



What lies beneath: Predicting seagrass below-ground biomass from above-ground biomass, environmental conditions and seagrass community composition

C.J. Collier^{a,*}, L.M. Langlois^a, K.M. McMahon^b, J. Udy^c, M. Rasheed^a, E. Lawrence^d, A. B. Carter^a, M.W. Fraser^e, L.J. McKenzie^a

^a Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER), James Cook University, Cairns, Australia

^b School of Science, Edith Cowan University, Perth, Australia

^c Queensland University of Technology, Brisbane, Australia

^d Data61, CSIRO, Brisbane, Australia

^e UWA Ocean's Institute and School of Biological Sciences, The University of Western Australia, Perth, Australia

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ABSTRACT

Seagrass condition, resilience and ecosystem services are affected by the below-ground tissues (BGr) but these are rarely monitored. In this study we compiled historical data across northern Australia to investigate biomass allocation strategies in 13 tropical seagrass species. There was sufficient data to undertake statistical analysis for five species: *Cymodocea serrulata*, *Halophila ovalis*, *Halodule uninervis*, *Thalassia hemprichii*, and *Zostera muelleri*. The response of below-ground biomass (BGr) to above-ground biomass (AGr) and other environmental and seagrass community composition predictor variables were assessed using Generalized Linear Models. Environmental data included: region, season, sediment type, water depth, proximity to land-based sources of pollution, and a light stress index. Seagrass community data included: species diversity and dominant species class (colonising, opportunistic or persistent) based on biomass. The predictor variables explained 84–97% of variance in BGr on the log-scale depending on the species. Multi-species meadows showed a greater investment into BGr than mono-specific meadows and when dominated by opportunistic or persistent seagrass species. This greater investment into BGr is likely to enhance their resistance to disturbances if carbohydrate storage reserves also increase with biomass. Region was very important for the estimation of BGr from AGr in four species (not in *C. serrulata*). No temporally changing environmental features were included in the models, therefore, they cannot be used to predict local-scale responses of BGr to environmental change. We used a case study for Cairns Harbour to predict BGr by applying the models to AGr measured at 362 sites in 2017. This case study demonstrates how the model can be used to estimate BGr when only AGr is measured. However, the general approach can be applied broadly with suitable calibration data for model development providing a more complete assessment of seagrass resources and their potential to provide ecosystem services.

1. Introduction

The biomass of below-ground tissue in seagrasses (BGr; rhizomes and roots) is one of the defining features of seagrass species growth strategies (Kilminster et al., 2015). It provides functions that confer resilience, including resistance to stress and recovery following decline (O'Brien et al., 2018). BGr is required for clonal growth (Marbà and Duarte, 1998, Duarte and Chiscano, 1999), storage of carbohydrates as sugars and starch (Alcoverro et al., 2001, Collier et al., 2009), nutrient uptake (Romero et al., 2006), anchorage and nutrient transfer (Prado et al.,

2008). It is pivotal to many of the ecosystem services that seagrasses provide, including foraging by dugongs using excavation (Marsh et al., 2011), storage of carbon in sediments (blue carbon) (Fourqurean et al., 2012, Lavery et al., 2013), and sediment stabilisation (Maxwell et al., 2017).

Seagrass meadows are under threat at a global scale (Orth et al., 2006, Waycott et al., 2009), and one of the key challenges researchers face in reversing this trend, is generating information that can support conservation strategies (Unsworth et al., 2019). Quantifying BGr and the conditions influencing BGr are important for several reasons. First,

* Corresponding author.

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accurate assessment of seagrass abundance and ecosystem services provided, requires quantification of seagrass biomass as a whole, including what is below-ground (Duarte and Chiscano, 1999, Zobel and Zobel, 2002). Second, management actions taken to protect seagrass meadows can be refined based on how much of the biomass is below-ground. For example, seagrass light requirements are influenced by morphological plasticity including changes in allocation of biomass to BGr or AGr (Ferguson et al., 2016). This is because the relative proportion of BGr and AGr affects plant carbon balance, including radiative transfer through the canopy, gross productivity of leaves, and the respiratory demands of both the BGr and AGr (Zimmerman, 2003, Ralph et al., 2007). For similar reasons, the relative allocation of biomass can also affect thermal optima for net productivity (Collier et al., 2017), and therefore accurately predicting productivity and the future distribution of seagrasses requires knowledge of biomass allocation strategies. Third, BGr can also be influenced by conditions and processes in the sediment such as nutrient concentrations, organic matter content and deposition rates and the reducing potential of the sediment (Ferguson et al., 2016, Ferguson et al., 2017) and the potential for the microbiome to protect root tips from sulphide intrusion (Martin et al., 2019). Therefore, improving our understanding of what influences below-ground processes and biomass allocation strategies can influence environmental management priorities and targets.

The BGr is not routinely assessed in most monitoring programs, and only half of the research studies measure it compared to above-ground biomass (AGr; shoots and stems) (Duarte and Chiscano, 1999, Marbà et al., 2013). BGr is difficult to access, requires destructive sampling, and is time-consuming and costly to analyse. By contrast, AGr can be assessed visually using remote sensing (Roelfsema et al., 2014), or on-ground visual assessment of cover (McKenzie et al., 2017), biomass (Rasheed et al., 2014), or tactile shoot counts (Collier et al., 2009). These are all non-destructive measures. Even in cases where destructive sampling is undertaken, it can be very difficult to accurately measure BGr (Zobel and Zobel, 2002). Models that can accurately predict BGr would circumvent the need for direct measurement.

In tropical seagrass habitat, meadows are often comprised of multiple seagrass species (Fig. 1). Seagrasses are not a taxonomic group but a functional grouping of monocotyledonous plants with a range of life-history strategies (Waycott et al., 2006), namely: colonising, opportunistic and persistent, based on their response to disturbances (Kilminster et al., 2015). One of the features that distinguishes the functional grouping of seagrass species is the amount they invest into below-ground tissues (Fig. 2). Persistent species, with large rhizomes and a large proportion of BGr, are better able to resist mortality when disturbances such as light reduction affect their capacity to photosynthesise (O'Brien et al., 2018). They do this by drawing on the sugars and starch stored in their rhizomes to support respiratory processes, including

growth (Collier et al., 2009). By contrast, colonising species expand rapidly, with more frequent turnover of tissues. They invest much smaller amounts into below-ground biomass and consequently have fewer storage reserves, leading to a lower capacity for resistance (Chartrand et al., 2018). However, they have high levels of sexual reproduction, including seed formation which facilitates rapid recovery. For the many seagrass species in northern Australia, there is very little information on morphological plasticity within these functional groupings, including how environmental conditions affect biomass allocation and how co-occurring species influence the biomass of each other.

The objectives of this analysis were to: 1. assess how environmental conditions and seagrass community composition influence seagrass investment into BGr; and 2. develop a tool to estimate BGr and seagrass resources of northern Australia from AGr. To do this, we compiled all available historical seagrass biomass data from tropical northern Australia and used Generalized Linear Models (GLM) to predict BGr from AGr, environmental, and community co-variables, and then predicted BGr from AGr in Cairns Harbour to demonstrate application of the model.

2. Materials and methods

2.1. Seagrass data sets

AGr and BGr biomass data were collated from multiple sources including published literature and unpublished data (Table 1) from subtropical and tropical locations of northern Australia, extending from Shark Bay in Western Australia to Moreton Bay in Queensland (Fig. 3). The sampling unit for biomass varied among studies (Table 1), but was standardized to equivalent units for this study (grams dry weight (gdw) m^{-2}). This assumes biomass sampled within a sampling unit was consistent at the one metre scale, and could be scaled up to these units. Here we will refer to the data that includes harvested BGr and AGr as 'biomass samples'. Most biomass samples came from mixed species meadows with biomass recorded for each species separately. The species were: *Amphibolis antarctica*, *Cymodocea angustata*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Enhalus acoroides*, *Halophila decipiens*, *Halophila ovalis*, *Halophila spinulosa*, *Halophila tricostata*, *Halodule uninervis*, *Syringodium isoetifolium*, *Thalassia hemprichii* and *Zostera muelleri*.

The collated data set spans 30 years, from 1987 to 2015, but is spatially and temporally disparate. Most individual studies were either one-off sampling events, or extended for a maximum of 19 consecutive sampling events over three years. The largest number of biomass samples were from the Great Barrier Reef, which spans 2,300 km of Queensland's east coast. At a location level, the greatest number of biomass samples were from Green Island (2329 data points), Moreton Bay (658), the Pilbara (395), Ellie Point in Cairns Harbour (363), and

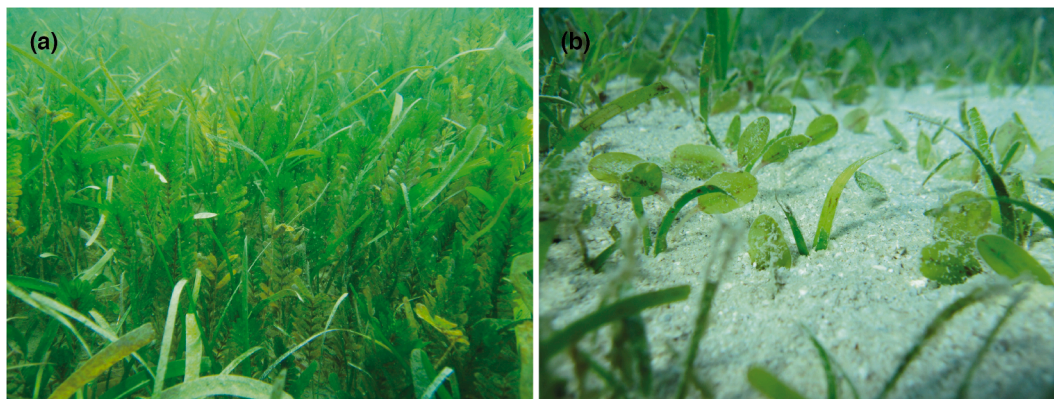


Fig. 1. Examples of tropical multi-specific seagrass meadows comprised of (a) *C. serrulata*, *H. uninervis*, and *H. spinulosa* at Magnetic Island, and (b) *H. ovalis* and *H. uninervis* at Green Island, Queensland, Australia.

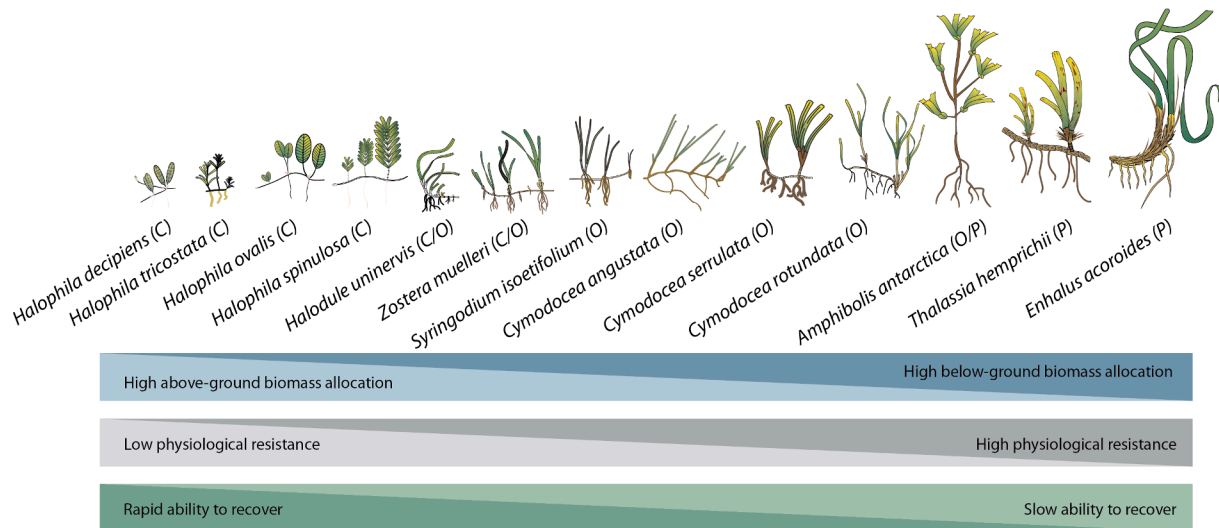


Fig. 2. Dominant traits among northern Australian seagrass species, with emphasis on their relative biomass allocation, and ability to either resist disturbances, or to recover following loss. Also indicated is the species classification as colonising (C), opportunistic (O), or persistent (P). Adapted from Kilminster et al. (2015).

Magnetic Island (288) (Fig. 3).

Five species had adequate data for statistical analysis (Table 1). *H. uninervis* and *H. ovalis* had the highest representation in the dataset (>1,000 data points each), and with both species broadly distributed throughout the study area. *Z. muelleri* had a large number of biomass samples (838) and was broadly distributed throughout Queensland (but not Western Australia), with the greatest number of biomass samples (363) from Ellie Point near Cairns. *T. hemprichii* had 903 biomass samples, but 80% were from Green Island. *C. serrulata* had 290 biomass samples that were patchily distributed from Moreton Bay to Green Island along the Queensland coast. *C. rotundata* had a large number of biomass samples but was excluded from statistical analysis as 95% were from one location at Green Island. The species *A. antarctica*, *C. angustata*, *E. acoroides*, *H. spinulosa*, *S. isoetifolium*, *H. decipiens* and *H. tricostata* had insufficient biomass samples to undertake statistical analysis.

2.2. Community data

Two variables were used to describe the seagrass community for each biomass sample (Table 2). These were species diversity and dominant species class (Dom_{cl}). Species diversity was the number of species present in a sample and Dom_{cl} was defined according to whether the species with the highest total biomass (AGr + BGr) in a sample was categorized as colonising, opportunistic or persistent according to Kilminster et al. (2015) (Fig. 2).

2.3. Environmental covariates

Six environmental covariates were used to describe environmental conditions for each of the biomass samples (Table 2). This included the season when sample collection occurred, depth category, region, sediment type, proximity to land-based sources of pollution, and light stress (Table 2). The Shark Bay, Pilbara and Kimberley regions in Western Australia were defined by the Integrated Marine and Coastal Regionalisation of Australia (Integrated Marine and Coastal Regionalisation of Australia (IMCRA) v4 2006). In Queensland within the GBR, region was defined according to Natural Resource Management boundaries because these are in common use within Queensland to report on marine condition (e.g. Reef Water Quality Protection Plan Secretariat, 2016). Outside of the GBR, bay names were used to describe the region. Benthic

sediment type was visually assessed and defined according to broad categories and listed from most to least dominant and then simplified into three categories based on the dominant type as either mud, sand, or coarse sand/rubble.

A light stress index (LSI) was developed to assess the effect of water quality on historical biomass where environmental data (such as *in situ* light or remote sensing data) was not available. The index was developed using a risk-based approach to score light stress for each site adapted from Waterhouse et al. (2017) and used a combination of within-canopy light data from existing monitoring programs, and expert opinion. It is based on the average long-term conditions of the site, and not the quality of water at the time of biomass collection, i.e. it does not account for temporal variation. Light data from long-term monitoring of intertidal seagrass populations was used to define the benthic light characteristics of five reference sites, which formed the basis for defining five water quality categories (McKenzie et al., 2018; Reason and Rasheed, 2018) (Table 3). Expert judgement was then used to assign water quality categories based on visual assessments of water quality, seagrass species present, and depth of seagrass species occurrence. Water quality (WQ) categories were assigned a WQ multiplier from 1 to 5. Site depth was also scored from 1 (intertidal) to >4 m depth (Table 3). The score range was limited to 4 because although there are expansive seagrass meadows in northern Australia that extend below 4 m depth, there were few samples in this category within the collated data. The light stress value for each site was calculated as the product of that site's water quality multiplier and its depth category score. This resulted in a LSI that ranged from 1 to 16 (scores did not extend to 20 because no seagrass found >2 m LAT where WQ = 5; Table 3).

2.4. Statistical analyses

We assessed whether below-ground biomass (BGr) could be predicted for each species. Generalized Linear Models were fitted to BGr and the variables listed in Table 2 using a Gaussian error distribution with identity link. The natural logarithm of AGr and BGr were taken to improve model fits and accommodate the uneven spread of those values in the data. For factor variables, only those with sufficient data points were kept to prevent unbalanced bias (Table A1). Extreme outliers were removed (BGr > 800 for *H. ovalis*, BGr > 1000 for *H. uninervis*, BGr > 600 for *Z. muelleri*). Finally, sediment was not included in any models,

Table 1

Biomass data used in this study including: sample location, data source, number of biomass samples for each species, collection method, study duration and number of sampling events. Species codes: Aa *Amphibolis antarctica*; Ca *Cymodocea angustata*; Cr *Cymodocea rotundata*; Cs *Cymodocea serrulata*; Ea *Enhalus acoroides*; Hd *Halophila decipiens*; Ho *Halophila ovalis*; Hs *Halophila spinulosa*; Ht *Halophila tricostata*; Hu *Halodule uninervis*; Si *Syringodium isoetifolium*; Th *Thalassia hemprichii*; Zm *Zostera muelleri*. Letters in brackets indicate the species classification of colonising (c), opportunistic (o) or persistent (p) (Kilminster et al., 2015). * Species included in statistical analysis. See Fig. 3 for location map.

Location	Number of samples													Collection method	Study duration	Sampling events	Data source
	Aa (o)	Ca (o)	Cr (o)	Cs* (o)	Ea (p)	Hd (c)	Ho * (c)	Hs (c)	Ht (c)	Hu* (o)	Si (o)	Th* (p)	Zm* (o)				
Shark Bay	38									38				0.25 m corer	2011	2	Fraser et al. (2012)
Green Island & Moreton Bay			47	77			38	5		84	41	24	34	0.17 m corer	2014–2015	2	Collier et al. (2017)
Multiple sites, GBR			99	112			6			329	26	121		0.17 m corer	2008–2010	7	Collier et al. (2010)
Multiple sites, GBR-wide			3	18		18	46	30	27	68	11		28	0.25 m ² quadrat	1987–1988	1	Coles et al. (2001c,d,e)
Green Island			18	20			8			41	1	25		0.25 m ² quadrat	1993	1	McKenzie et al. (2014)
Ellie Point													337	0.25 m ² quadrat	1998–1990	19	McKenzie (1994)
Green Island			517	13			151			327		583		0.0035 m ² corer	2001–2005	17	McKenzie and Coles (unpubl)
Multiple sites, GBR-wide			42	23			332	1		280		46	162	0.25 m ² quadrat	2005–2008	5	McKenzie (unpubl)
Pilbara		50					150	40		100	10	45		0.11 m corer	2013–2014	5	Vanderklift et al. (2017)
Moreton Bay							155							0.0625 m ² quadrat	2002–2003	13	McMahon (2005)
Hervey Bay													90	0.0625 m ² quadrat	2002	1	McMahon (2005)
Ellie Point													27	0.25 m ² quadrat	1995	1	Rasheed (1999)
Green Island			7	3			1			7	3			0.25 m ² quadrat	1995	1	Rasheed (2004)
Moreton Bay													59	0.15 m corer	1997–1998	5	Udy et al. (unpubl)
Moreton Bay				24			137	30		46	14		160	0.15 m corer	2012–2013	1	Samper-Villarreal et al. (2016)
Kimberley					59							59		0.04 m ² quadrat	2013–2015	3	Kendrick et al. (2017)
TOTAL no. samples	38	50	733	290	59	18	1024	106	27	1320	106	903	897				

as the simple descriptors tended to cluster with species leading to unbalanced models (e.g. most *Z. muelleri* samples tended to be labelled as 'mud'). Model selection (a comparison of models containing a different number of the explanatory variables) was used to identify the optimum models as defined by the Akaike Information Criteria (AIC) in a stepwise process (Zuur et al., 2016). When multiple models had very similar AIC (between 2 and 10 AIC points difference) the simplest model was selected. K-fold cross-validation ($k = 10$) was also used to confirm the model selection process, specifically to assess the quality of the model for predicting below-ground biomass (Zhang, 1993). This showed that the simplest model chosen had the same predicting capabilities as more complicated ones. Interactions of all variables were tested (as a maximum of 3-way interactions), but were not included in any of the final models because they did not significantly improve model prediction when they were tested using cross validation, even if they had slightly lower AICs. Residuals were checked for homogeneity of variance and normality. The final models for each species are in Table 4. All analyses were performed in RTM version 3.5.0 using the *stats* package (R Core Team, 2018).

2.5. Cairns Harbour case study

To demonstrate each species models' application, we provide a case study to predict BGr within the seagrass meadows of Cairns Harbour. AGr for Cairns Harbour meadows was visually assessed in October and November 2017 as a part of routine annual monitoring (McKenna et al., 2015; Reason and Rasheed, 2018). AGr, including the contribution of each species, was assessed in three random 0.25 m² quadrats within a 5 m (radius) site which were averaged for the site and resulted in 362 AGr samples (Fig. 6). Species present included *C. serrulata*, *H. ovalis*, *H. uninervis* and *Z. muelleri*. *H. decipiens* was present at 9 of the sites, but could not be included in the prediction of total BGr using the models because there was insufficient biomass data to develop a model for this species. These species models were then used to predict BGr for each species. BGr was then summed for all species to calculate total BGr per site. Predictions were undertaken in R and plotted using the *ggmap* package (Kahle and Wickham, 2013). We were not able to validate the Cairns Harbour predictions against measured BGr at the time of biomass sampling, as this data was unavailable, but provide this case study as an

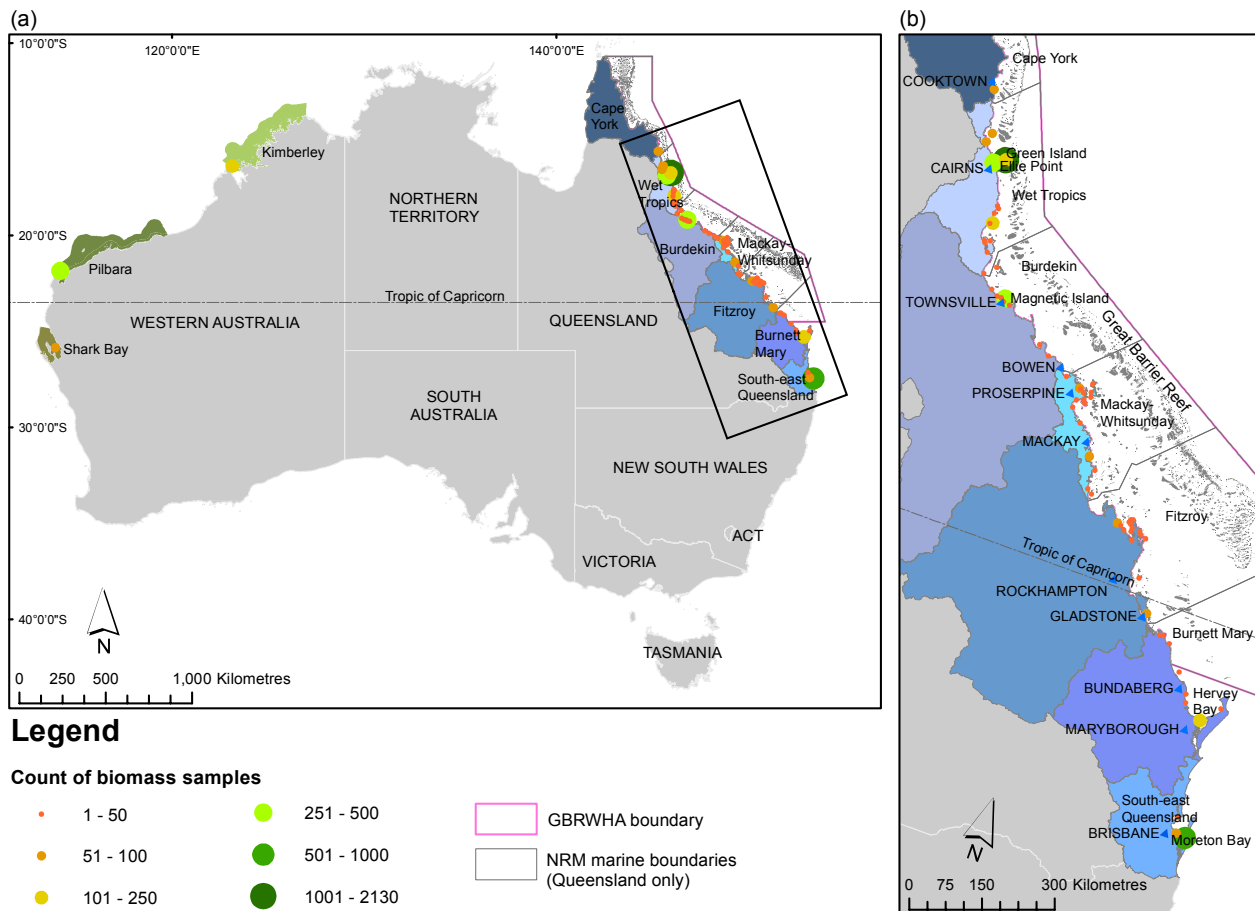


Fig. 3. Spatial distribution of biomass samples. Biomass sample data was collated from within the sub-tropics and tropics of northern Australia from Shark Bay (Western Australia) to Moreton Bay (South-east Queensland). Regions were defined for (a) Western Australia using the Integrated Marine and Coastal Regionalization of Australia, and (a, b) Queensland using Natural Resource Management (NRM) boundaries. GBRWHA: Great Barrier Reef World Heritage Area.

Table 2
Variables included in the model. NA – Not applicable.

Variable type	Variable Name	Abbreviation	Type	Units	Description and levels	Source
Seagrass	Above-ground biomass	AGr	Continuous log scale (natural log)	gDW m ⁻²	Seagrass above-ground (leaves/shoot) biomass	Sources listed in Table 1
Environmental covariates	Season	Season	Factor	NA	Season levels for southern hemisphere: Summer = December-February Autumn = March-May Winter = June-August Spring = September-November	Sources listed in table 1
	Depth	Depth	Factor	NA	Two depth levels: intertidal (experiences exposure to air) shallow subtidal (<10 m MSL)	Carter et al. (2018)
	Region	Region	Factor	NA	Queensland (within GBR): Natural Resource Management region Queensland (outside GBR): Bay name Western Australia: Integrated Marine and Coastal Regionalisation regions (IMCRA4.0)	Integrated Marine and Coastal Regionalisation of Australia (IMCRA) v4 (2006) See Table 3
	Light stress index	LSI	Discrete continuous	Score	Index where 1 = very low stress and 16 = very high stress.	
Community covariates	Sediment type (simple)	Sed _s	Factor	NA	Three broad levels: mud (silt and clay, mean diameter <<0.0625 mm), sand (very fine to coarse, mean diameter > 0.0625 to < 1 mm), coarse sand/rubble (mean diameter > 1 mm). Based on Wentworth (1922) categories.	Sources listed in Table 1 , where possible. Gaps filled using expert knowledge.
	Proximity to land-based sources of pollution	Proximity to land	Factor	NA	Three levels: estuarine, coastal, reef.	Carter et al. (2018)
	Species diversity	Diversity	Discrete continuous	Count	Number of species present in each sample	Sources listed in Table 1
	Dominant species classification	Dom _{cl}	Factor	NA	Three levels: colonising, opportunistic or persistent	Kilminster et al. (2015)

Table 3

Light stress index and calculation method. All sites within the biomass data set were assigned one of five water quality categories defined from long-term (5–10 years) within-canopy light monitoring (WQ multiplier), and one of four depth categories based on lowest astronomical tide (LAT). The light stress value for each site is the product of that site's WQ multiplier and its depth category score. NA = not applicable, no seagrass growing > 2 m LAT where WQ = 5.

Water quality (WQ) categories	WQ multiplier	Depth category score			
		Intertidal	<2m LAT	2–4 m LAT	>4m LAT
		1	2	3	4
Clean water, infrequently (<5% days) drops below light thresholds. Example site: Green Island, mean daily light = 17.4 mol m ⁻² d ⁻¹	1	1	2	3	4
Usually clear water, but occasionally exposed to low light conditions. Example site: Low Isles, mean daily light = 15.6 mol m ⁻² d ⁻¹	2	2	4	6	8
Chronic low light but not due to very high turbidity. Able to support subtidal seagrass > 4 m. Example site: Magnetic Island/Picnic Bay, daily light = 14.8 mol m ⁻² d ⁻¹	3	3	6	9	12
Visually turbid and brown, but able to support very shallow subtidal seagrass populations. Example site: Cairns Harbour, daily light = 12.9 mol m ⁻² d ⁻¹	4	4	8	12	16
Very turbid, generally only able to support intertidal seagrass populations. Example site: Shelley Beach Townsville, daily light = 8.4 mol m ⁻² d ⁻¹	5	5	10	NA	NA

Table 4

Best fit GLMs for five seagrass species where the response is BGr. See Table 2 for explanation of predictor abbreviations.

Model	Species	Response	Predictors
1	<i>C. serrulata</i>	BGr	AGr + Season
2	<i>H. uninervis</i>	BGr	AGr + Season + Depth + Habitat + Region + LSI + Diversity + DOM _{cl}
3	<i>H. ovalis</i>	BGr	AGr + Season + Depth + Region + LSI + Diversity
4	<i>T. hemprichii</i>	BGr	AGr + Region + LSI + DOM _{cl}
5	<i>Z. muelleri</i>	BGr	AGr + Region + LSI + DOM _{cl}

example of how the model could be applied in a management context.

3. Results

BGr represented a smaller proportion of total biomass than AGr in three species. The proportion was lowest in *H. tricostata* (34%), followed by *C. angustata* and *H. decipiens* (Fig. 4). *A. antarctica* had an equal allocation of biomass. BGr was a greater proportion of total biomass for the remaining nine species, reaching an average of 88% in *T. hemprichii* (Fig. 4). There was a general increase in total biomass for each genera along the species traits model (Fig. 2), with the lowest total biomass for opportunistic *Halophila* genera, particularly *H. decipiens* and *H. tricostata*

(6 gDW m⁻²) that occupy deep subtidal waters, while *E. acoroides* has the highest total biomass. There was large within-genera variation for *Halophila* and *Cymodocea* for total biomass and the proportion of BGr. For example, *C. angustata* had a much lower total biomass (16 gDW m⁻²) and contribution of BGr (41%) than *C. serrulata* and *C. rotundata*, where mean total biomass > 100 gDW m⁻² and contribution of BGr to total biomass was 74% (Fig. 4).

3.1. Variables affecting below-ground biomass

AGr was a consistently strong positive predictor of BGr for the five species we modelled (Table 4). AGr did not act in isolation however; between one (*C. serrulata* model) and seven (*H. uninervis* model) additional environmental and/or community covariates were significant predictors of BGr in the models. Sediment type was the only variable that did not contribute to BGr predictions for any species. Region and LSI were significant predictors of BGr in all but the *C. serrulata* model.

The models accounted for between 84% and 98% of the variance on the log-scale, and between 67% and 80% when predicted on the normal scale (Fig. 5). Once transformed to the normal scale, the uneven spread in the data was more apparent (clustered towards lower values) and there was a small under-prediction of below-ground biomass (Fig. 5).

The estimates given in Table A2 provide an indication of the direction of the effect each variable has on BGr predictions. The estimates are based on all data used in each model, and are affected strongly by measured AGr and need to be carefully interpreted. For example, a positive estimate for BGr in winter (e.g. for *H. uninervis*) doesn't necessarily imply that BGr was higher in winter compared to spring, but that the prediction of BGr from AGr requires a positive offset because AGr is typically reduced in winter (7 g DW m⁻² in winter compared to 13 g DW m⁻² in spring), but BGr is not reduced relatively as much (52 g DW m⁻² winter and 56 g DW m⁻² in spring). In addition, as AGr strongly influenced the models, many of the apparent trends among factors or variables are not important in the simplified models. For example, there is a much higher BGr for *C. serrulata* in Moreton Bay compared to other regions (Fig. A1); AGr explains this, so region is not important in the model for predicting BGr in this species. Furthermore, the AGr and BGr were log transformed for this analysis, and therefore the estimates in Table A2 can be applied to log transformed biomass data only.

BGr of *C. serrulata* increased with AGr (Tables 5, A2) explaining 94% of the variance (R² = 0.9469, Fig. 5) in (log)BGr. Despite *C. serrulata*'s occurrence throughout Queensland, and with data included in this analysis from the Wet Tropics to Moreton Bay, there was no significant effect of region on this prediction, or of any other variable other than season because AGr was such a strong predictor on its own.

For *H. ovalis*, BGr increased with AGr and was also affected by season, depth, region, LSI and species diversity, and these combined, explained 84% of the variance in (log)BGr (Table 4, A2, Figs. A1–A3). BGr was significantly greater in the Wet Tropics than in all other regions except for neighbouring Cape York. BGr was also significantly greater in the intertidal compared to the shallow subtidal depth category. BGr significantly decreased as the light stress index increased, and increased with species diversity; for example, when four or five species were present, BGr was at least double that compared to monospecific biomass samples of *H. ovalis* (Fig. A3).

The BGr of *H. uninervis* increased significantly with AGr, and was also affected by season, depth, region, LSI, species diversity and Dom_{cl} and these combined, explained 93% of the variance in (log)BGr (Tables 5, A2, Figs. A1–A3). BGr was greatest in summer and similar in all other seasons, but due to an increase of BGr relative to AGr in both summer and winter (compared to spring), the prediction of BGr from AGr requires a positive offset in both of these seasons. BGr was significantly greater in shallow subtidal than in intertidal depths. BGr was greater in reef and lower in estuary compared to coastal, but due to a relative decrease in AGr and BGr in estuaries, an offset is not required in the prediction (p > 0.05). The BGr of *H. uninervis* increased with species

Table 5

Generalised linear models (analysis of variance summary) for the prediction of (log)BGr in five seagrass species from northern Australia. Complete results with estimates are in the Appendix (Table A2).

Variable	DF	SS	MS	F value	P	Variable	DF	SS	MS	F value	P
<i>C. serrulata</i>						<i>H. uninervis</i>					
AGr	1	832.0	832.0	1221.0	<0.001	AGr	1	3423.4	3423.4	4109.9	<0.001
Season	3	9.7	3.2	4.7	0.003	Season	3	41.3	13.8	16.5	<0.001
Residuals	263	179.2	0.7			Depth	1	84.6	84.6	101.5	<0.001
<i>H. ovalis</i>						<i>Z. muelleri</i>					
AGr	1	1690.8	1690.8	2703.9	<0.001	AGr	1	740.5	740.5	1905.2	<0.001
Season	3	23.0	7.7	12.2	<0.001	Region	4	126.9	31.7	81.6	<0.001
Depth	1	142.7	142.7	228.2	<0.001	LSI	1	1.9	1.9	4.8	0.030
Region	7	103.5	14.8	23.6	<0.001	DomCl	1	3.7	3.7	9.6	0.002
LSI	1	14.8	14.8	23.7	<0.001	Residuals	780	303.2	0.4		
Diversity	1	20.4	20.4	32.6	<0.001						
Residuals	986	616.6	0.6								
<i>T. hemprichii</i>											
AGr	1	1779.2	1779.2	2252.5	<0.001						
Region	2	10.0	5.0	6.3	0.002						
LSI	1	90.6	90.6	114.7	<0.001						
DomCl	1	61.1	61.1	77.4	<0.001						
Residuals	801	632.7	0.8								

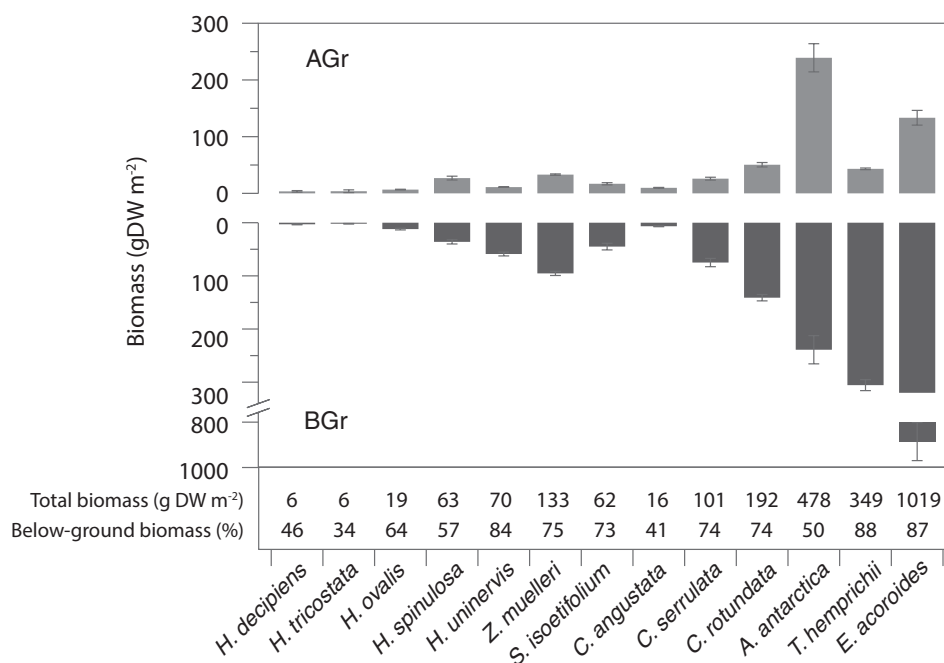


Fig. 4. Above-ground and below-ground biomass ± standard error (SE) of thirteen seagrass species in northern Australia, based on collated data. N = 18 to 1320 depending on species (see Table 1). Total biomass (g DW m⁻²) is mean AGr + BGr for each species. BGr (%) is percent contribution of BGr to total biomass for each species. Arranged in order used in species traits model (Fig. 2).

diversity; BGr was up to two times greater when there were 2–5 species, compared to when *H. uninervis* was the only species. BGr was significantly greater when the dominant species (Dom_{Cl}) was opportunistic or persistent rather than colonising. BGr significantly decreased as LSI increased; for example, BGr ranged from 83 to 89 gDW m⁻² at LSI 1 to 2, and 2 to 12 gDW m⁻² at LSI 10 to 16. BGr was the lowest in the Pilbara region and highest in Cape York but when predicted from AGr, a larger offset was required for the Burdekin region (Table A2).

Only one persistent species was able to be analysed – *T. hemprichii* – because there was insufficient data for *E. acoroides*. The BGr of *T. hemprichii* increased with AGr, and also was affected by region, LSI, and Dom_{Cl} (Tables 5, A2, Figs. A1–A3). BGr was significantly greater in the Kimberley region compared to the Wet Tropics. Although BGr was lower in the Burdekin region, a positive offset is also required when predicting BGr from AGr in the Burdekin region because of the influence of other variables in that region, in particular AGr. BGr was significantly

higher in samples dominated by persistent rather than opportunistic species.

In northern Australia, *Z. muelleri* is constrained to the Queensland coast. For this study our sample sites with *Z. muelleri* ranged from Ellie Point (near Cairns) south to Moreton Bay. Despite this broad latitudinal distribution, and the large number of sample locations along this stretch of coast, the variables included in the model accounted for >97% of the variance in the (log)BGr for *Z. muelleri*. BGr increased with AGr, and also varied with region, LSI and Dom_{Cl} (Tables 5, A2, Figs. A1–A3). BGr was significantly affected by region, being higher in the Fitzroy region and in Moreton Bay compared to the Wet Tropics (Table A2).

3.2. Cairns Harbour case study

BGr was predicted at 362 sites within Cairns Harbour using the GLMs for each species present. The largest predicted BGr was for *Z. muelleri*

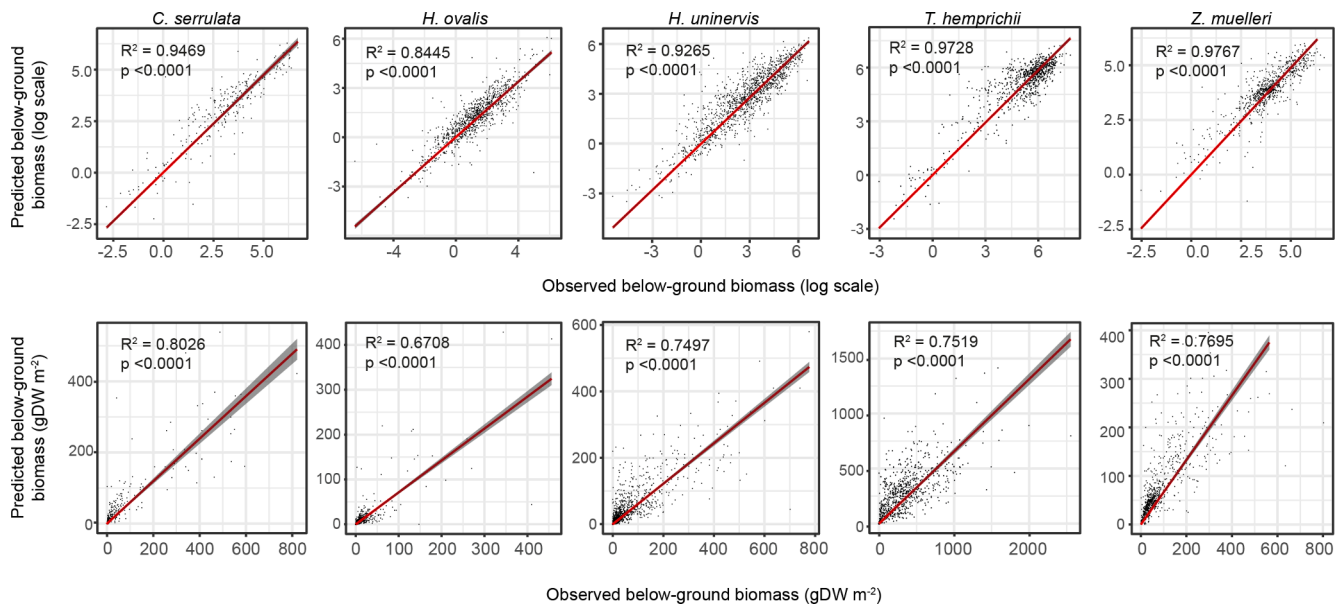


Fig. 5. Fitted generalised linear models showing predicted vs observed below-ground biomass (BGr) in the log scale (top row), and after transformation to the normal scale (bottom row) for five species occurring in northern Australia.

and *C. serrulata* (Fig. 6). Total BGr was highest in the western portion of the Harbour, where composition was dominated by *Z. muelleri* and *C. serrulata*. *H. uninervis* occurred at the greatest number of sites, but had lower BGr. The upper and lower standard errors are presented in Fig. A4.

4. Discussion

This study has demonstrated that the below-ground biomass (BGr) of five common seagrass species in northern Australia, *C. serrulata*, *H. ovalis*, *H. uninervis*, *T. hemprichii* and *Z. muelleri*, is strongly related to above-ground biomass (AGr) and various combinations of environmental conditions and seagrass community composition variables. These relationships suggest that predictions of BGr are possible when BGr is not directly measured. In the Cairns Harbour case study, the results of the model were applied to each site and estimates of BGr and a modelled picture of BGr was produced. The strength of the model leads to a reasonable confidence in the predictions but further field validation (in addition to the K-fold cross-validation applied here) of the predictive capability of the model would be the next logical step in the process. These models are a substantial advance on previous BGr predictions (e.g. Duarte and Chiscano, 1999) because they take into account local site conditions and include species-specific equations. As a result, the amount of explained variance was very high. Traditional methods to measure BGr can be labour-intensive, and destructive to harvest and process, and may also have levels of error associated with its measurement (Zobel and Zobel, 2002). Therefore, these models may enable us to predict BGr with relatively high confidence, and with further validation of their predictive capacity could be used for broad-scale assessments of seagrass resources at the scale of northern Australia or the Great Barrier Reef. These models can therefore be used to vastly improve estimates of seagrass resources, which is important because evidence for how much seagrass is present and whether biomass is going up or down underpins environmental management actions and targets for both the habitat and the ecosystem services that seagrass meadows provide (e.g. Great Barrier Reef Marine Park Authority, and Queensland Government, 2015). This approach to modelling BGr using AGr, environmental variables and community variables, could be applied in the management of any seagrass habitat—including outside of northern Australia—with suitable model calibration data.

Species diversity and/or the dominant species affected predictions of

BGr, particularly in the structurally small species *H. ovalis*. There were two indications that seagrasses in meadows that have formed stable and diverse communities have a greater investment into below-ground biomass. These indicators were: the increase in BGr prediction when the dominant species class was opportunistic or persistent compared to colonising, and increasing BGr as diversity increased. Diversity affected BGr of *H. ovalis* and *H. uninervis* while dominant species influenced the prediction of BGr for *H. uninervis*, *T. hemprichii* and *Z. muelleri*. The effect was largest in *H. ovalis*, which is the structurally smallest species and it may therefore suffer more from resource competition. Such morphological plasticity can reduce the degree to which size asymmetry affects access to resources by increasing the chances of accessing limited resources (Schwinning and Weiner, 1998).

Below-ground tissues, in particular the rhizome, store starch and sugars which are energy reserves that can be used to support metabolism and growth under conditions of stress including light limitation (Mackey et al., 2007; Collier et al., 2009; McMahon et al., 2013) or physical disturbance (Gacia et al., 2003). BGr is therefore an indicator of resistance capacity such that species that have greater BGr can tolerate light deprivation and ‘resist’ mortality (Duarte and Chiscano, 1999; Kilminster et al., 2015; O’Brien et al., 2018). This is typically used to differentiate resilience strategies among different species (Kilminster et al., 2015). Previous studies identified that on average seagrass invested similarly into above-ground and below-ground tissues, but varied among species (Duarte and Chiscano, 1999) whereas in our new data compilation of biomass, we found that nine out of 13 species had a greater investment into below-ground biomass. This would suggest that ‘resistance’ strategies are important in most species of northern Australia.

This analysis furthers our understanding of resilience in northern Australian seagrass species, highlighting that the amount of below-ground biomass can vary within a species depending on environmental and community co-variables. Therefore the capacity to resist disturbances is not simply a species-dependant trait, but one that can adapt. Meadows that have features of stability (opportunistic or persistent dominated species, higher diversity), have larger investment into below-ground biomass and are likely to have greater resistance to disturbances. When colonizing species are not dominant, they allocate relatively more to BGr highlighting that they can adopt more resistance-like traits in meadows that have resistance-like features. Therefore it

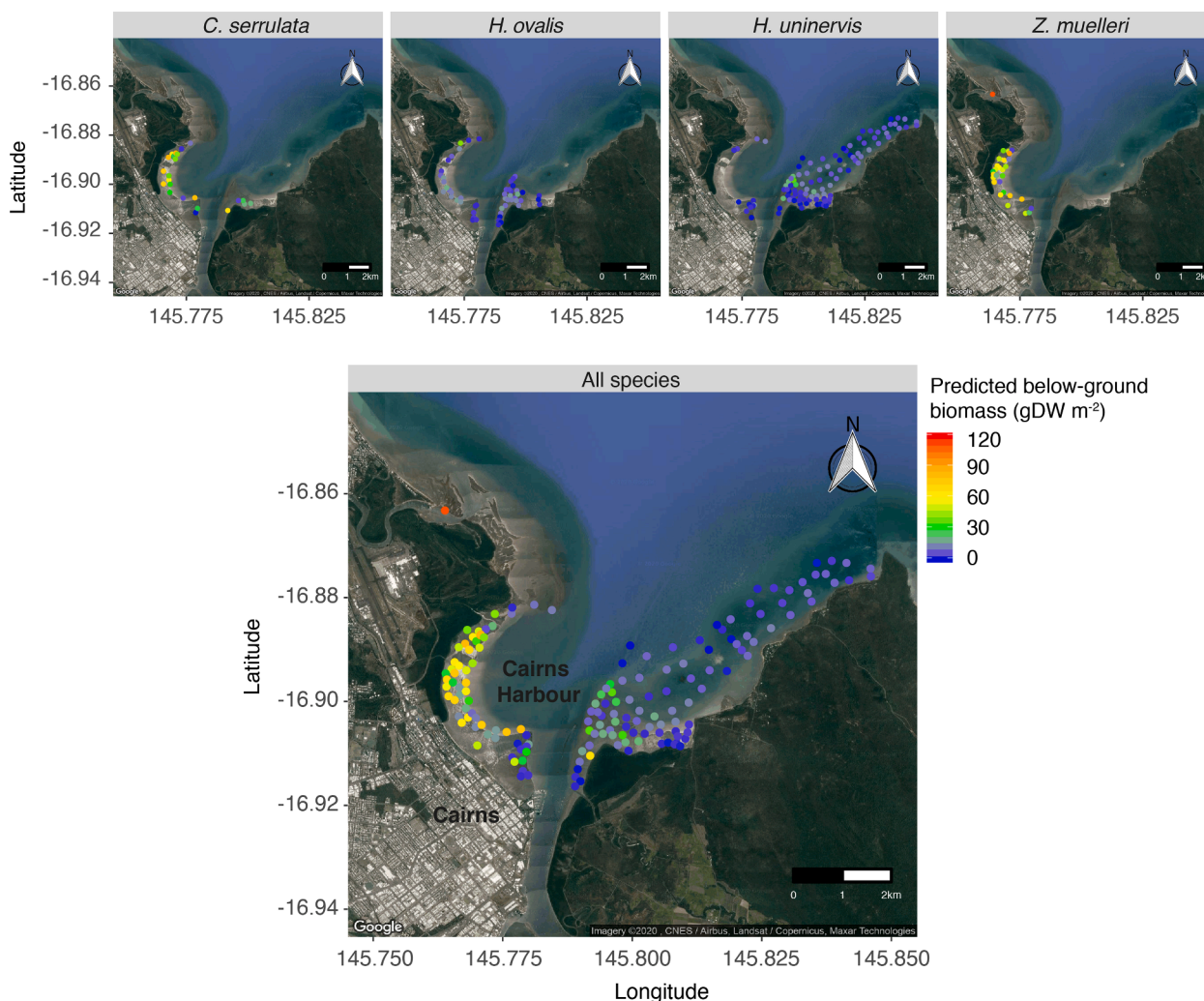


Fig. 6. Below-ground biomass (BGr) at sites within Cairns Harbour, October/November 2017, predicted using generalised linear models for each species (Table 5) and visually estimated above-ground biomass from 2017 surveys (Reason and Rasheed, 2018). Blue points refer to very low BGr, as there are no zero values (seagrass absence) shown. Map image source: CNES/Airbus, DigitalGlobe, Landsat/Copernicus.

appears that there is a positive feedback, in that if conditions enable meadows to be stable and diverse, increased investment into below-ground biomass might further promote resistance and stability. Recognition of these potential feedbacks is critical for the success of management strategies for conservation and planning (Maxwell et al., 2017).

Seagrass biomass allocation strategies also need to be investigated at a scale at which management strategies will be implemented. This analysis was undertaken on samples from locations spanning northern Australia and over a long time-series to demonstrate that a tool for predicting seagrass resources at that scale can be developed. It included a large number of co-variables to capture the diversity of habitat conditions across that range. As such the environmental condition data were compiled at a relatively coarse level, which is likely to have influenced how important the factors were in the models. For example, the sediment factor was reduced to a simple three level factor to reduce complexity in the category data, but because it tended to cluster by species it was not useful for the models. However, we know from focused local-scale assessments that sediment type and sediment conditions influence seagrass morphology (Ferguson et al., 2016, 2017) and diversity of seagrass communities (Collier et al., 2020). This, in turn, can affect seagrass light requirements. Therefore when setting local-scale management plans, for example in protection of a seagrass meadow from coastal development, seagrass biomass and environmental conditions should be measured at a scale appropriate for the management plan.

Similarly, light stress was approximated using the light stress index (LSI), which had a significant effect on BGr in four out of five species. The LSI did not improve the model for *C. serrulata* even though biomass allocation is affected by both acute light stress (Collier et al., 2012) and gradients in light availability (Ferguson et al., 2016, 2017), including in this species. Under short-term light stress, leaves and shoots are typically shed, resulting in a fairly consistently reported increase in the relative proportion of BGr (Abal et al., 1994; McMahon et al., 2013; York et al., 2013). However, under persistent gradients in light, such as those from shallow to deeper water or across gradients in water quality, BGr generally declines in conjunction with total biomass, but the relative amount of BGr to AGr can be influenced by local-scale conditions (Collier et al., 2007; Ferguson et al., 2016). The LSI is a very simple risk of exposure to these natural gradients and did not contribute to estimates of BGr in a consistent and predictable manner for all species, as would be expected for short-term light stress. The effect of measured light availability, rather than a risk index, would also provide a more robust assessment of biomass allocation across gradients if the data were available (e.g. Magno-Canto et al., 2019), and is recommended in future analyses. This analysis was unable to account for short-term change as the sampling was mostly not repeated and there was no measure of changing water quality included in the model. Therefore, this model is unsuitable for predicting local-scale changes in BGr in response to short-term changes in water quality, but this could be added with appropriate

input data.

Due to the strong influence of AGr in the model, future applications to predict below ground biomass should also incorporate a good understanding of any local acute pressures that can have a major impact on AGr while leaving BGr largely unaffected. In tropical Australia, grazing by green turtles that crop the leaves can lead to such local impacts (Scott et al., 2020) as well as tidal exposure events leading to “burning” and loss of leaves for large species such as *E. acoroides* (Unsworth et al., 2012). Under these circumstances the modelled relationship would likely breakdown at the local meadow scale, however these impacts are usually obvious and could be accounted for during model application if observed and recorded during monitoring.

While BGr was strongly affected by AGr, other variables had a considerably smaller effect on the prediction of BGr. Therefore if information on these other variables is not available (e.g. the light stress index), then BGr can still be predicted. The absence of interactions in the models ensures that missing information will not influence how the other variables are used to estimate BGr. One exception is that the ‘region’ in which the samples were collected accounted for large effects on BGr, and in the most widely distributed species, *H. ovalis* and *H. uninervis*, these effects were greater than any of the other predictor variables. For example, in *H. uninervis* the estimate for the Pilbara region was considerably larger than any of the other factors or regions because it was a narrow leaf form of the species. This indicates that there are conditions within each of the regions that affect the BGr (e.g. nutrient availability, tidal range), biological features (e.g. narrow leaf *H. uninervis*), or ecological features (e.g. grazing pressure) that are not covered in the model through the other predictor variables. The importance of region to the model means that these predictive models should be used with caution outside of northern Australia. These models provide a robust framework for estimating seagrass BGr, but more accurate assessments could be developed with increased data availability and resolution.

In conclusion, the BGr of seagrasses can be predicted with a high degree of confidence for these five species in northern Australia using AGr and other variables on environmental conditions and community composition. This is useful given the range of techniques for assessing AGr such as remote sensing, percent cover and visual estimates of AGr. This provides a means to estimate broad-scale seagrass resources and accurately assess the ecosystem services provided by seagrass meadows. The data used in this analysis was historical data, and much of it did not have environmental data recorded alongside the biomass samples. We recommend ongoing measurement of BGr, in conjunction with associated environmental data to further develop the models over time and increase confidence in BGr estimates; however, even with further model improvements, some *in-situ* validation is likely to be necessary.

CRedit authorship contribution statement

C.J. Collier: Conceptualization, Methodology, Investigation, Data curation, Writing - original draft, Writing - review & editing. **L.M. Langlois:** Methodology, Validation, Formal analysis, Data curation, Visualization, Writing - original draft, Writing - review & editing. **K.M. McMahon:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **J. Udy:** Project administration, Funding acquisition, Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **M. Rasheed:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing. **E. Lawrence:** Methodology, Writing - original draft, Writing - review & editing. **A.B. Carter:** Methodology, Writing - original draft, Visualization. **M.W. Fraser:** Methodology, Writing - original draft. **L.J. McKenzie:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107156>.

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