the central region of the GBR; Scoffin and Tudhope 1985; 75–85% for the Gulf of Aqaba, Red Sea; Rasheed et al. 2003). At One Tree Beach, the carbonate content of <5% indicated that sediments were most likely composed of silicate sands and is in agreement with previous carbonate values reported for this location (Javier et al. 2013).

Conclusions

Seagrass meadows at Lizard Island, GBR, assessed in 2011/2012 were representative of Indo-Pacific mid-shelf coral reef seagrass meadows. There was spatial variability in the distribution of species over location and depth, which appeared to be relatively consistent between 2011 and 2012, and less so between 1995 and 2011. The sediment organic content was higher than reported for coral reef habitats, and higher than the average value reported for seagrass in Australia; yet, it was at the low end of the range for seagrass worldwide, as expected in relatively low-nutrient waters occurring in a mid-shelf coral reef environment. The aboveground biomass was at the low end of reported values, but was within the range of values documented for seagrass habitats globally. The extent of seagrass mapped in 2011 was 46% less than that reported from 1995 (McKenzie et al. 1997), following a similar trend documented for other sites on the GBR. However, the magnitude of loss reported may have been less if consistent mapping methods had been used between years. The results reported here may be used to assess future changes driven by environmental or anthropogenic factors in seagrass distribution, abundance, and function.

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Bionotes



Megan I. Saunders

The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia
m.saunders1@uq.edu.au

Megan I. Saunders is a research fellow in the Global Change Institute and Marine Spatial Ecology Lab at The University of Queensland, Australia. Her interests include the effects of human stressors on coastal marine ecosystems and conservation ecology of seagrass meadows, coral reefs, mangroves and kelp beds.



Elisa Bayraktarov

The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia

Elisa Bayraktarov is a research fellow in the Global Change Institute at the University of Queensland, Australia. Her research interests include ecology and restoration of coastal marine habitats.



Chris M. Roelfsema

School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Qld 4072, Australia

Chris M. Roelfsema is a Research Fellow and Lecturer Remote Sensing in the Biophysical Remote Sensing Group, School of Geography, Planning and Environmental Management, The University of Queensland, Australia. His interests include pure and applied research in remote sensing of coastal habitats.



Javier X. Leon

The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Qld 4072, Australia

Javier X. Leon is a Lecturer in Physical Geography at the University of the Sunshine Coast, Australia. His interests include remote sensing of shallow coastal marine environments and effects of sea-level rise on shorelines.



Jimena Samper-Villarreal

Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia

Jimena Samper-Villarreal is a PhD Student in the Marine Spatial Ecology Lab in the School of Biological Sciences, at The University of Queensland, Australia. Her interests include carbon sequestration in coastal vegetated habitats such as seagrass and mangroves.



Stuart R. Phinn

The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and School of Geography, Planning and Environmental Management, The University of Queensland, St Lucia, Qld 4072, Australia

Stuart R. Phinn is a Professor of Geography and Director of the Centre for Spatial Environmental Research in the School of Geography, Planning and Environmental Management at the University of Queensland, Australia. He uses satellite and airborne imaging systems to develop approaches for mapping, measuring and monitoring changes in the earth's environments.



Catherine E. Lovelock

The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and The School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia

Catherine E. Lovelock is a Professor in the School of Biological Sciences at the University of Queensland, Australia. Her research focuses on the influence of environmental change on the ecology of coastal and marine plant communities, and in providing knowledge to underpin conservation and restoration of these systems now and in the future.



Peter J. Mumby

The Global Change Institute, The University of Queensland, St Lucia, Qld 4072, Australia; and Marine Spatial Ecology Lab, School of Biological Sciences, The University of Queensland, St Lucia, Qld 4072, Australia

Peter J. Mumby is a Professor in the School of Biological Sciences at the University of Queensland and head of the Marine Spatial Ecology Lab. His research focuses on delivering science to improve the management of coral reef environments.