Present Estimation and Future Prediction of Seagrass Distribution and Carbon Storage in Andaman Coast of Thailand

Milica Stankovic

A Thesis Submitted in Fulfillment of the Requirements for the Degree of Doctor of Philosophy in Biology
Prince of Songkla University
2018

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Thesis Title	Present Estimation and Future Prediction of Seagrass Distribution and Carbon Storage in Andaman Coast of Thailand
Author	Miss Milica Stankovic
Major Program	Biology

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Dean of Graduate School

This is to certify that the work here submitted is the result of the candidate's own investigations. Due acknowledgement has been made of any assistance received.

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Major Advisor

....Signature
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Candidate

I hereby certify that this work has not been accepted in substance for any degree, and is not being currently submitted in candidature for any degree.

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Thesis Title Present Estimation and Future Prediction of Seagrass Distribution and Carbon Storage in Andaman Coast of Thailand

Author Miss Milica Stankovic

Major Program Biology

Academic Year 2017

ABSTRACT

Seagrass meadows have one of the largest carbon sink capacities in coastal ecosystems, trapping more than 18% of marine carbon sequestration. Their role in mitigation of climate change is vital, as they are responsible for assimilation of 2% of CO_2 from anthropogenic sources, which remains trapped in the ecosystem for millennia and centuries. The aim of this study was to estimate carbon storage of these ecosystems in present time, to determine important variables influencing the carbon storage, to develop the predictions of the seagrass distribution and to estimate gains and losses of carbon within these meadows in the future climates. The study was conducted in diversely characterized (disturbed vs undisturbed, exposed vs sheltered, high density vs low density) seagrass ecosystems, in uniform (*Enhalus acoroides*) and mixed species (*E. acoroides* and *Thalassia hemprichii* or *Cymodocea serrulata*) meadows, along the Andaman coast of Thailand, in Phuket, Krabi and Trang provinces. The results suggested that higher amounts of organic carbon were stored in uniform meadows than in mixed, in undisturbed comparing to disturbed, while exposed and sheltered seagrass meadows had similar amounts. Organic carbon storage was highly influenced by meadow type and disturbance, suggesting that undisturbed, uniform and high density meadows store the highest amount of organic carbon. In the future climates, mixed meadows were constantly expanding their areas, while uniform meadows expanded their distributions by 2025 and then underwent decrease until several of meadows completely disappeared. The increase of the mixed meadows in the future climates had important influence on the climate, as the newly occupied areas assimilated large amounts of carbon from the ocean and atmosphere, consequently mitigating the climate

change. However, uniform meadows had the opposite trend, loss of the areas, which released large amounts of carbon back to the ocean, and via direct ocean-atmosphere exchange the concentrations of CO_2 in atmosphere were affected. Our results presented the essential knowledge required to understand and set the baseline for proper management and conservation in the present time, and to more effectively address the importance of the natural carbon sinks in the mitigation of climate change.

ACKNOWLEDGEMENT

I am sincerely grateful to a large number of people who generously contributed their time and effort, without whom this work, and thesis would not be finished.

Firstly, and foremost, I would like to express my gratitude to my adviser Assoc. Prof. Dr. Anchana Prathep, who inspired me to become seagrass nerd, and for her valuable encouragement, advices, suggestions and her immense support throughout my studies. Besides my adviser, I would like to express sincere appreciation for my co-adviser Dr. Naruemon Tantipisanuh from Conservation Ecology Program at King Mongkut's University of Technology Thonburi. Without her patient guidance and persistent help, I would be lost in statistical world.

I would like to express special gratitude towards Dr. Kitsanai Charoenjit and his team, who selflessly contributed their time, knowledge and patience towards novel use of drone technology

Also, I am very grateful for immense help from Assoc. Prof. Gregory Nishihara, who generously contributed his time and knowledge to advise me in species distribution modeling.

Moreover, I hold enormous gratitude towards Seaweed and Seagrass Research Team at PSU, as without their help on the field and in the laboratory and without their valuable suggestions when my thoughts got stuck, this study would not be complete.

I am sincerely thankful to my dear friend Janmanee Panyawai, who was my right hand throughout the studies.

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My deepest appreciation is towards my boyfriend, Dejan Davidovic, who was always beside me, giving me valuable advices and selflessly providing me time to finish my studies.

Finally, my deepest appreciations are to my parents, grandmother and sister for their unconditional understanding and support throughout the years.

Milica Stankovic

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LIST OF PAPERS AND MANUSCRIPTS

This thesis has been published in the following Papers (1, 2 and 3) and there is a manuscript in preparation (Manuscript 1).

Published papers:

1. Stankovic, M., Panyawai J., Jansanit K, Upanoi T. and Prathep A. 2017. Carbon content in different seagrass species in Andaman Coast of Thailand. *Sains Malaysiana,* 49(9): 1441–1447.
2. Stankovic, M., Tantipisanuh N., Rattanachot E. and Prathep A. 2018. Model-based approach for estimating biomass and organic carbon in tropical seagrass ecosystems. *Marine Progress Series*, 596:61–70.
3. Stankovic, M., Tantipisanuh N. and Prathep A. 2018. Carbon storage in seagrass ecosystems along the Andaman coast of Thailand. *Botanica marina*, under review.

Manuscripts in preparation:

1. Stankovic, M., Nishihara G.N., Tantipisanuh N. and Prathep A. 2018. Change of seagrass distribution in future climate change scenarios.

LETTERS OF ACCEPTANCE

Paper 1: **<u>Stankovic, M.,</u> Panyawai J., Jansanit K, Upanoi T. and Prathep A. 2017.** Carbon content in different seagrass species in Andaman Coast of Thailand. *Sains Malaysiana*, 49(9): 1441–1447.

Mohd. Salmi Md. Noorani <msn@ukm.edu.my> Tue, Jan 17, 2017, 3:20 PM
to me

Dear Prof Milica Stankovic,

It gives me great pleasure to announce that your paper

Carbon content in different seagrass species in Andaman coast of Thailand

is accepted for publication in Journal Sains Malaysiana pending for some minor corrections (see attachment). Please look into these corrections carefully.

Also, we hope to get your paper published before the end of 2017. For this, please look at the formatting of your paper. As a guide, we have provided you a sample paper from a recent issue. You may also look at the website: http://www.ukm.my/jsm/contents.html

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Thank you for your patience and thank you for choosing Sains Malaysiana.

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Editor

Journal Sains Malaysiana

Paper 2: **<u>Stankovic, M</u>., Tantipisanuh N., Rattanachot E. and Prathep A. 2018.** Model-based approach for estimating biomass and organic carbon in tropical seagrass ecosystems. *Marine Progress Series*, 596:61–70.

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3 messages

Anchana Prathep <a_prathep@hotmail.com> Thu, Apr 12, 2018 at 4:07 PM
To: "svesemenja ." <svesemenja@gmail.com>, June Tantipisanuh <ttpisanu@gmail.com>

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Thank you for your careful attention to the reviewers comments. I am pleased to accept your manuscript for publication in MEPS. Your documents have been forwarded to our Production Department, and you will hear from them soon.

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In case of questions, please send an email to Angela Fromm (angela@int-res.com) at the Editorial Office.

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Paper 3: **<u>Stankovic, M</u>., Tantipisanuh N. and Prathep A. 2018.** Carbon storage in seagrass ecosystems along the Andaman coast of Thailand. *Botanica marina*, under review.

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Kind regards,

Dr. Siti Maryam Yaakub
Guest Editor, Botanica Marina

Reviewer(s)' Comments to Author:
Reviewer: 1
Comments to the Corresponding author
The authors have done an excellent job at revising their manuscript in reference to most of my prior comments. Their in-depth response is much appreciated but the authors still had not sufficiently addressed my comment on the "biomass-carbon" model methodology (re: comment #2 in my first review). The authors referred heavily on Stankovic et al. 2017b, which I duly note had recently been accepted (my congrats to the authors, and therefore this reference should be edited to Stankovic et al. 2018 (accepted) in the revised draft). That paper and this BM manuscript should be taken as independent in the sense that BM readers can replicate the study without heavy reference to Stankovic et al. 2017b. I therefore recommend (at least) some minor elaboration on this biomass-carbon" model to improve the current draft.

Reviewer: 2
Comments to the Corresponding author
Thank you for the edits. The paper is clearer after revision. All the best for your research.

SUMMARY OF CONTENTS

1. General introduction

1.1. Seagrass ecosystems

Seagrasses are mixed group of flowering plants that thrive in shallow oceanic and estuarine environments around the world. Although they are one of the poorest taxa, these plants play many important roles in coastal and marine ecosystems. They occupy oceanic and estuarine waters on all continents, apart from Antarctica. The countries which extend to both temperate and tropical climates, have the greatest species diversity, such as Australia (29 species), the United States (23 species) and Japan (16 species). On the other hand, the greatest diversity in countries with one climate zone, occurs in tropical region such as India and Philippines (both with 14 species). Indo-Pacific bioregion, specifically Philippines, Papua New Guinea and Indonesia, is considered as the center of global seagrass biodiversity (Green and Short, 2003). Moreover, Southeast Asia has been hypothesized to be the origin for tropical seagrass species (Ooi et al. 2014).

1.2. Diversity, distribution and ecosystem services

Seagrasses comprise of about 60 closely related species, belonging to 12 generas and four families of monocts (Duarte 2000). As they are distributed worldwide, about half of the species can be founded in tropical region, while another half is temperate species (Short et al. 2007). The global estimated cover of the seagrass meadows is between 300 000 – 600 000 km^2 (Duarte et al. 2013a), covering around 1% of the world's ocean. Many seagrass meadows consist only of one species, although mixed stands containing up to 14 species maybe found in the tropics, particularly in the Indo-Pacific region (Short et al. 2007).

Seagrass communities in Thailand are highly variable in terms of diversity and structure, as uniform and mixed meadows are reported throughout the country. Most of the seagrass species are associated with uniform and mixed species meadows, such as *Enhalus acoroides, Thlalasia hemprichii, Cymodocea serrulata, Cymodocea rotundata, Halophila ovalis, Halodule uninervis* etc., while *Halophila decipines* is commonly associated only with uniform meadows (Rattanachot et al. 2008). In the mixed meadows, competition for the available resources might occur, which can lead to the decrease of shoot density, growth and survival (Duarte et al. 2000), while in the uniform meadows there is abundance of available resources. However, in the mixed species meadows, species provide a “tradeoff” to each other, as the studies showed that the shoot density of *E. acoroides, C. rotundata, C. serrulata* and *H. uninervis* decreased when other species from mixed meadows are removed (Duarte et al. 2000), suggesting that there is a complex interaction within meadows.

The ecosystem services of the seagrass meadows lie in their “engineer” characteristics, which includes physical and geochemical modification of their environment. Their primary services include: primary production (Buapet et al. 2013), nutrient recycling (Costanza et al. 1997), providing food and habitat for fish (Cullen-Unsworth et al. 2014) and, invertebrates (Cullen-Unsworth et al. 2014; Nordlund and Gullström 2013), nursery grounds for juveniles (Jackson et al. 2015). These ecosystems can attenuate the wave action (Christianen et al. 2013; Ondiviela et al. 2014), stabilize the sediments (Christianen et al. 2013; Newell and Koch 2004), prevent the sediment resuspension (Gacia and Duarte, 2001) and accrete the sediment (Van Keulen and Borowitzka 2003). Their ecosystem services provide at least US$33 trillion dollars annually (Costanza et al. 1997). Moreover, they play a vital role in the mitigation of climate change, as they create large carbon sinks within the meadows (Fourqurean et al. 2012; Macreadie et al. 2014).

1.3. Organic carbon in seagrass ecosystems

The seagrass meadows are autotrophic ecosystems, where excess organic carbon is exported to other communities or is buried (Duarte et al. 2013b). The higher net productivity of the meadow suggests higher carbon inputs as well as higher burial rate (Lavery et al. 2013). They are one of the most productive ecosystems, with the global net productivity of 400 Tg yr^{-1} (Duarte et al. 2005). However, 80% of their primary production is not consumed (Duarte et al. 2013b) but is exported to adjacent ecosystems, (24%; Duarte and Cebrián 1996) or buried in the sediment (30-50%; Duarte et al. 2005). Unlike terrestrial ecosystems, carbon sequestered and stored in the coastal soils can be trapped for a long period of time (centuries and millennia) (Duarte et al. 2005). They are responsible for more than 18% of total marine carbon sequestration (Kennedy et al. 2010), with the sink capacity of 0.08 – 0.22 Pg C yr^{-1} (Duarte et al. 2013a). However, their global distribution is rapidly declining at the annual rate of 7% (Waycott et al. 2009), with the estimated loss of 30 – 40 % in the next 100 years (Pendleton et al. 2012).

Loss and/or degradation of these ecosystems exposes the sediment to oxygen, which increases nutrient cycling (Liu et al. 2017) and microbial activity (Trevathan-Tackett et al. 2017), resulting in higher respiration and detrital decay (McLeod et al. 2011), leading to decrease in carbon sequestration. Moreover, the carbon sequestration capacity is directly affected by the disturbance, leading to the loss of trapping ability, loss of the carbon in the living vegetation and in the sediment. The oxidized sediment is remineralized (Macreadie et al. 2014) and released back into the ocean (Fourqurean et al. 2012; Marbà et al. 2015). The increased concentration of ocean carbon disturbs ocean-atmosphere equilibrium and by their direct exchange, CO_2 concentrations in the atmosphere are affected. Recent estimates suggest an average release of 0.15 Pg of CO_2 y^{-1} from the loss of seagrass ecosystems, which would affect global economy by 6.1 billion US\$ y^{-1} (Pendleton et al. 2012).

There are many factors which directly affect carbon sink (Mateo et al. 2006; McLeod et al. 2011), from which the most influential are: grain size (Dahl et al. 2016; Serrano et al. 2016), species complexity (Samper-Villarreal et al. 2016) , species composition (Gillis et al. 2017), landscape configuration (Ricart et al. 2017), productivity of the plants (Armitage and Fourqurean 2016), sediment density (Gullström et al. 2017) and disturbance (Rozaimi et al. 2017). On the other hand, changes of environmental factors associated with climate change indirectly influence carbon storage through the species growth, productivity, composition, distribution and abundance, which consequently shift the carbon balance and sequestration. Changes in temperature have effect on photosynthesis and productivity (Short and Neckles 1999; Pedersen et al. 2016), causing the changes in species distribution and abundance. The sea level rise in the future will increase the depth and conseqently reduce light conditions, especially in the lower distribution limit. The decrease of the light availability has effect on species growth, photosynthesis and distribution (Short and Neckles 1999), which is especially noticable in the species having narrow depth ranges (Duarte 1991). Moreover, the sea level rise will cause changes in tidal range, increasing the exposure stress to UV-B radiation (Short and Neckles 1999). Elevated UV-B leads to inhibition of photosynthetic efficiency (Unsworth et al. 2012) via decrease of chloroplast density (Short and Neckles 1999). As seagrass biomass and distributuion are negatively correlated with the tidal exposure and amount of solar radiation (Stapel et al. 1997; Unsworth et al. 2012), their upper distribution limit will be highly affected as well. The risk of sea level rise increases the frequency of extreme waves and storm surges, which can cause marine heatwaves and consequently the loss of seagrass meadows (Arias-Ortiz et al. 2018). Moreover, the increase of the flooding frequency causes erosion of the coastal areas and increase of the sediment run off, which affects seagrass richness, biomass and community structure (Terrados et al. 1998).

1.4. Climate change

In the last 650,000 years the Earth's climate had seven cycles of climate change (IPCC 2014). However, most of these changes attributed minimal variations, comparing to the current warming trend, as CO_2 concentrations levels are the highest ever recorded. The main drivers of the increase of CO_2 emissions are extremely likely due to global economic and population growth (IPCC 2014). Annual greenhouse gas (GHG) emissions have continued to increase, despite the policies, to 1.0 Gt CO_2 y^{-1} from 2000 to 2010 (IPCC 2014). The emissions from fossil fuel combustion, cement production and flaring have tripled, while the emissions from land use changes have increased by 40% in the last 40 years (IPCC 2014). However, as the Earth has natural carbon sinks (ocean, tropical, temperate and boreal forests, and coastal ecosystems such as mangrove forests, seagrass meadows and tidal salt marshes) only 40% of anthropogenic CO_2 emissions (880 ± 35 $GtCO_2$) have remained in the atmosphere since 1740 (IPCC 2014). The ocean has absorbed more than 30% of the emitted CO_2, causing ocean acidification (ocean pH decreased from 8.16 to 8.06 in the last 100 years, IPCC 2014)). Despite the natural carbon sinks, this increase of CO_2 emissions rose the average surface and ocean temperature by 0.85°C with one century (IPCC 2014). As the atmosphere warmed, ice sheets and glaciers have been losing mass at the rate of 3.5 – 13.6% per decade (IPCC 2014). Moreover, the area of snow cover has been decreasing by 11.7% per decade over the last 40 years. Increase rate of the ice mass loss caused the rise in the sea level, which rose by 0.19 m over the last 100 years, at the rate of 3.2 mm y^{-1} (IPCC 2014). Continued GHG emissions will cause additional warming of the atmosphere and oceans, which can have devastating consequences and irreversible impacts on ecosystems. By 2100, it is estimated that CO_2 concentrations will be more than double, up to 1,000 ppm, while the emissions will triple (IPCC 2014), causing the increase in temperature by 2.5°C, 0.70 m increase of sea level and decrease of ocean's pH by 0.5.

However, the Earth's natural carbon sinks, have high capacities of the carbon storage, especially coastal ecosystems with 237.6 Tg of carbon burial y^{-1} (Duarte et al. 2005). The seagrass ecosystems alone, are responsible for accumulating more than 2% of global anthropogenic CO_2 emissions (IPCC 2014). Their proper management, conservation and restoration are more than necessary, as restored meadows have the capacity to store more carbon in the sediment than naturally occurring vegetation (Thorhaug et al. 2017).

1.5. Mapping of the seagrass ecosystems

Various monitoring approaches have been conducted using scuba and snorkeling surveys (Gotceitas et al. 1997), ground based sampling (Moore et al. 2000) and mapping using hovercraft (Mckenzie 2003). As the technology is being developed, many studies have used remote sensing approaches to frequently monitor and quantify seagrass coverage and meadow's health (Knudby and Nordlund 2011; Lyons et al. 2015; Phinn et al. 2008; Roelfsema et al. 2014). Additionally, dynamics of the seagrass meadows (Baumstark et al. 2013), changes of the seagrass extent (Knudby et al. 2010) and fluctuations of the biomass (Misbari and Hashim, 2016) have been quantified. Moreover, the use of acoustics, such as side scan sonar, has been used to estimate cover of seagrass meadows (Hossain et al. 2014). However, the main limitation of these techniques is the spatial resolution, which restricts the study to mapping of the seagrass extent. Even with the finer scale resolution satellites mapping of the individual seagrass species is limited. Additionally, the inability of the satellite's measurement to capture fine scale patterns of the seagrass distribution and sparsely vegetated area, led to the novel approaches using small unmanned vehicles (UAVs), commonly known as drones. The rapid growth of the lightweight low-cost drone technology has been a novel addition to the ecological and environment studies. In the recent years, drone technology has been widely used in hydrology (DeBell et al. 2015), forestry (Inoue et al. 2014), wildlife monitoring (Chabot et al. 2015; Hodgson et al. 2013) and in polar studies (Ryan et al. 2015). The flexibility and capabilities of drones increased their utilization in coastal environments, for monitoring of the beaches and dunes (Gonçalves and Henriques 2015), classification of the habitats as nurseries for fishes (Ventura et al. 2016), mapping coral reefs (Chirayath and Earle, 2016) and seagrass meadows (Duffy et al. 2018).

The newly adopted technologies can provide knowledge of seagrass extent, coverage and biomass, which is enough for monitoring of seagrass health. However, to set appropriate conservation and management priorities, knowledge of seagrass ecosystem services has to be associated with the seagrass health, in a manner to produce spatially organized area as a “hot spot” of ecosystem services/carbon storage. Although the studies of carbon storage in seagrass ecosystems have been exponentially increasing since 2009 (Alongi 2018), there is still lack of basic knowledge of seagrass habitats in tropical region and a regional overview of the carbon inventories. Moreover, the knowledge about the factors influencing carbon storage in this region is limited as well and how the seagrass meadows will be influenced by the climate change. Thus, as Southeast Asian region is failing to keep up the pace with the global researchers, this study has been conducted to provide the key information of the carbon storage, seagrass distribution, factors influencing carbon storage, changes that seagrass meadows facing under climate change and the fate of the organic carbon in these ecosystems in future climates.

2. Research questions and objectives

The main research question of this study was:

- How future climate change scenarios will influence the seagrass meadows and currently stored carbon within these meadows?

In order to answer the main question, the study is divided into three minor frameworks with specific objectives:

Framework 1: Current biomass and organic carbon storage in the seagrass meadows
Objectives:

- To estimate current biomass and organic carbon storage in seagrass meadows
- To map the current biomass and organic carbon storage in seagrass meadows
- To estimate total carbon storage in seagrass meadows, which is the sum of carbon storage within living vegetation and sediment
- To determine which environmental factors, influence seagrass biomass and organic carbon storage

Framework 2: The status of the seagrass meadows, in terms of biomass and organic carbon, in the future climate change scenarios
Objectives:

- To determine the change of the seagrass meadows in the different future climate change scenarios
- To estimate total carbon storage in the future climate change scenarios
- To determine which meadows will continue to have high carbon storage

Framework 3: Estimations of the lost, gained organic carbon and biomass and its emissions
Objectives:

- To estimate change of biomass between seagrass meadows in present and in the future climates
- To estimate change of organic carbon budget between seagrass meadows in present and in future climates

- To estimate the amount of carbon that will be lost
- To estimate the CO_2 emission and assimilation
- To determine which meadows will have highest loss of organic carbon

3. Study sites

The study was conducted along the west coast of Thailand in Phuket, Krabi and Trang provinces (Fig 1). In total, five seagrass meadows were selected, and eight survey areas were classified based on disturbance, geomorphology and meadow type (Table 1). More information about study sites can be read in Paper 3 (Appendix 3).

Table 1. Location of the survey areas. Modified from Paper 3 (Appendix 3)

Survey areas				Study site	Mean depth (m)
Disturbed	Exposed	Uniform	High density	Krabi, Koh Sriboya	-1.9±0.02
			Low density	Krabi, Koh Sriboya	
		Mixed	High density	Krabi, Koh Sriboya	
			Low density	Krabi, Koh Sriboya	
	Sheltered	Uniform	High density	Phuket, Pa Klok	-2.0±0.2
			Low density	Phuket, Pa Klok	
		Mixed	High density	Phuket, Tang Khen Bay	-5.4±0.5
			Low density	Phuket, Tang Khen Bay	
Undisturbed	Exposed	Uniform	High density	Trang, Libong island site 1	-1.9±0.01
			Low density	Trang, Libong island site 1	
		Mixed	High density	Trang, Libong island site 1	
			Low density	Trang, Libong island site 1	
	Sheltered	Uniform	High density	Trang, Libong island site 2	-2.0±0.06
			Low density	Trang, Libong island site 2	
		Mixed	High density	Trang, Libong island site 2	
			Low density	Trang, Libong island site 2	

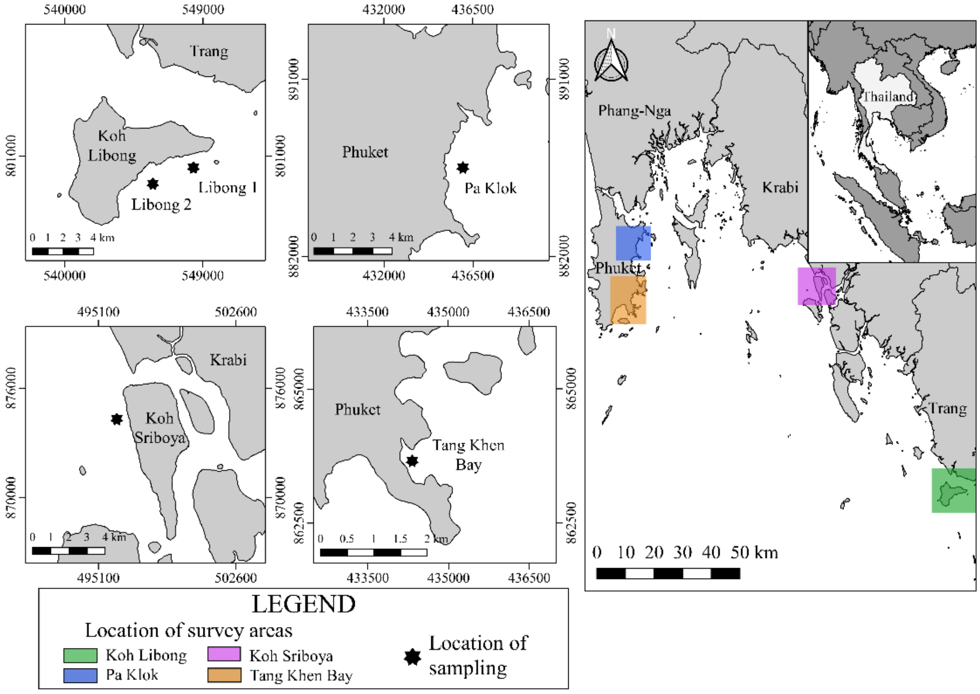
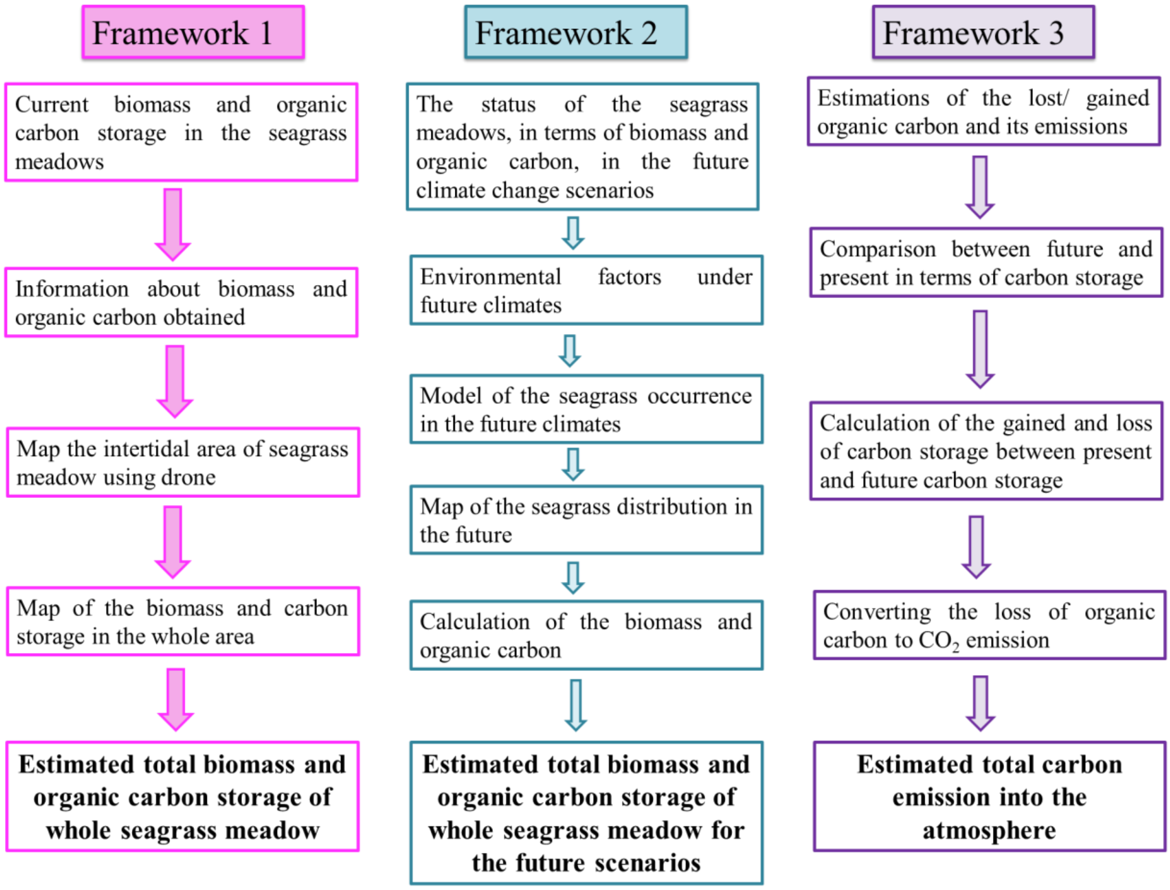


Figure 1. Map of the study sites and survey areas. Modified from Paper 3 (Appendix 3)

4. Results and discussion

The summary of the results and discussion for each framework are provided here. Full details, including literature review, methodology, details of the results and discussion are presented in the attached published Papers 1, 2, 3 (Appendix 1, 2 and 3) and Manuscript 1 (Appendix 4). Furthermore, the brief descriptions of the frameworks' results are summarized in the following diagram.



4.1. FRAMEWORK 1: Current biomass and organic carbon storage in the seagrass meadows (Paper 1, 2 and 3 in Appendix 1, 2 and 3)

4.1.1. Seagrass area

Total seagrass area had a range from 5.55 – 101.56 ha (Table 2). In each of the study sites, except for Tang Khen Bay, both types of meadows were recorded (Fig 2). For Libong site 2, drone images could not be used for classification as they were too blurry, and the water was too dark for seagrasses to be seen. For obtaining the seagrass area of this survey area, previous studies in this area were used.

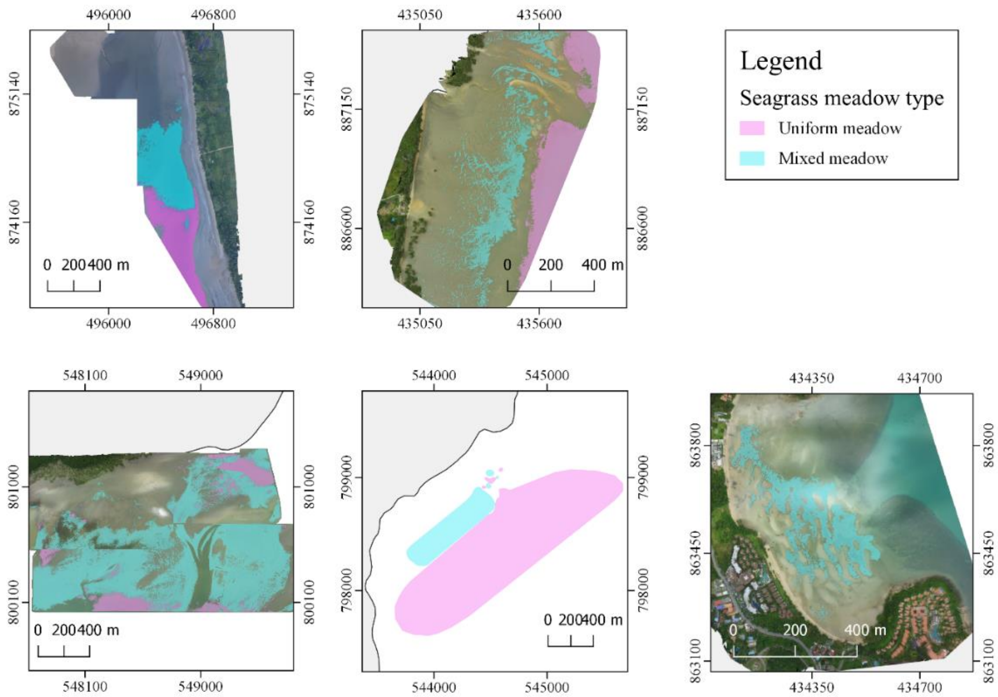


Figure 1. Seagrass area with two types of the meadows in all survey areas (From Manuscript 1)

Although high resolution imagery was used to map the seagrass areas, there were certain limitations. The main problem was that images can be obtained only in the intertidal zone during low tide. However, at Koh Sriboya, most of the *E.acoroides* meadows were located in the subtidal zone. This was resolved by taking the pictures in the middle of summer and early morning, when the ocean water was the clearest. On the other hand, at Libong site 2 getting the first light images were not successful, as the village is nearby and the fisherman disrupted the water after their finishing trips. The second low tide was in the late afternoon, but even then, the water was too dark to obtain the images. This is one of the biggest limitations of remote sensing, as currently there are no available satellites or small unmanned vehicles that could acquire proper images in these conditions. However, the use of sonar after the use of remote sensing could help in defining the areas of seagrass in dark, murky waters.

Table 2. Total area covered in seagrass in each of surveyed areas

Survey area			**Seagrass area (ha)**
Disturbed	Exposed	Uniform	25.18
		Mixed	20.18
	Sheltered	Uniform	11.82
		Mixed	5.54
Undisturbed	Exposed	Uniform	17.84
		Mixed	101.56
	Sheltered	Uniform	15.7
		Mixed	13.1

4.1.2. Biomass

Total average recorded biomass (from root, rhizome and leaves) was 283.1±178.4 g DW m^{-2}. The highest recorded total biomass was in uniform undisturbed exposed high density meadows, while the lowest recorded was in mixed disturbed sheltered low density meadows (Table 3, Fig 3). When observing from each parts of the seagrass, total average root biomass was 43.8±32.0 g DW m^{-2}, with highest recorded biomass in uniform disturbed exposed high density and lowest in uniform disturbed exposed low density (Table 3, Fig 3). Average recorded rhizome biomass was 208.0±135.3 g DW m^{-2}, while the highest was in uniform undisturbed exposed high density meadows and lowest in mixed disturbed sheltered low density meadows (Table 3, Fig 3). Average leaves biomass was 51.8±30.0 g DW m^{-2}, with highest recorded biomass in uniform disturbed sheltered high density meadows and lowest in uniform disturbed sheltered low density meadows (Table 3, Fig 3). More details about biomass of the seagrass meadow were presented in the Paper 1 and 3 (Appendix 1 and 3).

The reported values of the biomass for uniform meadows are falling in the range of the estimations of Vermaat et al. (1995) and Duarte and Chiscano (1999), while leaf biomass is higher than in Vermaat et al. (1995) and Duarte and Chiscano (1999). On the other hand, biomass in mixed meadows had similar values as in Rattanachot and Prathep (2015), with higher leaf biomass than in Koedsin et al. (2016) and much lower than reported by Prathep, Rattanachot, and Tuntiprapas (2010). The highest recorded values of biomass and all vegetation parts were in uniform high density areas, as the species which occupies these areas are bigger in size, robustness and higher productivity (Vermaat et al. 1995). On the other hand, lower recorded values of biomass and the vegetation parts were in disturbed and low density areas, suggesting that disturbance has high impact on the seagrasses with the small coverage, i.e at the edges of the meadows or in newly expanded areas.

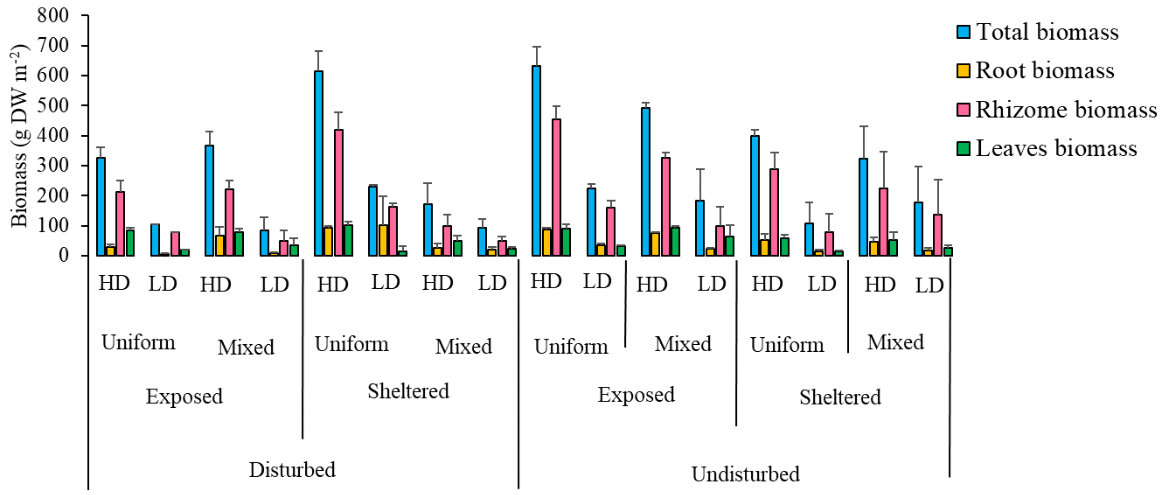


Figure 2. Average values of total biomass, root biomass, rhizome biomass and leaves biomass in all survey areas.

Table 3. Average values of total, root, rhizome and leaves biomass in each survey area

Survey areas	Total biomass (g DW m^{-2})	Root biomass (g DW m^{-2})	Rhizome biomass (g DW m^{-2})	Leaves biomass (g DW m^{-2})
Uniform disturbed exposed high density	324.4±37.2	27.6±110	213.6±35.8	82.2±9.6
Uniform disturbed exposed low density	103.2±2.5	6.4±2.6	77.4±0.5	19.4±0.6
Mixed disturbed exposed high density	368.0±48.8	66.9±29.6	221.4±29.6	79.6±9.2

Mixed disturbed exposed low density	82.6±45.8	8.9±0.9	50.2±33.5	33.5±23.4
Uniform disturbed sheltered high density	614.3±66.5	102.5±96.0	420.3±58.5	100.2±13.3
Uniform disturbed sheltered low density	231.1±3.6	93.9±5.3	162.3±11.4	14.0±1.8
Mixed disturbed sheltered high density	172.9±68.2	27.2±11.9	97.6±38.1	48.1±18.2
Mixed disturbed sheltered low density	91.5±29.4	18.7±9.9	48.4±15.5	24.3±4.1
Uniform undisturbed exposed high density	633.0±63.3	88.3±4.7	454.1±44.0	90.7±14.5
Uniform undisturbed exposed low density	225.0±14.6	33.5±7.7	160.3±22.0	31.2±2.7
Mixed undisturbed exposed high density	490.7±19.1	74.3±5.4	324.6±19.0	91.8±5.6
Mixed undisturbed exposed low density	184.5±103.8	21.8±3.9	99.2±63.2	63.5±36.8
Uniform undisturbed sheltered high density	398.2±20.6	51.6±19.4	289.4±52.9	57.2±12.8
Uniform undisturbed sheltered low density	108.7±67.2	15.0±5.2	79.5±58.8	14.3±3.2
Mixed undisturbed sheltered high density	322.7±109.1	46.5±13.4	223.4±122.5	52.8±26.8
Mixed undisturbed sheltered low density	178.3±118.3	16.9±10.2	136.6±117.8	24.8±9.6

The total average biomass, as well as in roots, rhizomes and leaves is recorded in Table 3 and had a following trend (detailed information about the factors influencing the biomass were presented in the Paper 3 – Appendix 3):

- Uniform meadows had higher values than mixed ones (Fig 4A)
- Undisturbed meadows had higher values than disturbed meadows (Fig 4B)
- Exposed meadows had higher values than sheltered meadows (Fig 4C)

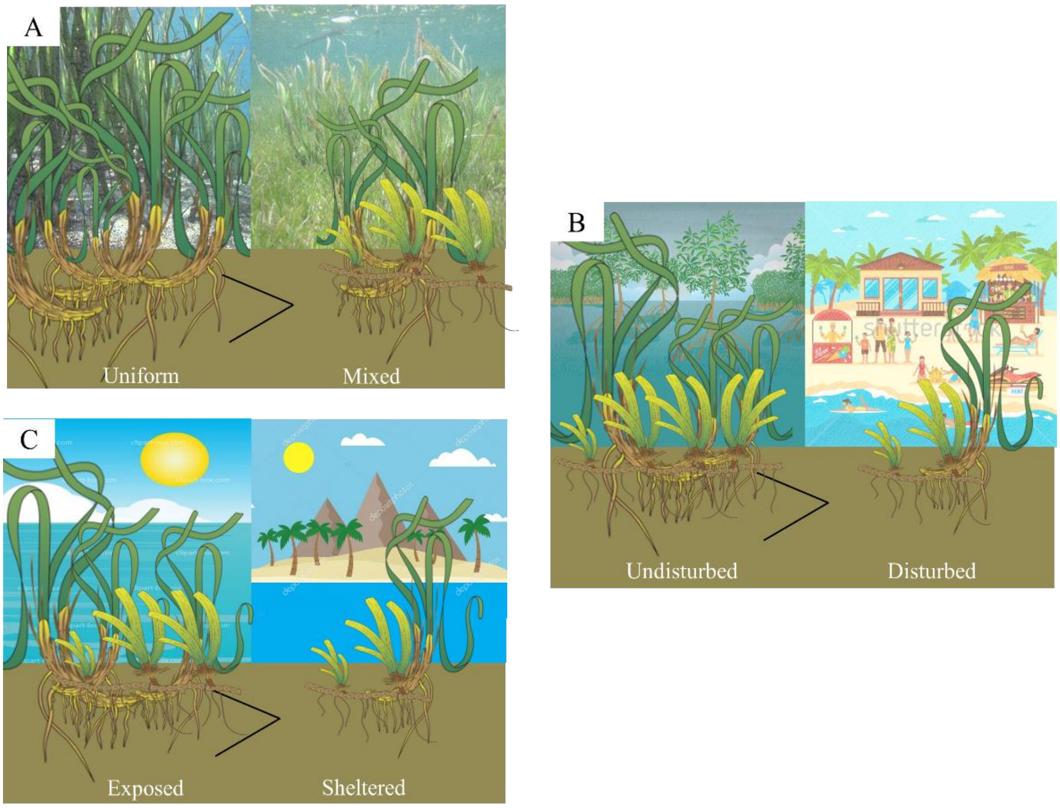


Figure 3. Trend of the higher and lower biomass in seagrass ecosystems

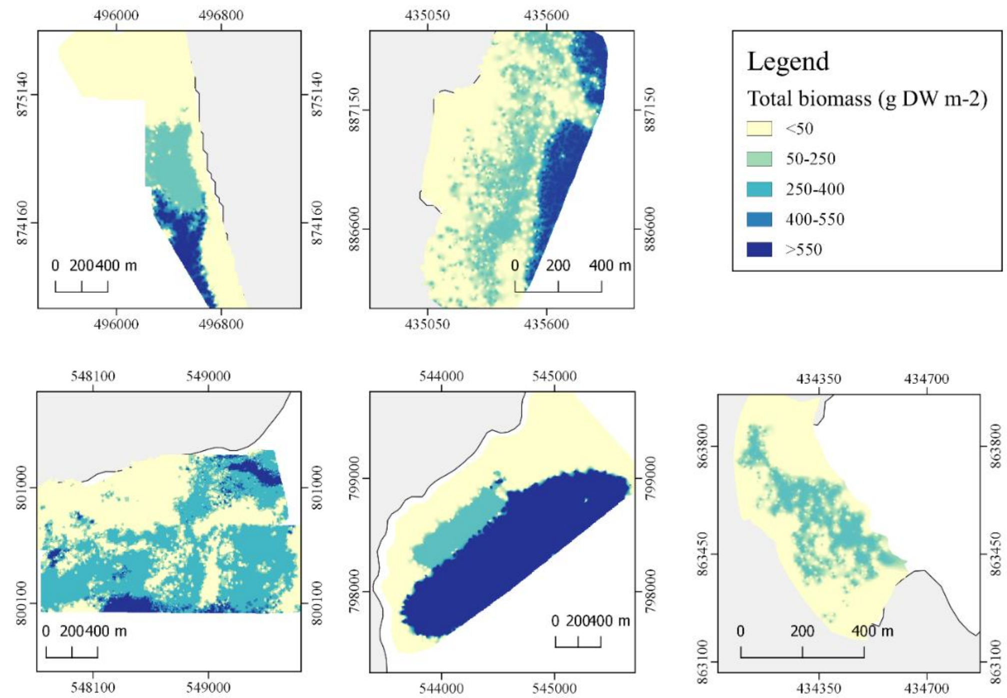


Figure 4. Maps of the total biomass in each of the surveyed areas

In all survey areas, total biomass highly varied across the meadow (Fig 5). Maps of the biomass in all survey areas were created using extracted seagrass area from drone images, which provided the input (coverage of the plants) for the series of the relationships that link coverage and biomass of the species. More information about the relationships between coverage of the plants and their biomass is presented in Paper 2 (Appendix 2). Total biomass was the highest in the areas where *E. acoroides* was present (in uniform meadows) and it was decreasing as the species was less abundant (edges of uniform meadows and mixed meadows). This species is considered bigger and more constant species, with longer life span, low mortality rates, longer-lived shoots and higher productivity (Vermaat et al. 1995). The difference in seagrass structure demonstrates direct influence of the species on the biomass and productivity of the seagrass meadow.

As seen on Fig 5, the areas of uniform meadows have significantly higher ($p < 0.05$) total biomass than areas of mixed species, which was presented in Paper 3 (Appendix 3). The difference in the biomass between the species supports roles of the species in the ecosystem and is direct influence of a different structure of the seagrass species.

4.1.3. Organic carbon storage

Total average organic carbon in living vegetation was 4.0±2.6 Mg ha^{-1}, with the highest values in uniform undisturbed exposed high density meadows, and the lowest in mixed disturbed exposed low density meadows (Table 4, Fig 6). Average organic carbon in roots was 0.5±0.3 Mg ha^{-1}, with the highest values in uniform disturbed sheltered high density meadows and lowest values in uniform disturbed exposed low density meadows (Table 4, Fig 6). Organic carbon in leaves had an average of 0.7±0.4 Mg ha^{-1}, with the highest recorded carbon in uniform disturbed sheltered high density meadows, while the lowest recorded carbon was in uniform disturbed exposed low density meadows (Table 4, Fig 6). The details of organic carbon in the living vegetation are presented in the Paper 1 and 3 (Appendix 1 and 3).

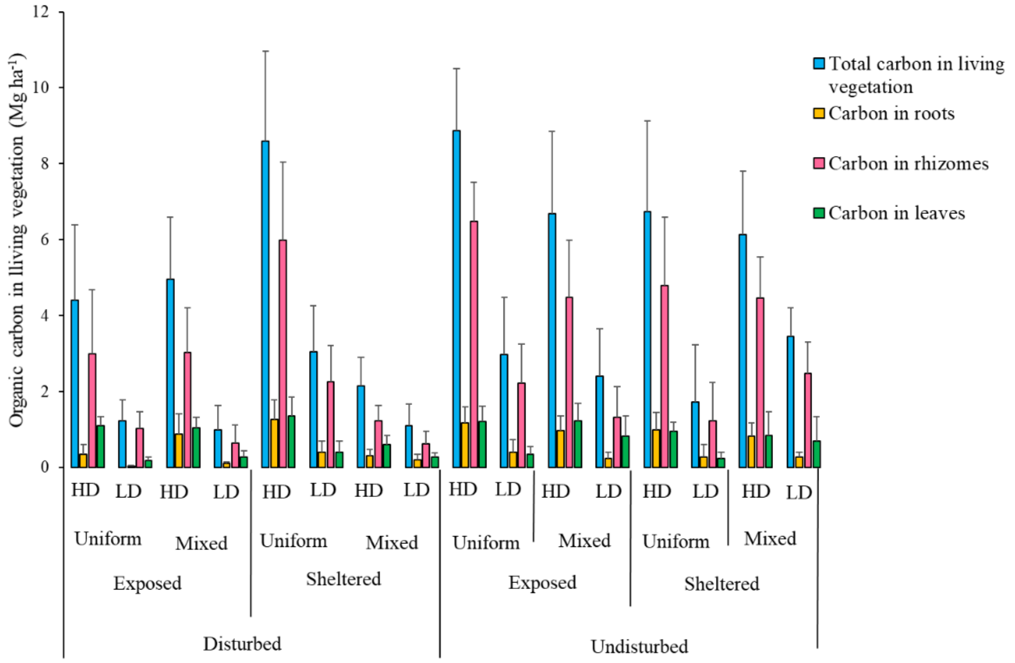


Figure 5. Average values of total carbon in living vegetation, as well as in roots, rhizomes and leaves in all survey areas

The reported values of the organic carbon in the vegetation fall within the range of the global estimates (Fourqurean et al. 2012), while it was 1.5 – 2 times higher than in Indonesia (Alongi et al. 2016), more than 7 times higher than in Singapore (Phang et al. 2015) and 2 times higher than in Micronesia (Kauffman et al. 2011). This suggests that seagrasses in the west coast of Thailand have high carbon uptake and assimilation, which provides higher carbon storages in the ecosystems.

Table 4. Average values of total organic carbon, as well as, in roots, rhizomes, leaves, sedimentary carbon and total carbon storage per area in each survey area.

Survey areas	Total carbon in living vegetation (Mg ha^{-1})	Carbon in roots (Mg ha^{-1})	Carbon in rhizomes (Mg ha^{-1})	Carbon in leaves (Mg ha^{-1})	Carbon in sediment (Mg ha^{-1})	Total carbon storage (Mg ha^{-1})	Total carbon per area (MgC)
Uniform disturbed exposed high density	4.4±1.9	0.3±0.2	3.0±1.6	1.1±0.2	124.7±7.5	125.9±8.1	3,105.6±12.9
Uniform disturbed exposed low density	1.2±0.5	0.3±0.02	1.0±0.4	0.1±0.07	100.1±27.9	104.4±29.8	
Mixed disturbed exposed high density	4.9±1.6	0.8±0.5	3.0±1.1	1.0±0.2	120.9±16.9	125.8±18.6	2,514.4±10.8
Mixed disturbed exposed low density	0.9±0.6	0.1±0.05	0.6±0.4	0.2±0.08	119.6±15.6	120.6±16.3	
Uniform disturbed sheltered high density	8.6±2.3	1.2±0.5	5.9±2.0	1.3±0.4	118.4±13.9	127.0±16.2	1,421.5±14.5
Uniform disturbed sheltered low density	3.0±1.2	0.4±0.3	2.2±0.9	0.4±0.2	100.6±22.5	103.7±23.7	
Mixed disturbed sheltered high density	2.1±0.7	0.3±0.1	1.2±0.4	0.6±0.2	52.9±6.5	54.0±7.1	290.5±6.68
Mixed disturbed sheltered low density	1.1±0.5	0.2±0.1	0.6±0.3	0.2±0.08	51.7±22.5	53.9±23.2	
Uniform undisturbed exposed high density	8.8±1.6	1.1±0.4	6.4±1.0	1.2±0.3	138.4±28.6	141.4±30.1	2,280.1±18.0
Uniform undisturbed exposed low density	3.0±1.5	0.4±0.3	2.2±1.0	0.4±0.2	112.1±19.7	121.0±21.3	

Mixed undisturbed exposed high density	6.7±2.2	1.0±0.4	4.5±1.5	1.2±0.5	123.1±26.1	129.8±28.3	12,676.8±18.2
Mixed undisturbed exposed low density	2.4±1.3	0.2±0.1	1.3±0.8	0.8±0.4	115.9±5.3	118.3±6.5	
Uniform undisturbed sheltered high density	6.7±2.4	1.0±0.5	4.8±1.8	1.0±0.2	165.5±29.5	169.0±31.9	2,605.1±15.9
Uniform undisturbed sheltered low density	1.7±1.5	0.3±0.1	1.2±1.0	0.2±0.05	162.2±47.2	164.3±48.7	
Mixed undisturbed sheltered high density	6.1±1.7	0.8±0.3	4.5±1.1	0.8±0.4	133.7±30.2	139.9±31.9	1,852.7±8.3
Mixed undisturbed sheltered low density	3.5±0.8	0.3±0.1	2.5±0.8	0.7±0.2	129.5±30.0	132.9±30.8	

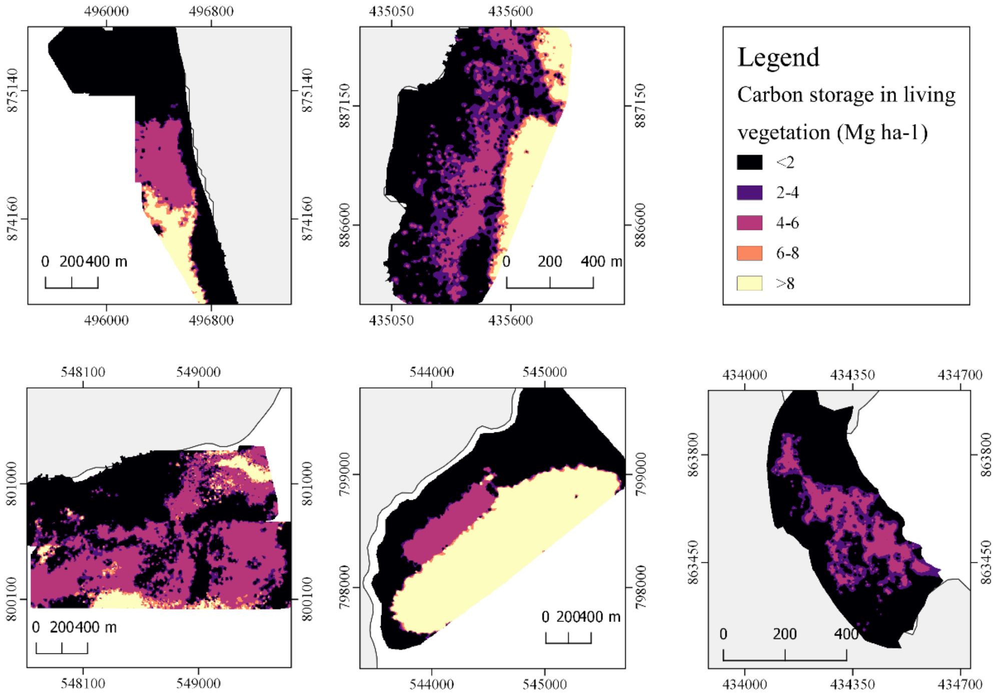


Figure 6. Map of the organic carbon storage in living vegetation in different survey areas

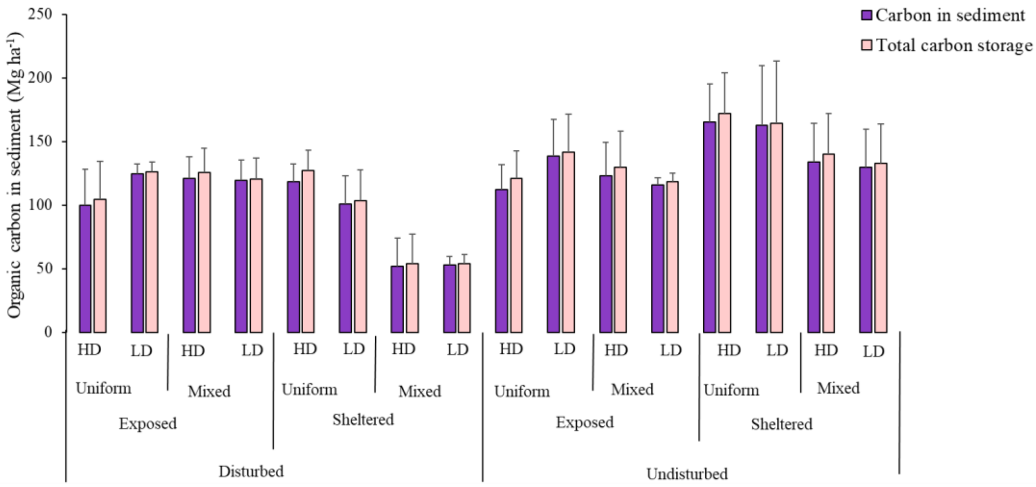


Figure 7. Average values of organic carbon in sediment and total carbon storage in seagrass meadows

When mapped, organic carbon storage in living vegetation had similar trend as biomass (Fig 7). The maps were created using linked linear regression equations between coverage of the plants and carbon within vegetation (Paper 2 – Appendix 2). Areas where uniform meadows had the highest carbon storage in vegetation, while areas of mixed meadows had lower values. This also corresponds to the structure of the species, as longer living species allocate their production into belowground and contributes more on carbon stock (Supriadi et al. 2014).

Average organic carbon in sediment was 116.7±30.6 Mg ha^{-1}, with highest recorded values in uniform undisturbed sheltered high density meadows and lowest in mixed disturbed sheltered low density meadows (Table 4, Fig 8). More information about sedimentary organic carbon are presented in Paper 3 (Appendix 3).

The recorded organic carbon in sediment is at least 1.8 times lower than the global estimates and 5 times higher than Indo-Pacific estimates (Fourqurean et al. 2012). On the other hand, carbon storage was 2 times higher in African region (Githaiga et al. 2016), while undisturbed sediments in Southeast Asia had similar values (Phang et al. 2015; Alongi et al. 2016). However, the reported sedimentary carbon storage in Thailand is much lower (Rattanachot and Prathep 2015; Panyawai 2017) suggesting that sedimentary organic carbon storage is highly variable throughout Thailand and that is influenced by multiple factors.

The highest total organic carbon storage per hectare (carbon stored in sediment and in the living vegetation) was recorded in uniform undisturbed sheltered high density meadows, while the lowest values were recorded in mixed disturbed sheltered low density meadow (Table 4, Fig 8). In the overall ecosystem scale, areas with high organic carbon storage were corresponding to the area where uniform meadows were (Fig 9), suggesting that bigger size species such as *E. acoroides* store more carbon than mixed species meadows, with medium size species. Their belowground parts are bigger, thicker, more robust and penetrate in much deeper layers of the sediment, up to 1 m depth (Marbà et al. 2010).

Total carbon storage per area in whole ecosystem highly varied as the area covered in seagrass was from 5 ha to 101.5 ha. The highest storage in ecosystem was in mixed undisturbed exposed meadows, while the lowest was in mixed disturbed sheltered meadows (Table 4).

Total carbon storage in ecosystems might be underestimated as it included only 5 seagrass meadows, excluding the meadows on the east coast and other meadows along the west coast. Although total carbon storage is higher than reported in the region (Lavery et al. 2013; Supriadi et al. 2014; Phang et al. 2015) , it is still considerably lower than the global records (Fourqurean et al. 2012).

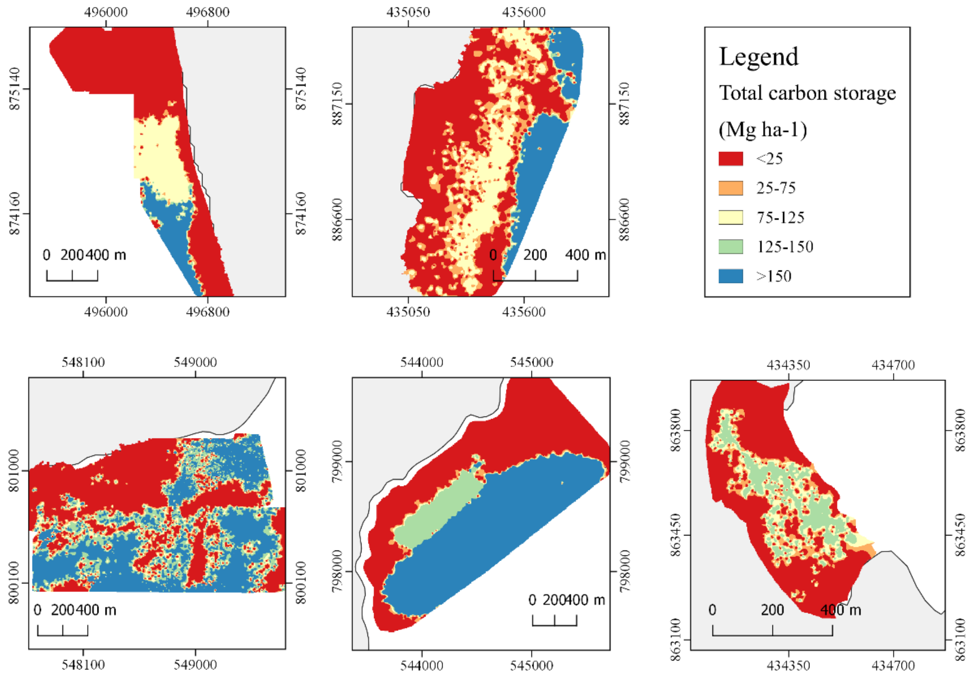


Figure 8. Map of the total carbon storage per hectare in each survey area

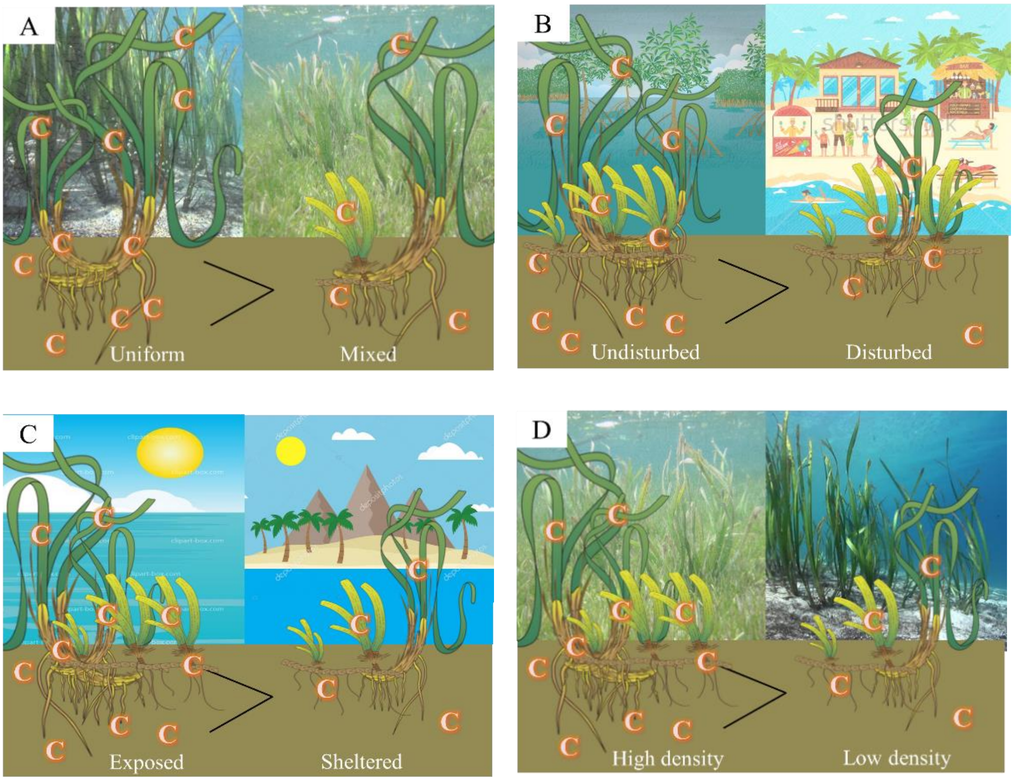


Figure 9. Trend of higher and lower organic carbon in seagrass ecosystems

Organic carbon storage in sediment and in living vegetation is recorded in Table 4 and 5, and it followed similar trend as the biomass (more detailed information about factors influencing organic carbon in the seagrass ecosystems is presented in Paper 3 – Appendix 3), with:

- Higher values in uniform than in mixed species meadows (Fig 10A)
- Higher values in undisturbed than in disturbed species meadows (Fig 10B)
- Higher values in exposed meadows comparing sheltered species meadow (Fig 10C)
- Higher values in high density areas than in low density area (Fig 10D)

Overall, meadow type highly influenced organic carbon storage. This suggests that structure, morphology of the species (Rozaimi et al. 2017) and species composition (Gillis et al. 2017) in the meadows are important factors which influence carbon storage and biomass in the ecosystem. Disturbance-geomorphology strongly influenced carbon storage in the seagrass meadows with undisturbed sheltered meadows supporting higher production and better ability to trap sediment. These meadows are under less influence of abiotic factors such as strong currents, waves and winds, and they together with limited human activity provide a suitable habitat for seagrass meadows. This reflects as a positive impact on the ecosystem health and services, thus increasing carbon sequestration and storage capacity in the meadows. The influence of the other environmental variables is presented in Paper 3 (Appendix 3).

4.2. FRAMEWORK 2: The status of the seagrass meadows, in terms of biomass and organic carbon, in the future climate change scenarios (Manuscript 1 – Appendix 4)

4.2.1. Seagrass area

Possible seagrass areas under RCP 4.5 and RCP 8.5 scenarios highly varied throughout the years. Unfortunately, future predictions for Tang Khen Bay were not possible, as the bay is very small and there was slight variation of the environmental factors, which was not enough to produce viable maps of the future seagrass areas. As many bays where seagrass meadows occur are small in size, using values of environmental factors from the satellites are not appropriate, so field data collection of them is necessary.

A. RCP 4.5 scenario

In 2025, lowest recorded area was in uniform disturbed exposed meadows, while the highest recorded area was in mixed undisturbed exposed meadows (Table 4). In 2050, the seagrass area of uniform disturbed exposed meadow will disappear from the surrounding area, while the mixed undisturbed exposed meadow will, continue to grow (Table 5). In 2075, uniform undisturbed sheltered seagrass meadow will as well disappear from the possible surrounding area, while mixed undisturbed exposed meadow will have the highest recorded area (Table 5). The probable seagrass distributions in the next 7, 32 and 57 years are presented on Fig 11, Fig 12 and Fig 13, respectively.

Table 5. Seagrass area in the future climate under RCP 4.5 scenario

Survey area			Seagrass area (ha)		
			2025	**2050**	**2075**
Disturbed	Exposed	Uniform	1.1	0	0
		Mixed	46.4	55.5	61.2
	Sheltered	Uniform	28.8	46.8	50.32
		Mixed	44.0	62.0	65.9
Undisturbed	Exposed	Uniform	27.0	12.6	9.8
		Mixed	172.5	204.6	211.7
	Sheltered	Uniform	57.2	5.1	0
		Mixed	26.1	39.8	50.8

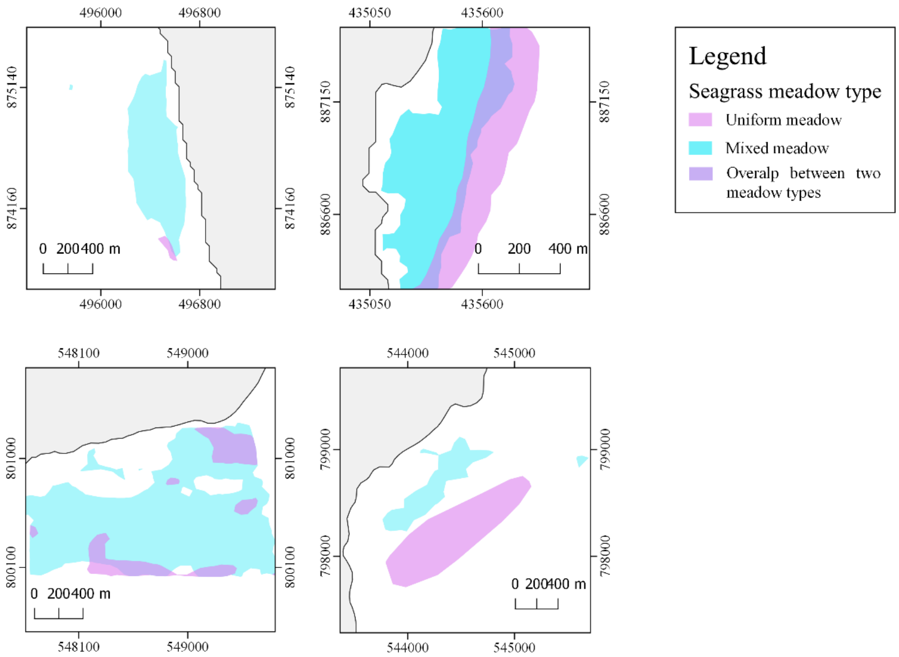


Figure 10. Seagrass area and meadow type in 2025 under RCP 4.5 climate change scenario

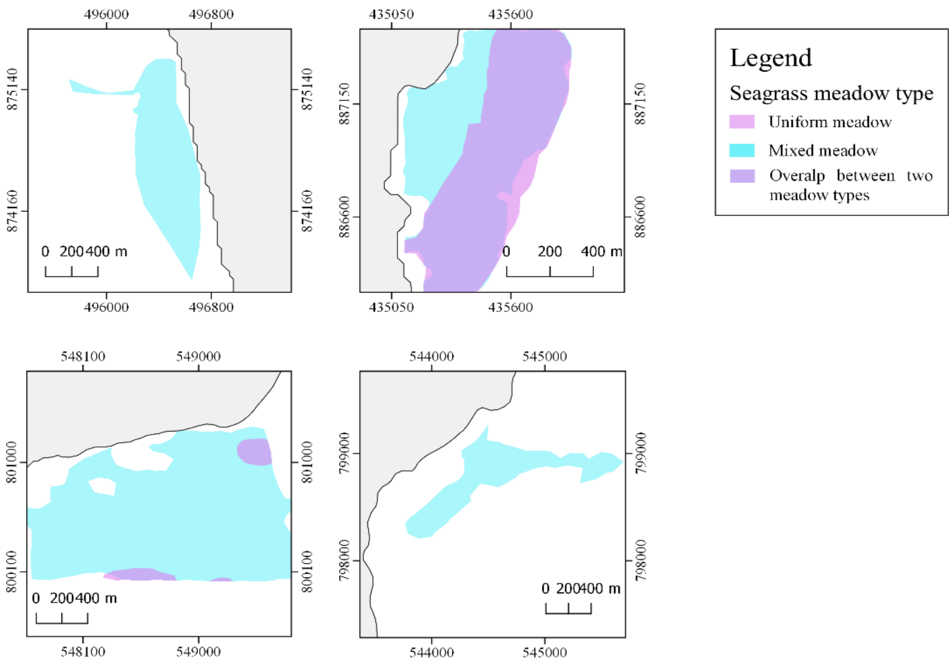


Figure 11. Seagrass area and meadow type in 2050 under RCP 4.5 climate change scenario (From Manuscript 1)

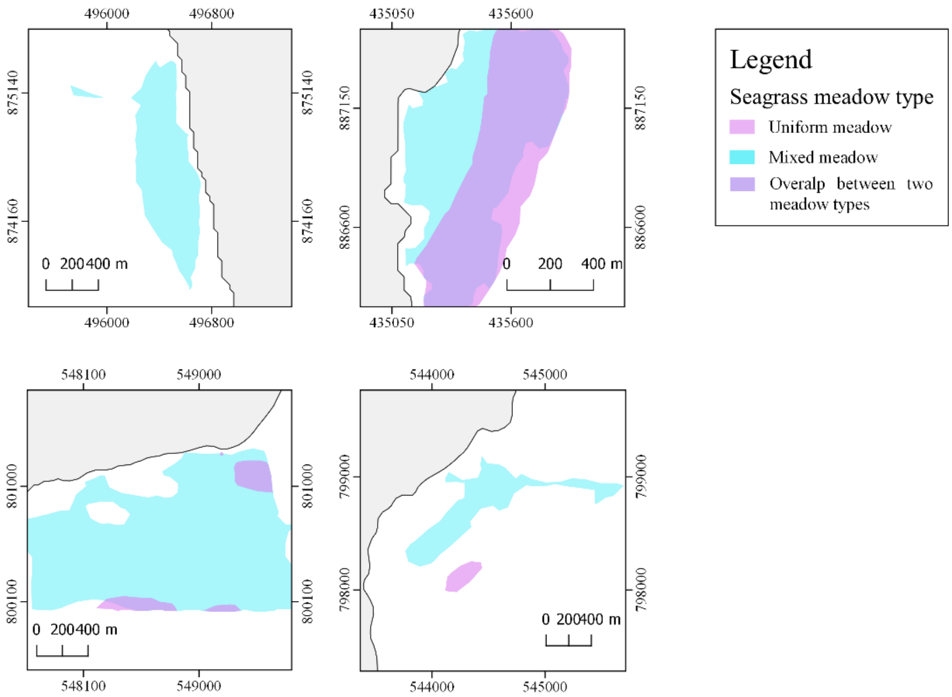


Figure 12. Seagrass area and meadow type in 2075 under RCP 4.5 climate change scenario (From Manuscript 1)

B. RCP 8.5 scenario

The lowest seagrass area in 2025 was in uniform disturbed exposed meadows, while the highest was in mixed undisturbed exposed meadow (Table 6). In 2050, the uniform disturbed exposed and undisturbed sheltered seagrass meadow disappeared from surrounding area, while mixed undisturbed meadow continued to expand (Table 6). In 2075, the area of uniform undisturbed exposed meadow decreased to only 8 ha, and it is highly probable that it will disappear from the area by 2100 (Table 6). The probable seagrass distribution in the year 2025, 2050 and 2075 are presented on Fig 14, Fig 15 and Fig 16, respectively.

Table 6. Seagrass area in the future climate under RCP 8.5 scenario

Survey area			**Seagrass area (ha)**		
			2025	**2050**	**2075**
Disturbed	Exposed	Uniform	0.3	0	0
		Mixed	48.5	61.8	64.3
	Sheltered	Uniform	32.8	70.5	71.0
		Mixed	48.3	53.7	64.9
Undisturbed	Exposed	Uniform	23.4	10.8	8.0
		Mixed	173.3	199.8	201.0
	Sheltered	Uniform	40.9	0	0
		Mixed	33.6	52.8	66.4

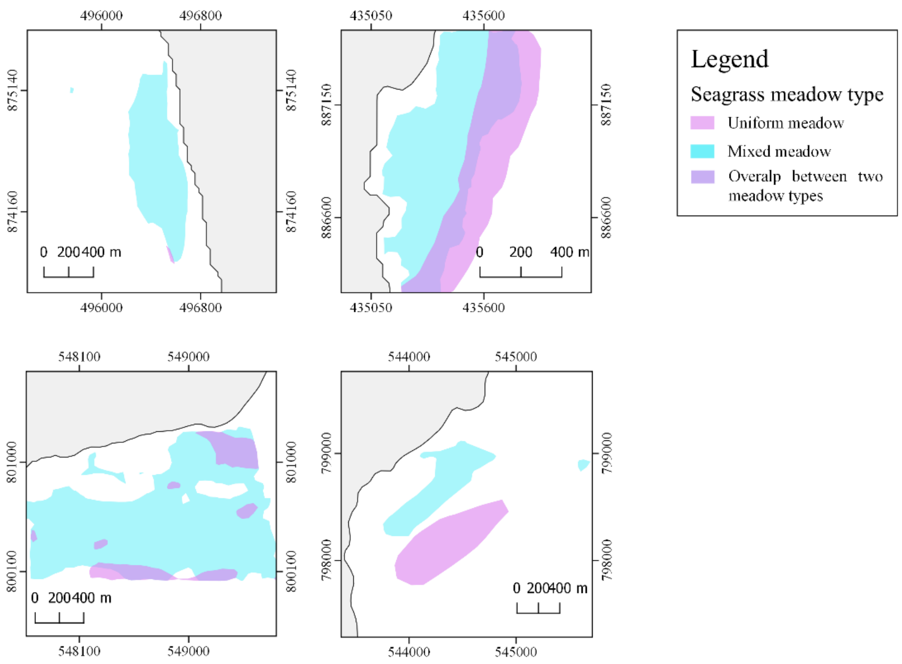


Figure 13. Seagrass area and meadow type in 2025 under RCP 8.5 climate change scenario (From Manuscript 1)

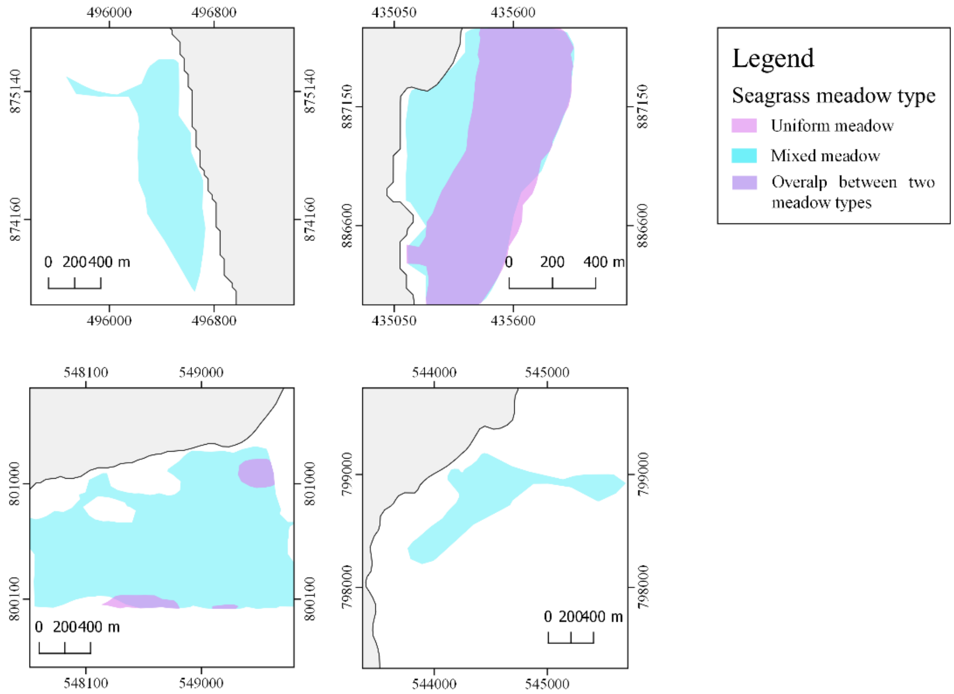


Figure 14. Seagrass area and meadow type in 2050 under RCP 8.5 climate change scenario (From Manuscript 1)

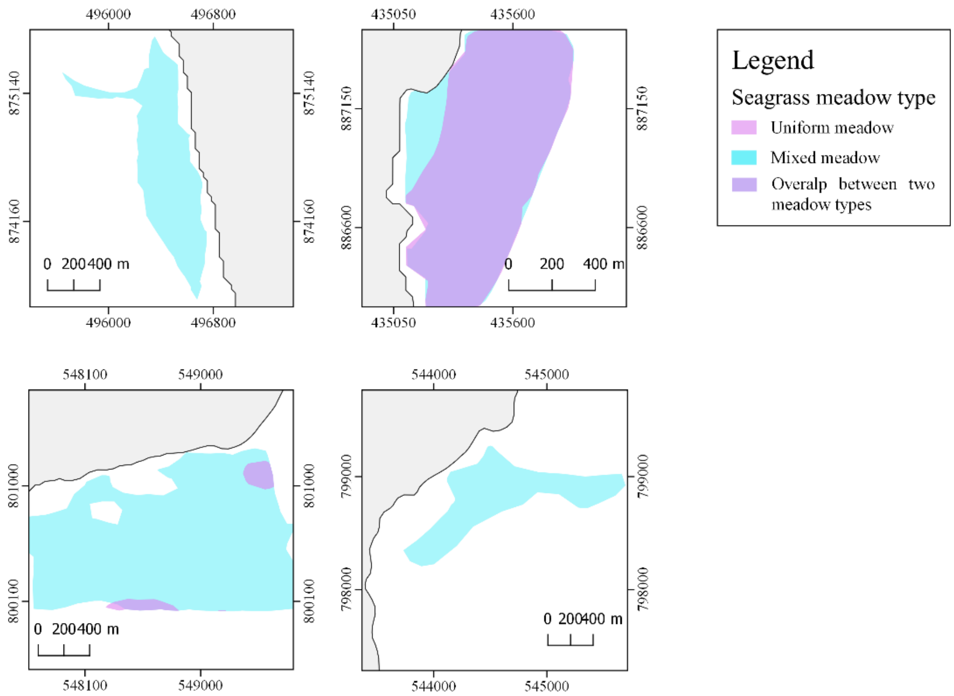


Figure 15. Seagrass area and meadow type in 2075 under RCP 8.5 climate change scenario (From Manuscript 1)

The area of the uniform and mixed meadows in some survey areas overlapped (Fig 11–16). Two types of overlapping were identified: overlapping in newly expanded areas, and in already occupied areas. Area overlap in newly expanded areas was recorded where in present time this was barren sand, while in the future this area could be occupied by both meadow types. In 2025, 2050 and 2075 at Pa Klok, Koh Sriboya, areas of uniform and mixed meadows expressed overlap in newly expanded areas, suggesting that these areas have suitable habitat characteristics for both types of the meadow to occupy. On the other hand, overlap areas in already occupied areas was identified as the area which was occupied by one meadow type in present time and in future prediction it provides suitable habitat for both meadow types. In the case of Libong site 1, the mixed species meadows are predicted to take over the area of uniform meadows even when uniform meadows are predicted inhabit the same area (Fig 11–16). In both overlapping cases there would be a competition between meadow types. The species in these meadows can be classified as persistent (*E. acoroides* and *T. hemprichii*) and opportunistic (*C. serrulata* and *C. rotundata*), based on their shoot turnover, genetic persistence, time to reach sexual maturity and seed dormancy (Kilminster et al. 2015). The opportunistic species have higher growth, elongation rates as well higher recruitment rate (Vermaat et al. 1995), which increases their ability to occupy newly expanded areas. Moreover, in the mixed meadows there is a positive “tradeoff” between the species, where each species is promoting the growth of the other one (Duarte et al. 2000).

Since mixed meadows consist of higher number of seagrass individuals of opportunistic species, there is high probability that they would occupy the overlapping areas in both cases.

As seen on the figures, the type of the meadow influenced on the trend of the seagrass:

- Uniform species meadows decreased throughout the years (Fig 17A)
- Mixed species meadows increased throughout the years (Fig 17B)

Although climate change provided suitable habitats for both meadow types, they had opposite trends. Mixed species meadow increased their area throughout the years, as these meadows consist of two species which provide positive “tradeoff” to each other. The studies in the mixed meadows showed that the shoot density of one species decreases when the other species are removed from the meadow (Duarte et al. 2000) On the other hand, uniform meadows were decreasing their area throughout the years in the future. This trend is probably due to intraspecific competition, as the study showed that leaf characteristics increase with the decrease of the number of shoots (Rattanachot et al. 2016).

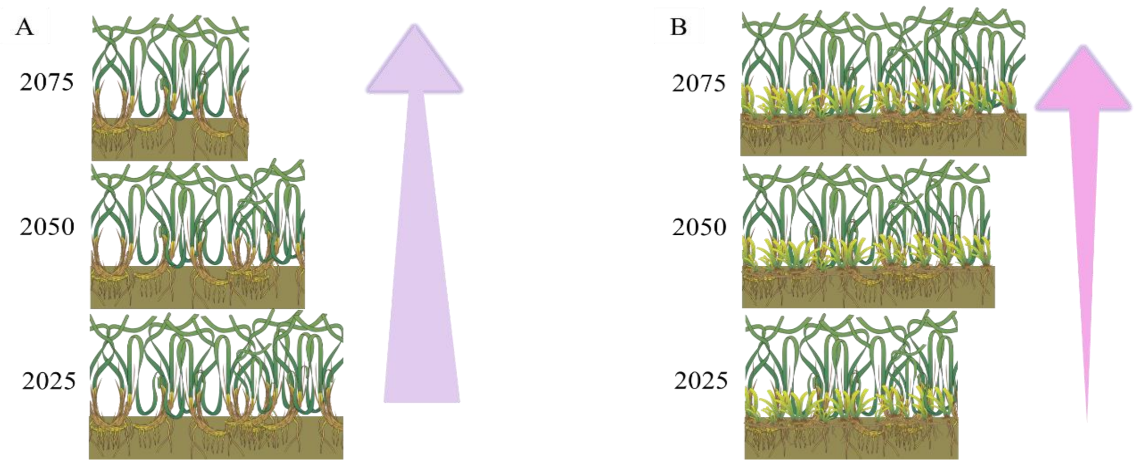


Figure 16. Seagrass area trend in uniform (A) and mixed (B) meadows

4.2.2. Biomass

A. RCP 4.5

Total, above- and belowground biomass on ecosystem scale highly varied among the survey areas (Table 7). In all three predicted years, it was the highest in mixed undisturbed exposed meadow, as this area expanded the most. On the other hand, the lowest values were in uniform disturbed exposed in 2025 and 2050, while in 2075 this meadow type and uniform undisturbed sheltered disappeared from the area. The probable seagrass total biomass across the meadows in the years 2025, 2050 and 2075 are presented on Fig 18, Fig 19 and Fig 20, respectively.

Table 7. Total, above- and belowground biomass variation in whole ecosystem following RCP 4.5 scenario

Year	Survey area	Total biomass per area (g DW)	Aboveground biomass per area (g DW)	Belowground biomass per area (g DW)
2025	Uniform disturbed exposed	753.3	117.6	635.7
	Mixed disturbed exposed	1,6632.8	4,000.7	12,632.1
	Uniform disturbed sheltered	19,204.7	2,997.1	16,207.6
	Mixed disturbed sheltered	15,766.3	3,792.3	11,974.0
	Uniform undisturbed exposed	18,004.9	2,809.9	15,195.0
	Mixed undisturbed exposed	61,786.7	14,861.7	46,925.0
	Uniform undisturbed sheltered	38,162.9	5,955.7	32,207.1
	Mixed undisturbed sheltered	9,353.0	2,249.7	7,103.3
2050	Uniform disturbed exposed	0.0	0.0	0.0
	Mixed disturbed exposed	19,902.1	4,787.1	15,115.0
	Uniform disturbed sheltered	31,210.2	4,870.7	26,339.5
	Mixed disturbed sheltered	22,229.6	5,347.0	16,882.7
	Uniform undisturbed exposed	8,445.8	1,318.1	7,127.8
	Mixed undisturbed exposed	73,281.1	1,7626.5	55,654.6
	Uniform undisturbed sheltered	3,413.0	532.6	2,880.4
	Mixed undisturbed sheltered	14,258.7	3,429.7	10,829.0
2075	Uniform disturbed exposed	0.0	0.0	0.0
	Mixed disturbed exposed	21,925.2	5,273.7	16,651.5
	Uniform disturbed sheltered	33,543.3	5,234.8	28,308.5
	Mixed disturbed sheltered	23,615.4	5,680.3	17,935.1
	Uniform undisturbed exposed	6,572.7	1,025.7	5,546.9
	Mixed undisturbed exposed	7,5819.9	1,8237.2	5,7582.7
	Uniform undisturbed sheltered	0.0	0.0	0.0
	Mixed undisturbed sheltered	1,8215.5	4,381.4	13,834.1

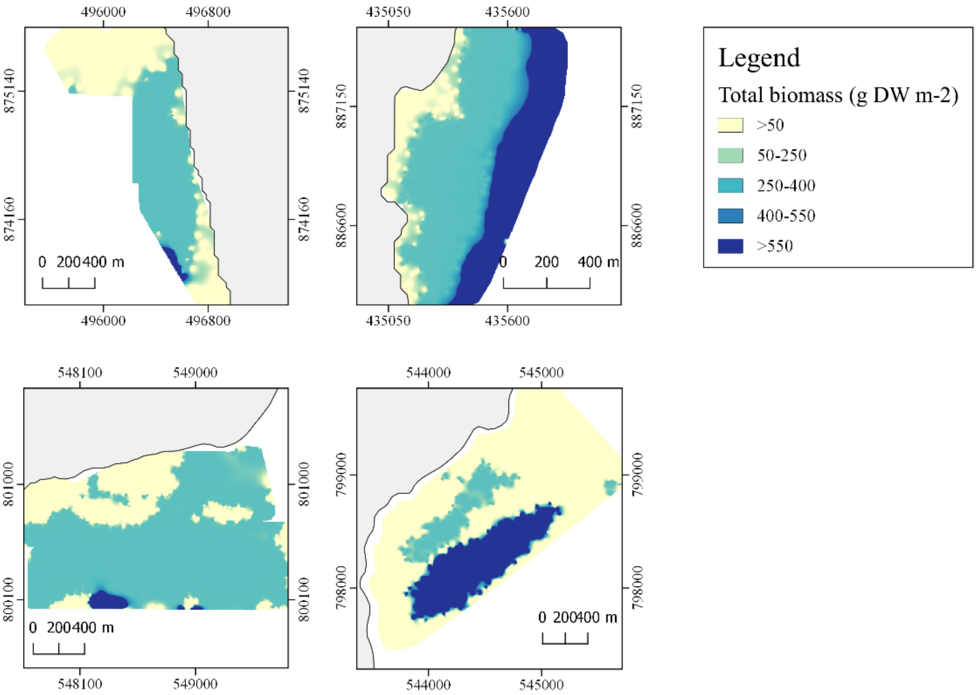


Figure 17. Seagrass total biomass in 2025 under RCP 4.5 climate change scenario

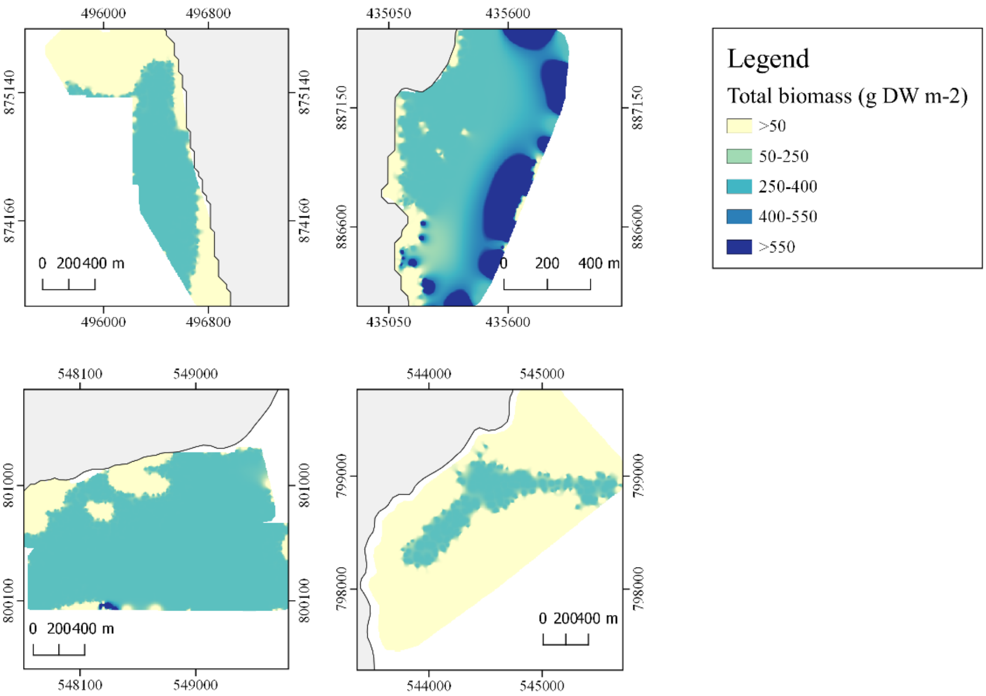


Figure 18. Seagrass total biomass in 2050 under RCP 4.5 climate change scenario

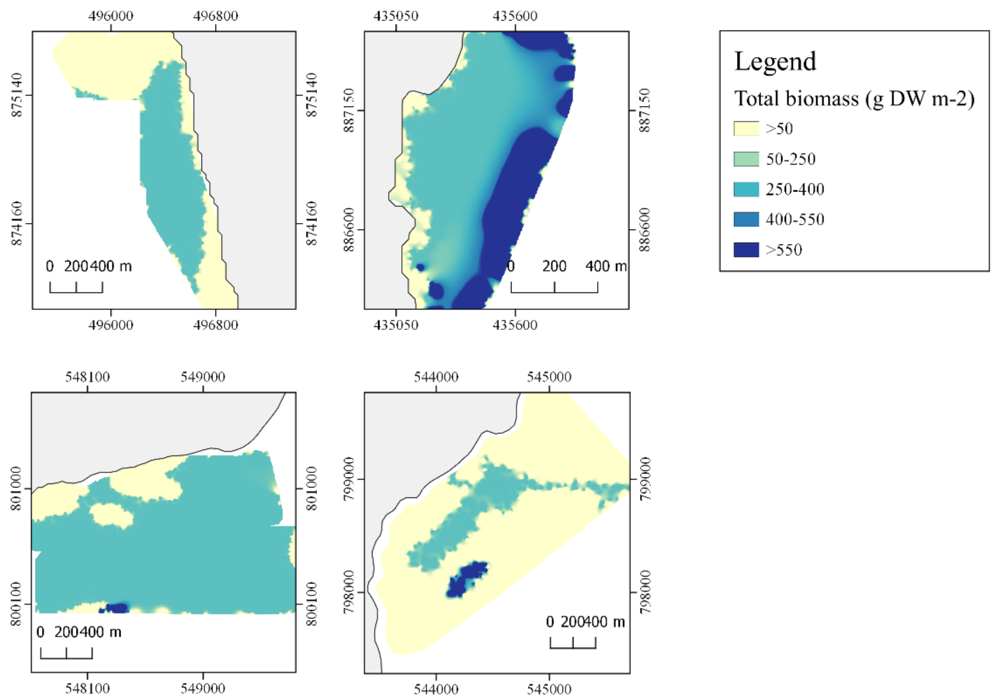


Figure 19. Seagrass total biomass in 2075 under RCP 4.5 climate change scenario

B. RCP 8.5

On the ecosystem scale, total, above- and belowground biomass varied among the survey areas (Table 8). In all three predicted years, same as in RCP 4.5, they were the highest in mixed undisturbed exposed meadows, as this area expanded the most. On the other hand, the lowest values were in uniform disturbed exposed in 2025, while in 2050 and 2075 this meadow type and uniform undisturbed sheltered disappeared from the area. The probable seagrass total biomass across the meadows in the years 2025, 2050 and 2075 are presented on Fig 21, Fig 22 and Fig 23, respectively.

Table 8. Total, above- and belowground biomass variation in whole ecosystem following RCO 8.5 scenario

Year	Survey area	Total biomass per area (g DW)	Aboveground biomass per area (g DW)	Belowground biomass per area (g DW)
2025	Uniform disturbed exposed	206.6	32.2	174.4
	Mixed disturbed exposed	1,7384.8	4,181.6	13,203.2

	Uniform disturbed sheltered	21,891.1	34,16.3	18,474.8
	Mixed disturbed sheltered	17,298.8	4,160.9	13,137.9
	Uniform undisturbed exposed	15,618.4	2,437.4	13,181.0
	Mixed undisturbed exposed	62,083.9	14,933.2	47,150.7
	Uniform undisturbed sheltered	27,277.3	4,256.9	23,020.4
	Mixed undisturbed sheltered	12,045.8	2,897.4	9,148.4
2050	Uniform disturbed exposed	0.0	0.0	0.0
	Mixed disturbed exposed	22,154.4	5,328.9	16,825.5
	Uniform disturbed sheltered	47,002.0	7,335.2	39,666.8
	Mixed disturbed sheltered	19,228.9	4,625.2	14,603.7
	Uniform undisturbed exposed	7,212.6	1,125.6	6,087.0
	Mixed undisturbed exposed	71,565.9	1,7213.9	54,351.9
	Uniform undisturbed sheltered	0.0	0.0	0.0
	Mixed undisturbed sheltered	18,935.3	4,554.6	14,380.7
2075	Uniform disturbed exposed	0.0	0.0	0.0
	Mixed disturbed exposed	23,046.0	5,543.3	17,502.7
	Uniform disturbed sheltered	47,381.9	7,394.5	39,987.5
	Mixed disturbed sheltered	23,271.6	5,597.6	17,674.0
	Uniform undisturbed exposed	5,339.5	833.3	4,506.2
	Mixed undisturbed exposed	75,916.5	18,260.4	57,656.1
	Uniform undisturbed sheltered	0.0	0.0	0.0
	Mixed undisturbed sheltered	23,801.6	5,725.1	18,076.5

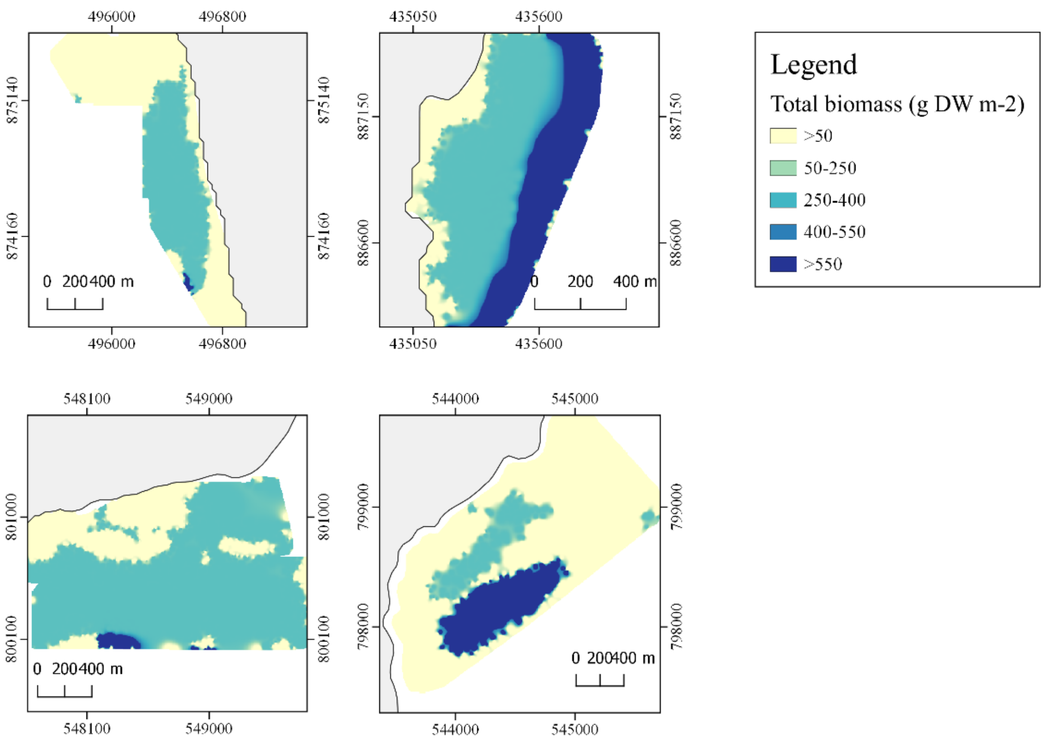


Figure 20. Seagrass total biomass in 2025 under RCP 8.5 climate change scenario

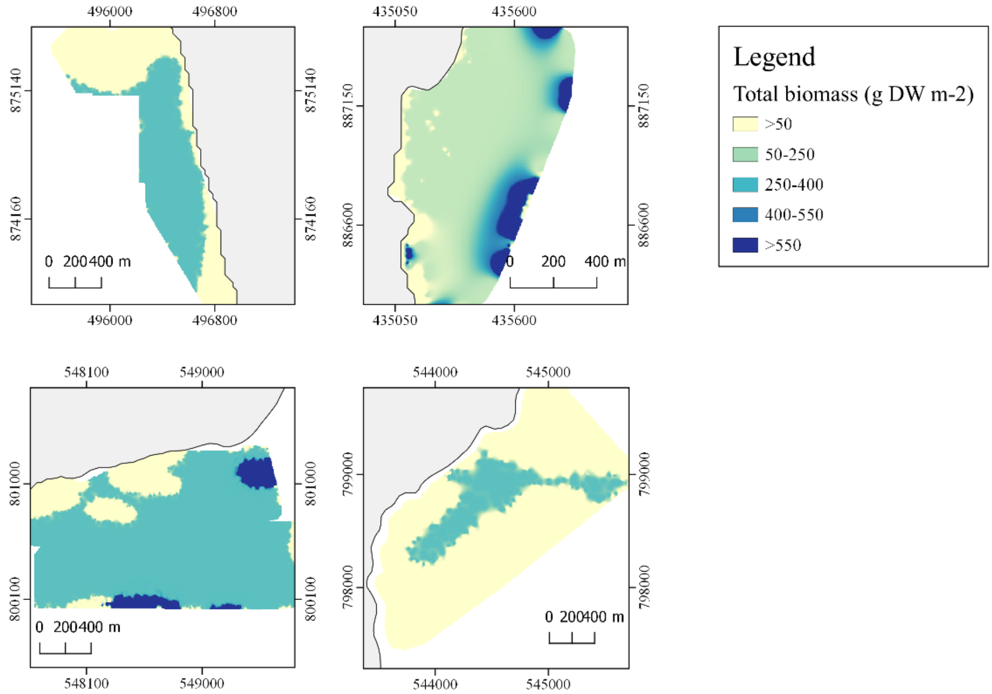


Figure 21. Seagrass total biomass in 2050 under RCP 8.5 climate change scenario

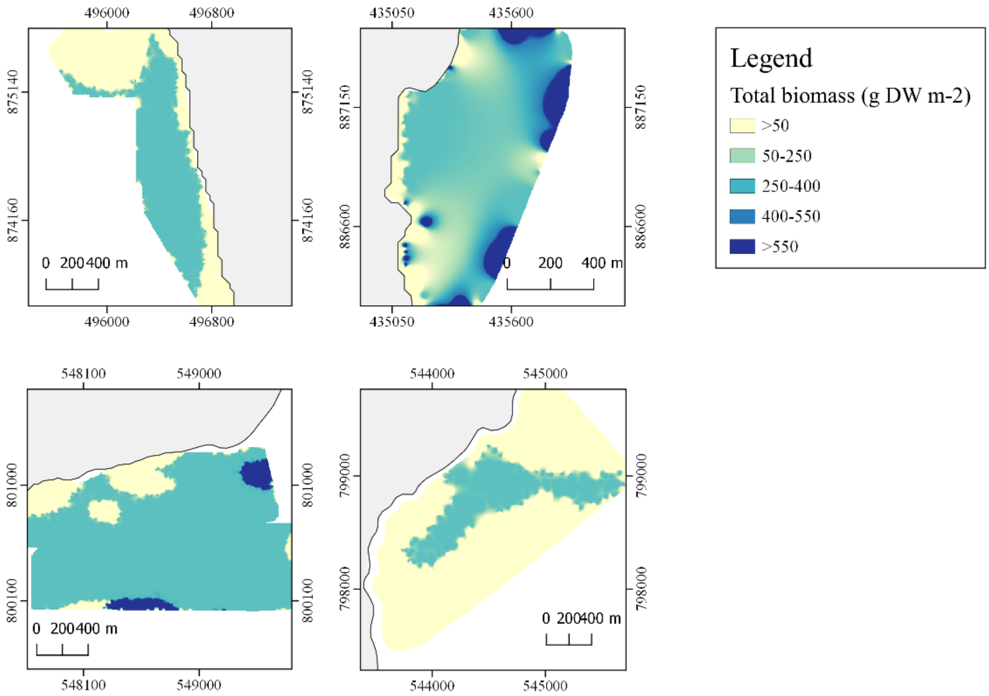


Figure 22. Seagrass total biomass in 2075 under RCP 8.5 climate change scenario

In the similar manner as the biomass in present time, the total biomass in the future years followed the same trend that: high biomass areas were corresponding to the areas of uniform meadow (with *E. acoroides*), and lower biomass areas were corresponding to the areas of the mixed species meadows.

4.2.3. Organic carbon storage

A. RCP 4.5

Total, above- and belowground carbon in the living vegetation on ecosystem scale highly varied among the survey areas (Table 9). In all three predicted years, it was highest in mixed undisturbed exposed meadows, as this area expanded the most. On the other hand, the lowest values were in uniform disturbed exposed in 2025, while in 2050 this meadow type disappeared from the area. In 2075, uniform undisturbed sheltered meadow disappeared from the area as well. The probable seagrass total carbon in the living vegetation across the meadows in the years 2025, 2050 and 2075 are presented on Fig 24, Fig 25 and Fig 26, respectively.

Table 9. Variation of total (above- and belowground) carbon in living vegetation, sedimentary organic carbon and total organic carbon storage (carbon in vegetation and in sediment) in whole ecosystem following RCP 4.5

Year	Survey area	Total carbon in living vegetation per area (Mg C)	Aboveground carbon in living vegetation per area (Mg C)	Belowground carbon in living vegetation per area (Mg C)	Organic carbon in sediment per area (Mg C)	Total organic carbon storage per area (Mg C)
2025	Uniform disturbed exposed	11.2	1.8	9.3	224.5	235.6
	Mixed disturbed exposed	226.7	53.0	173.7	6,342.3	6,549.5
	Uniform disturbed sheltered	284.4	46.4	238.0	5,722.5	6,006.9
	Mixed disturbed sheltered	214.9	50.2	164.7	6,011.9	6,208.2
	Uniform undisturbed exposed	266.6	43.5	223.1	5,365.0	5,631.6
	Mixed undisturbed exposed	842.0	196.7	645.3	23,560.0	24,329.6
	Uniform undisturbed sheltered	565.1	92.2	472.9	11,371.6	11,936.6
	Mixed undisturbed sheltered	127.5	29.8	97.7	35,66.4	3,682.9
2050	Uniform disturbed exposed	0.0	0.0	0.0	0.0	0.0
	Mixed disturbed exposed	271.2	63.4	207.9	7,588.9	7,836.8
	Uniform disturbed sheltered	462.1	75.4	386.7	9,299.9	9,762.0
	Mixed disturbed sheltered	303.0	70.8	232.2	8,476.4	8,753.3
	Uniform undisturbed exposed	125.1	20.4	104.7	2,516.6	2,641.7
	Mixed undisturbed exposed	998.7	233.3	765.4	27,942.9	28,855.7
	Uniform undisturbed sheltered	50.5	8.2	42.3	1,017.0	1,067.5
	Mixed undisturbed sheltered	194.3	45.4	148.9	5,437.0	5,614.6
2075	Uniform disturbed exposed	0.0	0.0	0.0	0.0	0.0
	Mixed disturbed exposed	298.8	69.8	229.0	8,360.3	8,633.4

	Uniform disturbed sheltered	496.7	81.0	415.6	9,995.1	1,0491.7
	Mixed disturbed sheltered	321.8	75.2	246.7	9,004.8	9,299.0
	Uniform undisturbed exposed	97.3	15.9	81.4	1,958.5	2,055.8
	Mixed undisturbed exposed	1033.3	241.4	791.9	28,911.0	29,855.3
	Uniform undisturbed sheltered	0.0	0.0	0.0	0.0	0.0
	Mixed undisturbed sheltered	248.2	58.0	190.3	6,945.8	7,172.7

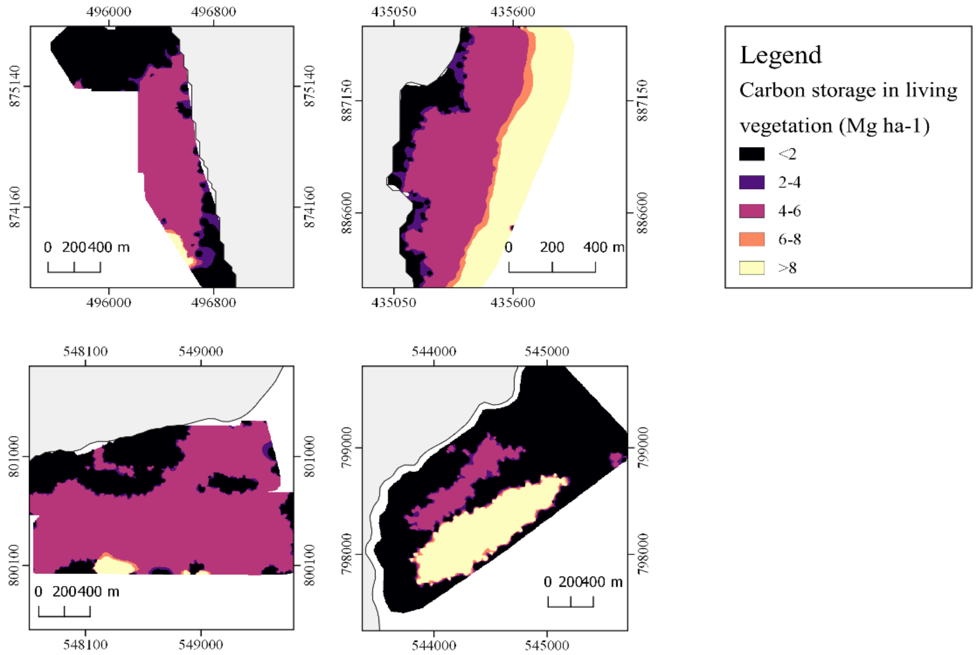


Figure 23. Seagrass total carbon storage in living vegetation in 2025 under RCP 4.5 climate change scenario

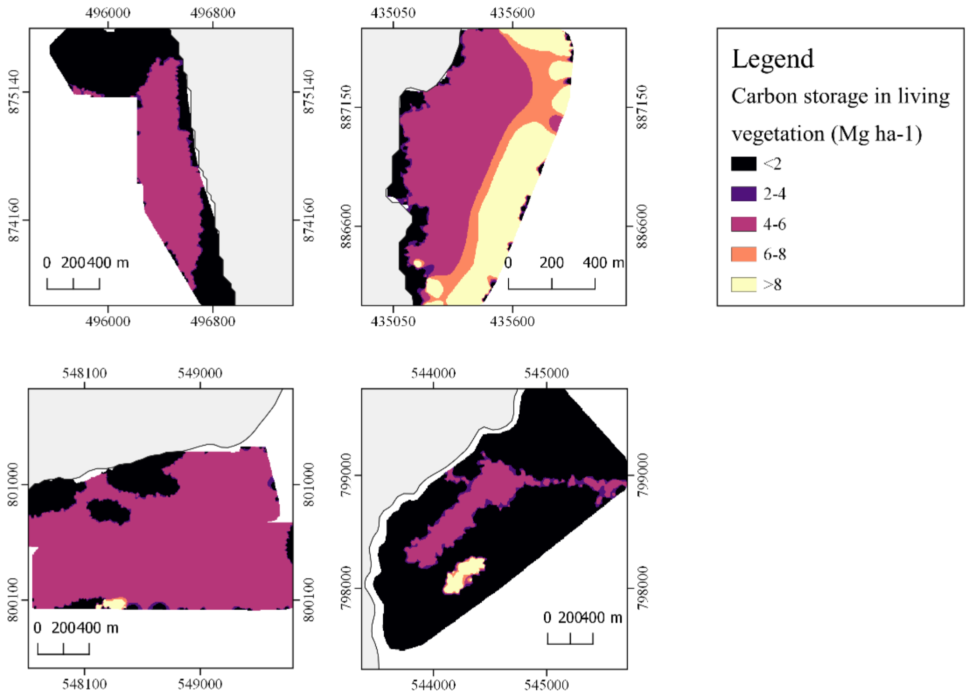


Figure 24. Seagrass total carbon storage in living vegetation in 2050 under RCP 4.5 climate change scenario

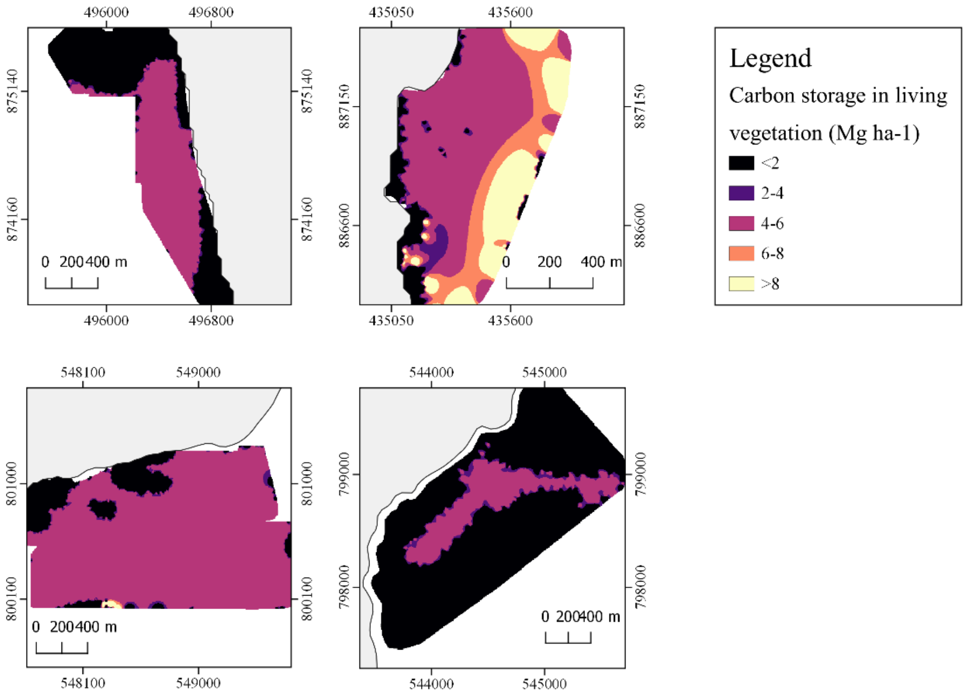


Figure 25. Seagrass total carbon storage in living vegetation in 2075 under RCP 4.5 climate change scenario

On ecosystem scale organic carbon in sediment highly varied among the survey areas (Table 9). It was the highest in mixed undisturbed exposed meadow, as this area expanded the most in all predicted years. On the other hand, the lowest values were in uniform disturbed exposed in 2025, while in 2050 this meadow type disappeared from the area. In 2075, uniform undisturbed sheltered meadow, as the previously mentioned meadow disappeared from the area.

Total organic carbon storage on the ecosystem scale varied as well between the survey areas (Table 9). It was the highest in mixed undisturbed exposed meadow, while the lowest values were in uniform disturbed exposed meadow in 2025. In 2050, this meadow type disappeared from the area, and in 2075, uniform undisturbed sheltered meadow disappeared from the area as well. The probable seagrass total organic carbon storage across the meadows in the 2025, 2050 and 2075 are presented on Fig 27, Fig 28 and Fig 29, respectively.

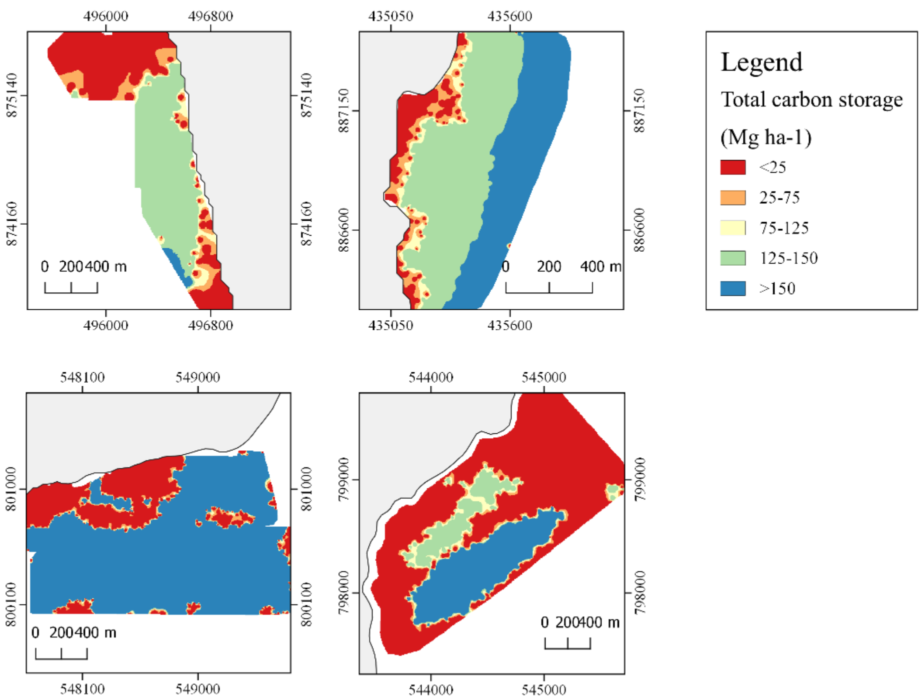


Figure 26. Total carbon storage in ecosystem in 2025 under RCP 4.5 climate change scenario

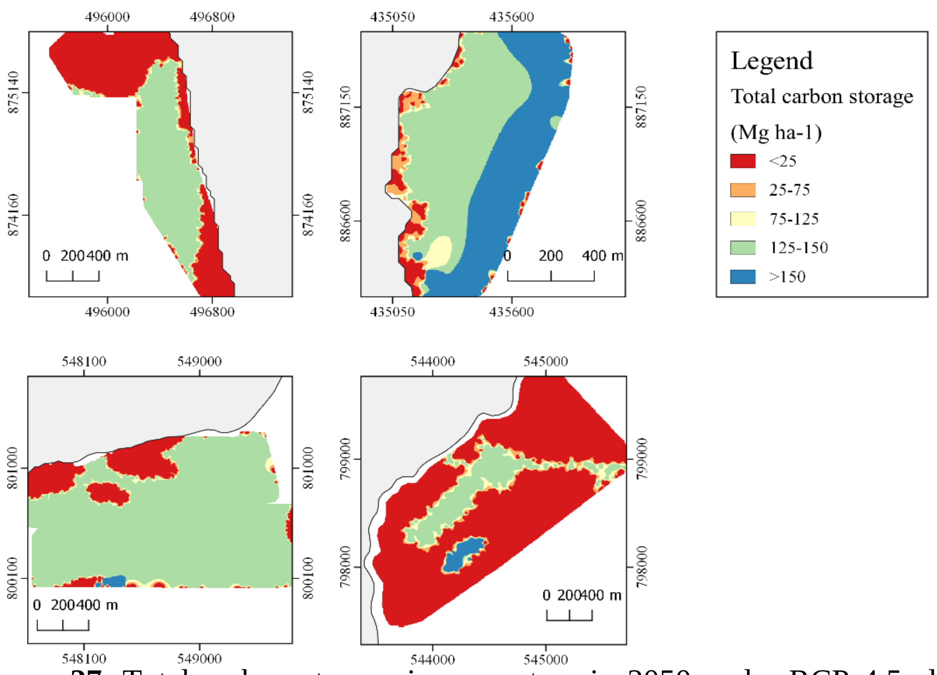


Figure 27. Total carbon storage in ecosystem in 2050 under RCP 4.5 climate change scenario

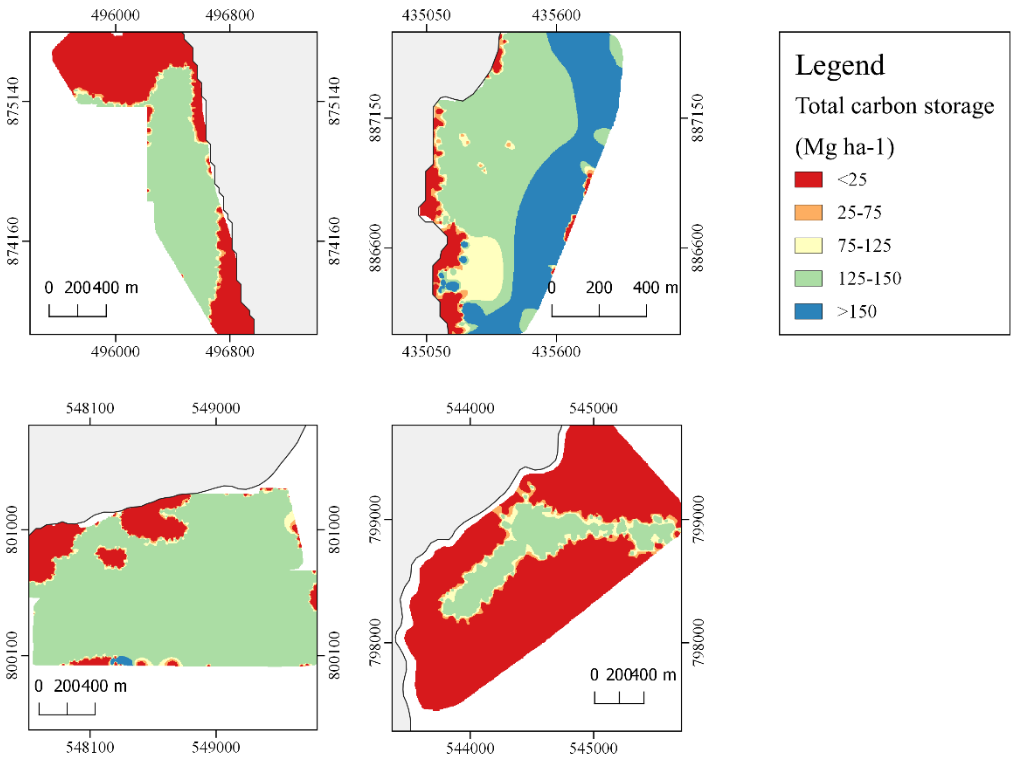


Figure 28. Total carbon storage in ecosystem in 2075 under RCP 4.5 climate change scenario

B. RCP 8.5

On ecosystem scale, total, above- and belowground carbon in the living vegetation varied between the survey areas (Table 10). In all predicted years, it was highest in mixed undisturbed exposed meadow, as this area expanded the most. On the other hand, the lowest values were in uniform disturbed exposed in 2025, while in 2050 this meadow type disappeared from the area. In 2075, uniform undisturbed sheltered meadow, same as previous meadow disappeared from the area. The probable seagrass total organic carbon storage within the living vegetation across the meadows in 2025, 2050 and 2075 are presented on Fig 30, Fig 31 and Fig 32, respectively.

Table 10. Variation of total (above- and belowground) carbon in living vegetation, sedimentary organic carbon and total organic carbon storage (carbon in vegetation and in sediment) in whole ecosystem following RCP 8.5

Year	Survey area	Total carbon in living vegetation per area (Mg C)	Aboveground carbon in living vegetation per area (Mg C)	Belowground carbon in living vegetation per area (Mg C)	Organic carbon in sediment per area (Mg C)	Total organic carbon storage per area (Mg C)
2025	Uniform disturbed exposed	3.1	0.5	2.6	61.6	64.6
	Mixed disturbed exposed	236.9	55.3	181.6	6,629.0	6,845.6
	Uniform disturbed sheltered	324.1	52.9	271.3	6,523.0	6,847.1
	Mixed disturbed sheltered	235.8	55.1	180.7	6,596.2	6,811.7
	Uniform undisturbed exposed	231.3	37.7	193.5	4,653.9	4,885.2
	Mixed undisturbed exposed	846.1	197.7	648.4	23,673.3	24,446.6
	Uniform undisturbed sheltered	403.9	65.9	338.0	8,127.9	8,531.8
	Mixed undisturbed sheltered	164.2	38.3	125.8	4,593.2	4,743.2
2050	Uniform disturbed exposed	0.0	0.0	0.0	0.0	0.0
	Mixed disturbed exposed	301.9	70.5	231.4	8,447.7	8,723.7
	Uniform disturbed sheltered	695.9	113.5	582.4	14,005.4	14,701.3

	Mixed disturbed sheltered	262.1	61.2	200.8	7,332.2	7,571.7
	Uniform undisturbed exposed	106.8	17.4	89.4	2,149.2	2,256.0
	Mixed undisturbed exposed	975.3	227.8	747.5	27,288.9	28,180.3
	Uniform undisturbed sheltered	0.0	0.0	0.0	0.0	0.0
	Mixed undisturbed sheltered	258.1	60.3	197.8	7,220.2	7,456.1
2075	Uniform disturbed exposed	0.0	0.0	0.0	0.0	0.0
	Mixed disturbed exposed	314.1	73.4	240.7	8,787.7	9,074.8
	Uniform disturbed sheltered	701.6	114.4	587.1	14,118.6	14,820.2
	Mixed disturbed sheltered	317.2	74.1	243.1	8,873.7	9,163.6
	Uniform undisturbed exposed	79.1	12.9	66.2	1,591.0	1,670.1
	Mixed undisturbed exposed	1034.6	241.7	792.9	28,947.8	29,893.4
	Uniform undisturbed sheltered	0.0	0.0	0.0	0.0	0.0
	Mixed undisturbed sheltered	324.4	75.8	248.6	9,075.8	9,372.3

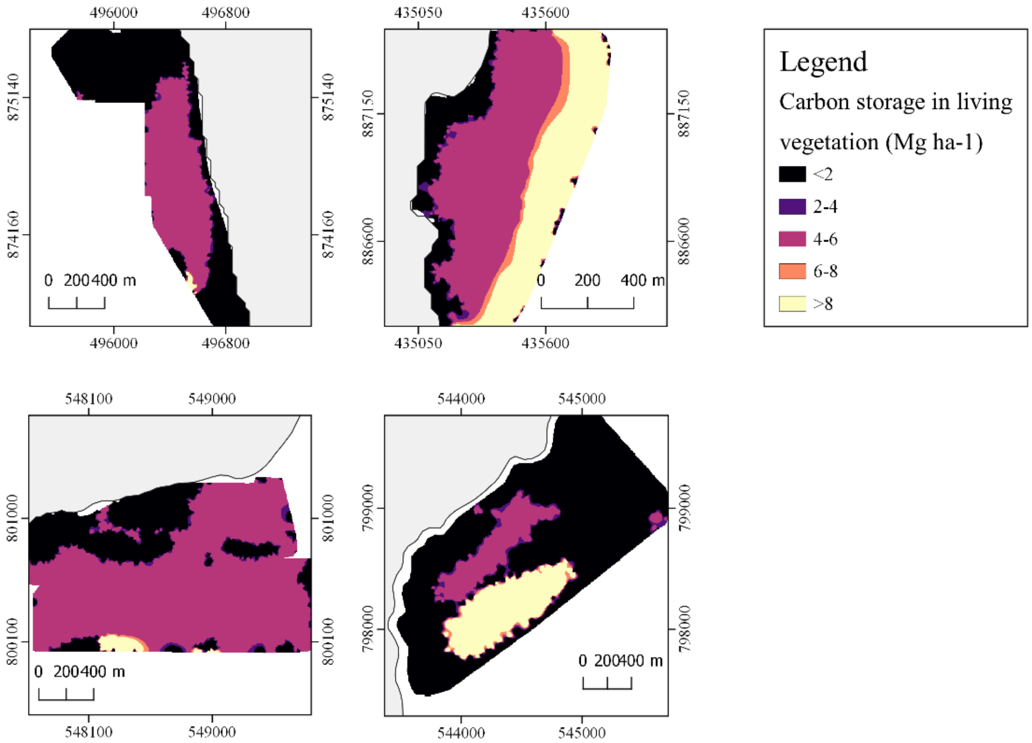


Figure 29. Seagrass total carbon storage in living vegetation in 2025 under RCP 8.5 climate change scenario

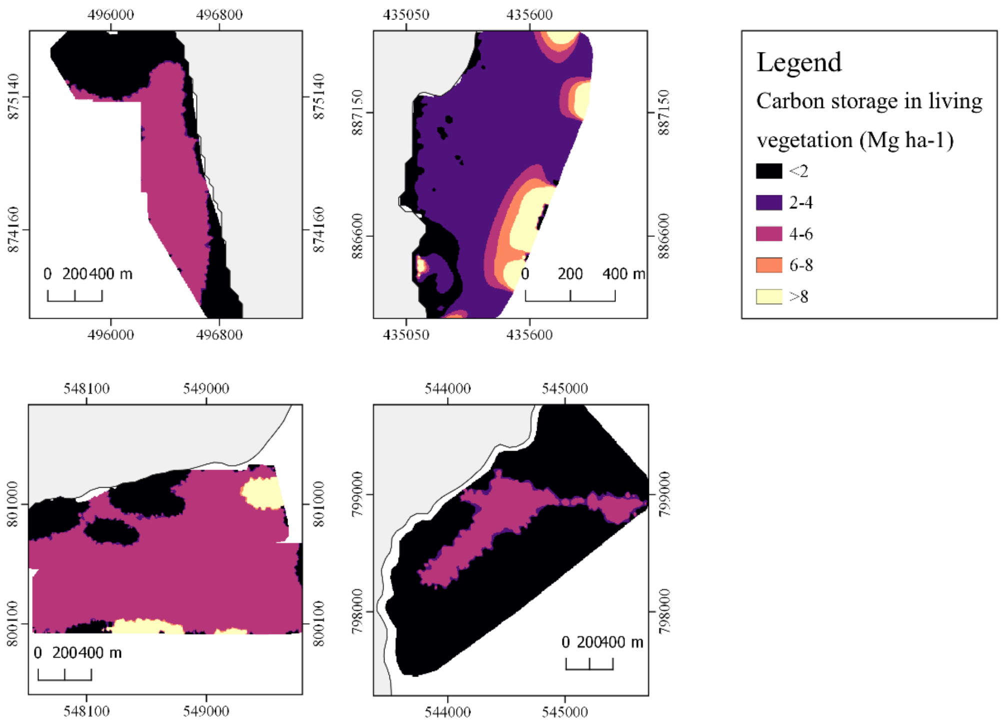


Figure 30. Seagrass total carbon storage in living vegetation in 2050 under RCP 8.5 climate change scenario

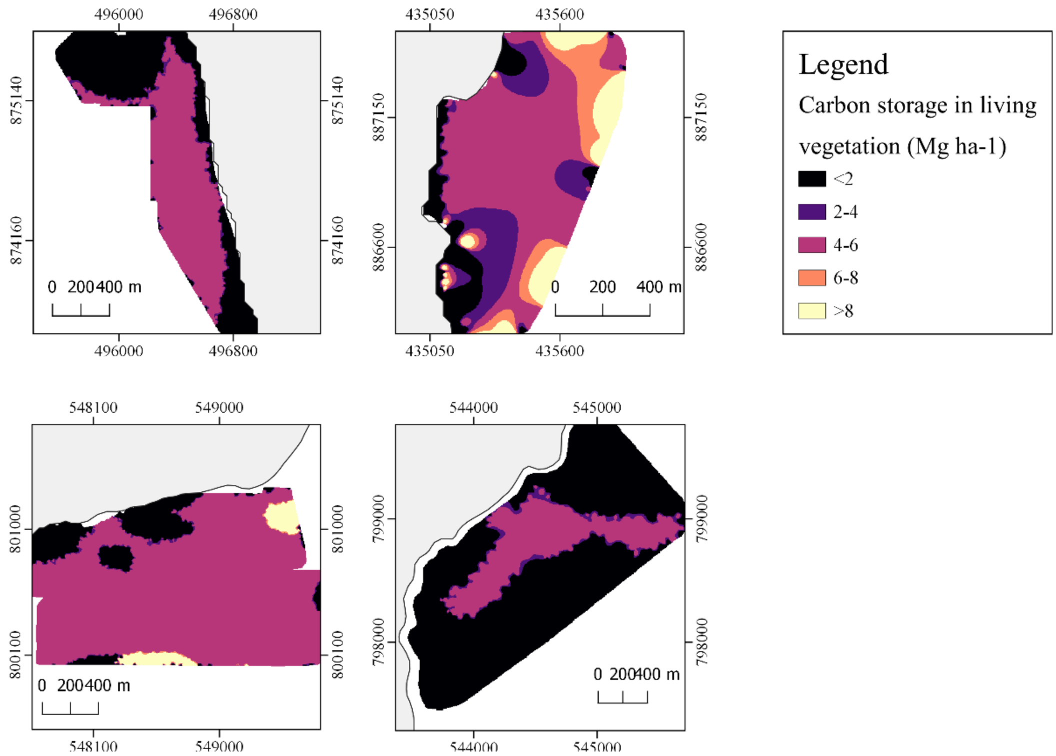


Figure 31. Seagrass total carbon storage in living vegetation in 2075 under RCP 8.5 climate change scenario

Organic carbon in sediment on the ecosystem scale varied among the survey areas (Table 10). In 2025, it was the highest in mixed undisturbed exposed meadows, and in 2025, it was the lowest in uniform disturbed exposed. In 2050 this meadow type disappeared from the area, and in 2075, uniform undisturbed sheltered meadow, as well disappeared from the area.

Total organic carbon storage on the ecosystem scale varied, as well between the survey areas (Table 10). It was the highest in mixed undisturbed exposed meadows, while the lowest values were in uniform disturbed exposed in 2025. In 2050, this meadow type disappeared from the area, and in 2075, uniform undisturbed sheltered meadow disappeared from the area. The probable seagrass total organic carbon storage across the meadows in 2025, 2050 and 2075 are presented on Fig 33 Fig 34 and Fig 35, respectively.

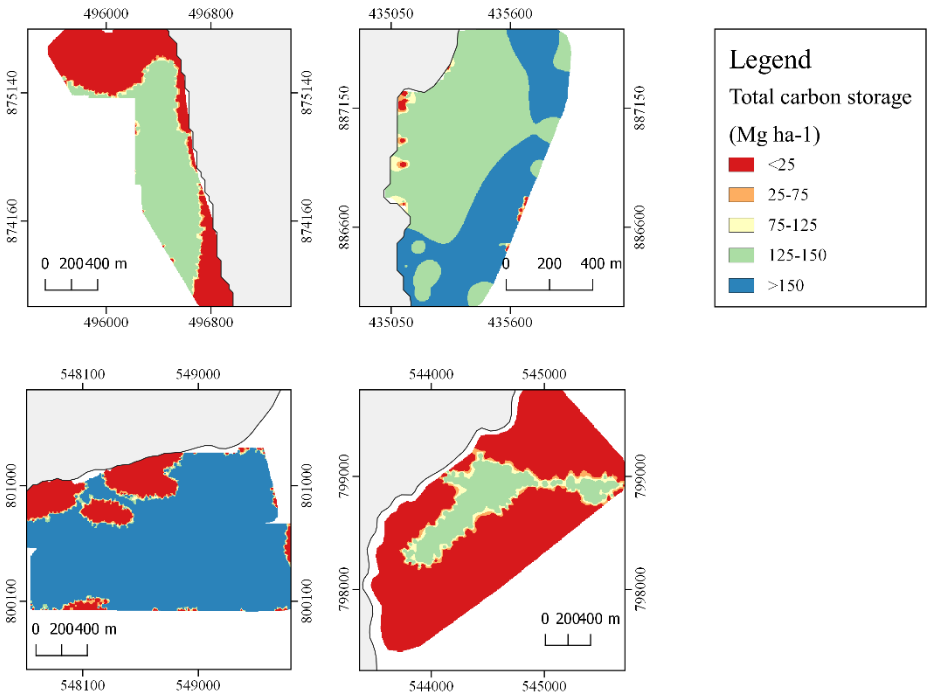


Figure 32. Total carbon storage in ecosystem in 2025 under RCP 8.5 climate change scenario

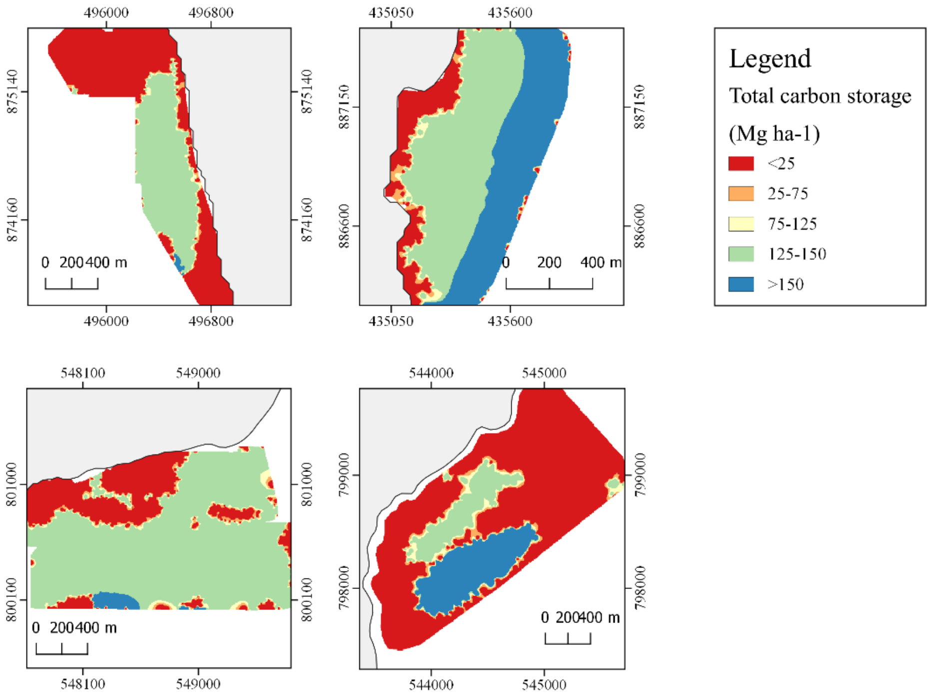


Figure 33. Total carbon storage in ecosystem in 2050 under RCP 8.5 climate change scenario

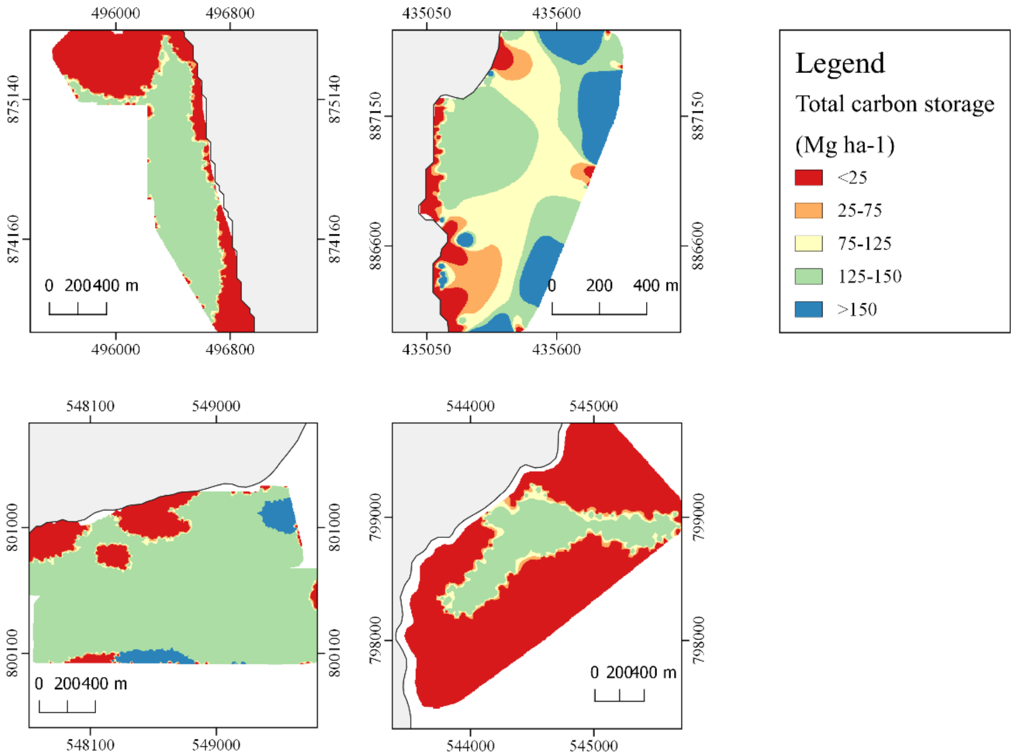


Figure 34. Total carbon storage in ecosystem in 2075 under RCP 8.5 climate change scenario

The loss of the meadow will not only affect carbon stored in the plants but more importantly it will trigger the release of the already buried carbon from the sediment (Marbà et al. 2015). The sediment becomes oxidized, stimulating the microbial remineralisation (Macreadie et al. 2014) and the stored carbon is released back into the ocean in the form of CO_2 (Fourqurean et al. 2012). The area of seagrass carbon sink becomes a major carbon source. The increase of the CO_2 concentration of ocean will disturb the equilibrium between air and water and by a direct ocean-atmosphere exchange the CO_2 of the atmosphere will be affected.

4.3. FRAMEWORK 3: Estimations of the lost, gained organic carbon and biomass and its emissions/assimilations

4.3.1 Seagrass area

The area of seagrass meadows varied throughout the years. Table 11 summarizes the increase (positive value) or decrease (negative value) of the seagrass area throughout the years in both RCPs. The biggest seagrass expansion was recoded in mixed undisturbed exposed, while the largest decrease in the meadow area was in uniform disturbed exposed (Table 10).

The expansions and losses of the meadow area had different trend based on the type of the meadow:

- In uniform meadows there was an increase of the area in 2025, followed by the decrease in 2050 and 2075 (Fig 36A)
- In mixed meadows there was constant increase of the seagrass area throughout the years (Fig 36B).

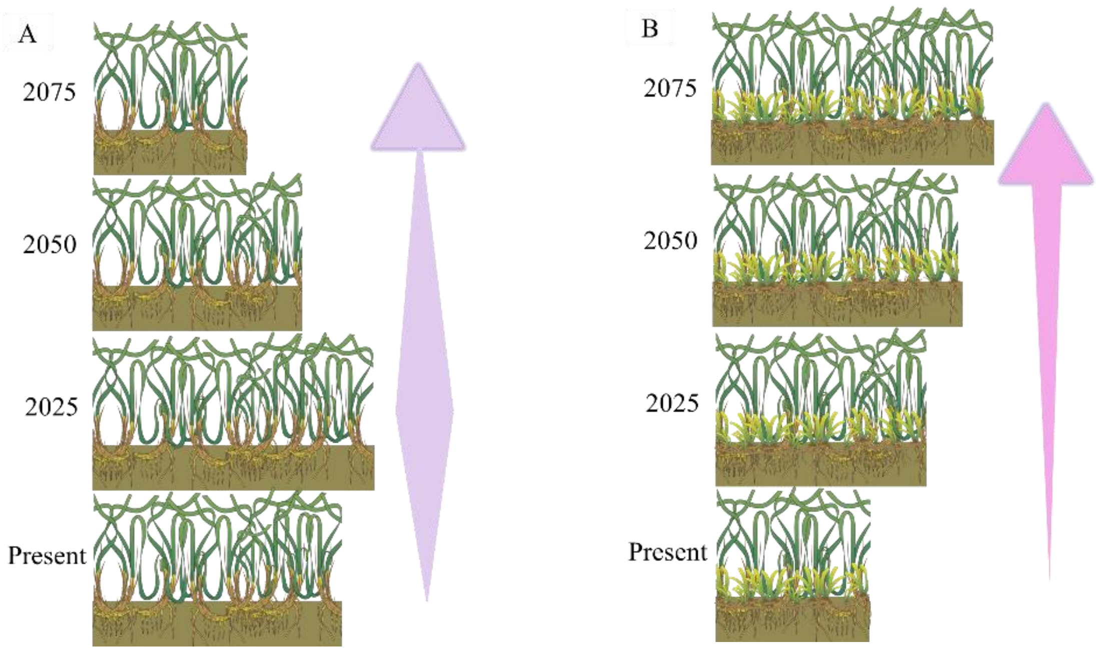


Figure 35. Trend of seagrass area change from present until 2075

Table 11. Seagrass area change throughout the years in RCP 4.5 and 8.5

Climate change scenario	**Year**	**Survey areas**	**Seagrass area change (ha)**
RCP 4.5	2025	Uniform disturbed exposed	-13.9
		Mixed disturbed exposed	444.3
		Uniform disturbed sheltered	276.3
		Mixed disturbed sheltered	434.8
		Uniform undisturbed exposed	252.3
		Mixed undisturbed exposed	1,623.9
		Uniform undisturbed sheltered	556.8
		Mixed undisturbed sheltered	248.1
	2050	Uniform disturbed exposed	-25.2
		Mixed disturbed exposed	535.6
		Uniform disturbed sheltered	456.4
		Mixed disturbed sheltered	615.3
		Uniform undisturbed exposed	108.9
		Mixed undisturbed exposed	1,944.9
		Uniform undisturbed sheltered	35.5
		Mixed undisturbed sheltered	385.1
	2075	Uniform disturbed exposed	-25.2
		Mixed disturbed exposed	592.1
		Uniform disturbed sheltered	491.4
		Mixed disturbed sheltered	654.0
		Uniform undisturbed exposed	80.8
		Mixed undisturbed exposed	2,015.8
		Uniform undisturbed sheltered	-15.7
		Mixed undisturbed sheltered	495.6
RCP 8.5	2025	Uniform disturbed exposed	-22.1
		Mixed disturbed exposed	465.3
		Uniform disturbed sheltered	316.6
		Mixed disturbed sheltered	477.6
		Uniform undisturbed exposed	216.5
		Mixed undisturbed exposed	1,632.2
		Uniform undisturbed sheltered	393.5
		Mixed undisturbed sheltered	323.3
	2050	Uniform disturbed exposed	-25.2
		Mixed disturbed exposed	598.5
		Uniform disturbed sheltered	693.3
		Mixed disturbed sheltered	531.5

		Uniform undisturbed exposed	90.4
		Mixed undisturbed exposed	1,897.0
		Uniform undisturbed sheltered	-15.7
		Mixed undisturbed sheltered	515.7
	2075	Uniform disturbed exposed	-25.2
		Mixed disturbed exposed	623.4
		Uniform disturbed sheltered	699.0
		Mixed disturbed sheltered	644.4
		Uniform undisturbed exposed	62.3
		Mixed undisturbed exposed	2,018.5
		Uniform undisturbed sheltered	-15.7
		Mixed undisturbed sheltered	651.6

* Negative values indicate loss seagrass area, while positive suggest gain of the meadow area

4.3.2. Organic carbon

In some seagrass meadows there was a loss of sequestration ability (where the meadows decreased and/or disappeared), and in those areas stored organic carbon in the ecosystem is being released back to the atmosphere or to adjacent ecosystems. On the other hand, as the meadows increases their extents, carbon storage in ecosystem increased. Table 12 summarizes the losses or gains of organic carbon in different meadow types. The biggest loss of carbon storage was recorded in uniform disturbed exposed meadow in all years, while the largest gain of carbon was in mixed disturbed sheltered meadow.

Table 12. Total organic carbon change in the seagrass meadows throughout the years in both climate change scenarios

Climate change scenario	Year	Survey areas	Total organic carbon change (Mg C)	Total organic carbon change (%)
RCP 4.5	2025	Uniform disturbed exposed	-749.6	-24.1
		Mixed disturbed exposed	62,980.1	2,504.8
		Uniform disturbed sheltered	58,647.4	4,125.7
		Mixed disturbed sheltered	61,791.8	21,270.8
		Uniform undisturbed exposed	54,035.8	2,369.9
		Mixed undisturbed exposed	23,0618.7	1,819.2

		Uniform undisturbed sheltered	116,761.2	4,482.0
		Mixed undisturbed sheltered	34,976.5	1,887.9
	2050	Uniform disturbed exposed	-3,105.6	-100.0
		Mixed disturbed exposed	75,853.4	3,016.8
		Uniform disturbed sheltered	96,198.2	6,767.4
		Mixed disturbed sheltered	87,242.3	30,031.8
		Uniform undisturbed exposed	24,136.9	1,058.6
		Mixed undisturbed exposed	275,879.7	2,176.3
		Uniform undisturbed sheltered	8,070.1	309.8
		Mixed undisturbed sheltered	54,293.5	2,930.5
	2075	Uniform disturbed exposed	-3,105.6	-100.0
		Mixed disturbed exposed	83,819.9	3,333.6
		Uniform disturbed sheltered	103,495.7	7,280.7
		Mixed disturbed sheltered	92,699.0	31,910.2
		Uniform undisturbed exposed	18,278.0	801.6
		Mixed undisturbed exposed	285,876.6	2,255.1
		Uniform undisturbed sheltered	-2,605.1	-100.0
		Mixed undisturbed sheltered	69,874.0	3,771.5
RCP 8.5	2025	Uniform disturbed exposed	-2,459.3	-79.2
		Mixed disturbed exposed	65,941.1	2,622.5
		Uniform disturbed sheltered	67,049.9	4,716.8
		Mixed disturbed sheltered	67,826.6	23,348.2
		Uniform undisturbed exposed	46,571.5	2,042.5
		Mixed undisturbed exposed	231,789.0	1,828.5
		Uniform undisturbed sheltered	82,713.1	3,175.0
		Mixed undisturbed sheltered	45,579.7	2,460.2
	2050	Uniform disturbed exposed	-3,105.6	-100.0
		Mixed disturbed exposed	847,22.3	3,369.5
		Uniform disturbed sheltered	145,591.9	10,242.1
		Mixed disturbed sheltered	75,426.5	25,964.4
		Uniform undisturbed exposed	20,279.6	889.4
		Mixed undisturbed exposed	269,125.8	2,123.0
		Uniform undisturbed sheltered	-2,605.1	-100.0
		Mixed undisturbed sheltered	72,708.1	3,924.4
	2075	Uniform disturbed exposed	-3,105.6	-100.0
		Mixed disturbed exposed	88,233.2	3,509.1
		Uniform disturbed sheltered	146,780.3	10,325.7
		Mixed disturbed sheltered	91,345.4	31,444.2
		Uniform undisturbed exposed	14,420.8	632.5
		Mixed undisturbed exposed	286,257.3	2,258.1
		Uniform undisturbed sheltered	-2,605.1	-100.0

		Mixed undisturbed sheltered	91,870.0	4,958.7

* Negative values indicate loss of the total organic carbon, while positive suggest gain of the total organic carbon in the ecosystem.

3.3.3 Emissions and assimilations

Many of the meadows, which store large amounts of organic carbon within their ecosystems, disappeared in the future climates, thus stored organic carbon stored was emitted back to the ocean and consequently to the atmosphere. The largest CO_2 emission was recorded in uniform disturbed exposed and uniform disturbed sheltered meadows (Table 13). In contrast, mixed meadows increased their carbon storage throughout the years, with the highest CO_2 assimilation in mixed undisturbed meadows (Table 13).

The released organic carbon from the ecosystems is in a form of CO_2, which increases the concentration of carbon dioxide in the ocean, and disturbs the equilibrium between air and water, in a manner that ocean is emitting increased concentration of inorganic carbon into the atmosphere. Although, the emissions of these seagrass meadows are large, they are below global average of 0.15 Pg CO_2 (Pendleton et al. 2012). On the other hand, with the extensions of the meadow areas, the equilibrium is shifted towards higher CO_2 absorption in the ocean from the atmosphere and decrease pf the carbon concentration in the atmosphere, consequently mitigating the climate change.

Table 13. Emission and assimilation of CO_2 in the seagrass meadows throughout the years in both climate change scenarios

Climate change scenario	Year	Survey areas	Emission/assimilation of CO_2 (Gg)
RCP 4.5	2025	Uniform disturbed exposed	-2.8
		Mixed disturbed exposed	231.1
		Uniform disturbed sheltered	215.2
		Mixed disturbed sheltered	226.8
		Uniform undisturbed exposed	198.3
		Mixed undisturbed exposed	846.4
		Uniform undisturbed sheltered	428.5
		Mixed undisturbed sheltered	128.4
	2050	Uniform disturbed exposed	-11.4
		Mixed disturbed exposed	278.4

		Uniform disturbed sheltered	353.0
		Mixed disturbed sheltered	320.2
		Uniform undisturbed exposed	88.6
		Mixed undisturbed exposed	1,012.5
		Uniform undisturbed sheltered	29.6
		Mixed undisturbed sheltered	199.3
	2075	Uniform disturbed exposed	-11.4
		Mixed disturbed exposed	307.6
		Uniform disturbed sheltered	379.8
		Mixed disturbed sheltered	340.2
		Uniform undisturbed exposed	67.1
		Mixed undisturbed exposed	1,049.2
		Uniform undisturbed sheltered	-9.6
		Mixed undisturbed sheltered	256.4
RCP 8.5	2025	Uniform disturbed exposed	-9.0
		Mixed disturbed exposed	242.0
		Uniform disturbed sheltered	246.1
		Mixed disturbed sheltered	248.9
		Uniform undisturbed exposed	170.9
		Mixed undisturbed exposed	850.7
		Uniform undisturbed sheltered	303.6
		Mixed undisturbed sheltered	167.3
	2050	Uniform disturbed exposed	-11.4
		Mixed disturbed exposed	310.9
		Uniform disturbed sheltered	534.3
		Mixed disturbed sheltered	276.8
		Uniform undisturbed exposed	74.4
		Mixed undisturbed exposed	987.7
		Uniform undisturbed sheltered	-9.6
		Mixed undisturbed sheltered	266.8
	2075	Uniform disturbed exposed	-11.4
		Mixed disturbed exposed	323.8
		Uniform disturbed sheltered	538.7
		Mixed disturbed sheltered	335.2
		Uniform undisturbed exposed	52.9
		Mixed undisturbed exposed	1,050.6
		Uniform undisturbed sheltered	-9.6
		Mixed undisturbed sheltered	337.2

* Negative values indicate emissions of CO_2 into the atmosphere, while positive suggest sequestration of CO_2 from the atmosphere

5. Concluding remarks

5.1. Organic carbon storage in seagrass ecosystems at the present time

Organic carbon storage in seagrass ecosystems was highly variable throughout the Andaman coast of Thailand. In comparison to the similar studies around Indo-Pacific, carbon storage in the ecosystem of this study is leaning towards the upper limit, suggesting that the seagrass meadows in Thailand area are healthier than in nearby countries. Healthy seagrass meadows have high areal extents, high densities and with that high abilities to trap and sequester carbon from the environment, consequently retaining and storing higher amounts of carbon within their ecosystems. Most of the organic carbon, 98%, in the ecosystem was stored in the sediment, while small amounts were stored within living vegetation. This ability of the seagrass distinguishes them as a crucial ecosystem in the climate change mitigation, since the sedimentary carbon is trapped until seagrass area is lost.

Uniform meadows had higher carbon storage than mixed ones, which is supporting the concept that bigger size, constant species, with slow turnover rate have higher ability to store organic carbon in the ecosystems. Their long living shoots have higher capacity to longer retain resources and increase the rate of carbon sequestration. Although, it has been suggested that canopy complexity increases storage capacities, via carbon trapping and sequestration, the results of this study did not demonstrate this concept. Disturbed meadows had much lower carbon storage in the ecosystem than undisturbed meadows, suggesting that anthropogenic disturbance has high impact on carbon storage in the ecosystem. The human activities, which include boat anchoring, destructive fishing gears and shell collection, and runoff from the nearby agricultural fields and housing areas, have direct and indirect influence on the seagrass meadows. The destructive fishing and shell collection include placing out the seagrasses due to the search of the invertebrates; while the runoff indirectly influences the seagrass ecosystem. The increase of runoff will decrease light availability which is an important factor for seagrass growth and production. Although it was expected that sheltered meadows should store more carbon in the ecosystem, the results suggested that both meadows (sheltered and exposed) had similar amounts of carbon storage in the ecosystem. As seagrass meadows are highly connected with adjacent ecosystems through organic matter flow, it is highly probable that the organic carbon has been transported to nearby ecosystems. Overall, undisturbed uniform meadows stored highest amount of carbon, suggesting that disturbance and meadow type highly affects carbon storage. These meadows are characterized with limited anthropogenic activities, which provide not only suitable environment, but without external limiting factors, for larger seagrass species to grow, to have higher production rates and expand their extents, which directly reflects on the carbon storage of the ecosystem. Thus these ecosystems are highly important, as the healthier meadows are not only characterized by the high carbon storage, but in the high ecosystem services as well.

The importance of this study is to set up a baseline knowledge for the carbon studies in Thailand, as well to appeal for proper management and conservation of the seagrass meadows. Moreover, the produced maps can assess the carbon “hot spot” areas, which can be incorporated in the carbon credit schemes.

5.2. Organic carbon storage in seagrass ecosystems in future

The results of this study indicated that uniform and mixed meadows have different trends of expansion/reduction of their areas throughout the years in the future. The organic carbon storage in the ecosystem is directly affected by the change of the seagrass area, as the loss of the seagrass meadows decreases the ability to trap and sequester carbon from environment and to retain sedimentary carbon. The results suggested that mixed meadows increased their areas throughout the years in the future, and consequently the carbon storage of the ecosystems increased. However, uniform meadows had different trend than mixed ones, as they expanded their extents by 2025 and then started to diminish. The increase of the area indicated the increase in carbon storage, while the loss of the gained and original area decreased the meadow’s ability to trap, sequester and store carbon. Furthermore, few of the uniform meadows completely disappeared, suggesting that there was a big loss of stored carbon in the ecosystem. However, the increase of the mixed meadows is higher than the loss of the uniform meadows, suggesting that the carbon storage capacity will increase throughout the years in the future. The large seagrass area in the future will have higher carbon assimilation rates, reducing the carbon from the ocean environment. Through ocean-atmosphere direct exchange the high carbon concentration from atmosphere will be assimilated into ocean, consequently reducing the CO_2 concentrations in the atmosphere. The reduced atmospheric carbon concentrations will decrease atmospheric temperature, consequently leading to the stabilization of the sea level and environment, thus mitigating the climate change.

Species distribution model created in this study had certain limitations, as it only included two environmental variables (SST and MSL). In order to create more tangible future predictions of the distribution of seagrass meadows other environmental variables need to be included. Moreover, anthropogenic influence model should be created as the seagrass meadows are highly affected by the run off from the coast in Southeast Asia. Predicting the future distribution of the seagrass meadows can be used to create conservation and management priorities in present time, so they can “avoid” specific scenario and not face total disappearance.

5.3. Assimilation and emission of organic carbon in the seagrass ecosystem

This study presented that seagrass meadows extended their areas in the future climates. Since most of the meadows followed this trend, trapping and sequestration of carbon from adjacent ecosystems had great importance. The carbon from ocean and coastal ecosystems is being transferred to the seagrass meadows and sequestered, trapped and retained in the living vegetation and sediment, providing them higher assimilation rates of carbon from the atmosphere. The high expansions of the seagrass meadows throughout the years, suggest that more carbon will be trapped in the sink and more carbon can be assimilated to the ocean and coastal ecosystems, thus reducing the overall carbon concentration in the atmosphere. The concentrations of carbon in atmosphere will decrease, as it is being removed via natural carbon sinks, and consequently atmospheric temperature and other climate change associated variables will be reduced. However, uniform meadows expressed the decrease and disappearance of their areas in the future, which released the trapped carbon to the ocean and atmosphere, increasing already high inorganic carbon concentrations and aggravate effects of climate change.

6. Recommendation for future studies

This study presented that the seagrass meadows can be used as natural carbon sinks, which meadow type stores the highest amounts of carbon, how seagrass meadow would behave facing climate change and what could we expect from these meadows in terms of carbon in the future. However, this study provided only the baseline for various carbon studies, as more information is needed specifically on:

1. Carbon flux of the seagrass meadow, so the complete picture of the carbon storage can be obtained. This information can be used to improve carbon prediction methodologies, which can be useful in the assessment of the carbon "hot spots", proper management and conservation. Moreover, the knowledge of the complete carbon cycle would provide a step forward in the incorporation of the coastal organic carbon in carbon credit schemes.

2. Integration of other environmental variables in the modeling of climate change methodologies. The climate change is associated with various environmental factors and their addition to the models is crucial to predict the seagrass distribution as tangible as possible. This would provide enough knowledge for management and set conservation priorities, so the meadows can "avoid" specific scenario of the severe loss of seagrass meadows.

3. Creating an anthropogenic influence model, as seagrass meadows in Southeast Asia are highly affected by the coastal erosion and nutrient overload. The results from this model, together with the results of this study can create a better picture of the fate of seagrass meadows in this region.

4. Obtaining the information of the other seagrass meadows in the upper Andaman coast and moreover in the Gulf of Thailand, so full and complete image of Thailand's seagrass meadows can be gained. This would provide an overview of the carbon in the country and its access, which could lead to the increase of Thailand's carbon budget and its integration to the compulsory carbon market.

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APPENDICES

Appendix 1 – Paper 1

Sains Malaysiana 46(9)(2017): 1441–1447
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Carbon Content in Different Seagrass Species in Andaman Coast of Thailand

(Kandungan Karbon dalam Pelbagai Spesies Rumpai Laut di Teluk Andaman, Thailand)

MILICA STANKOVIC*, JANMANEE PANYAWAI, KAMARUDIN JANSANIT, TIPAMAT UPANOI & ANCHANA PRATHEP

ABSTRACT

*Seagrass meadows have one of the highest carbon sequestration and storage capacities than any other ecosystems. Carbon that is stored in the ecosystem is accumulated in the deposited sediment as well as in the living, above and below ground biomass, with a different rate of carbon sequestration and storage between the species. The objective of this research was to investigate carbon storage in the living plants and in the sediment among species of different size in tropical waters. The samples were collected from Phuket province, Thailand, in the high density monospecific patches of different size species (*Enhalus acoroides *as a big,* Thalassia hemprhicii *as a medium and* Halophila ovalis *as a small size species). Total carbon and carbon stored in above and below ground, was significantly different between the species (*$p<0.05$*), with the highest values in below ground parts of* E. acoroides *and* T. hemprichii *238.10±85.07 and 134±21.55 g Dw m*$^{-2}$*, respectively. Average organic carbon in the sediment was significantly different (*$p<0.05$*) as well, with* E. acoroides *having highest organic carbon content in the deeper layers of the sediment 1.14±0.25 %* C_{org}*, while the other two species had higher organic carbon in the top and medium layers of sediment. The results of this preliminary research propose that big size species have higher carbon content than smaller species, which reflects in higher sequestration rates of carbon from the ocean, thus reducing the ocean carbon budget. Moreover, it provides necessary information on size of the species which is the key for the future carbon storage studies in the region.*

Keywords: Above ground; below ground; organic carbon; seagrass; sediment

ABSTRAK

*Padang rumpai laut mempunyai keupayaan menyerap karbon dan kapasiti simpanan antara yang tertinggi berbanding ekosistem yang lain. Karbon yang disimpan di dalam ekosistem yang terkumpul di dalam sedimen didepositkan di dalam kehidupan, atas dan bawah tanah biojisim, dengan kadar penyerapan dan simpanan karbon yang berbeza antara spesies. Kajian ini bertujuan untuk mengkaji penyimpanan karbon dalam tumbuh-tumbuhan dan sedimen antara spesies berbeza saiz di perairan tropika. Sampel kajian telah dikumpul dari daerah Phuket, Thailand, dalam tompok monospesifik berkepadatan tinggi spesies dengan saiz yang berbeza (*Enhalus acoroides Thalassia hemprhicii *yang besar, sebagai medium serta* Halophila ovalis *sebagai satu spesies saiz kecil). Jumlah karbon dan karbon yang disimpan di atas dan bawah tanah, adalah berbeza antara spesies (*$p<0.05$*), dengan nilai tertinggi di bawah bahagian tanah* E. acoroides *dan* T. hemprichii *238.10±85.07 dan 134±21.55 g Dw m*$^{-2}$*, masing-masing. Purata karbon organik dalam sedimen adalah berbeza secara signifikan (*$p<0.05$*) dengan E. acoroides mempunyai karbon organik yang tertinggi di lapisan sedimen lebih dalam 1.14±0.25% Corg, manakala kedua-dua spesies lain mempunyai karbon organik yang lebih tinggi di lapisan atas dan sederhana enapan. Hasil kajian awal ini mencadangkan bahawa spesies saiz besar mempunyai kandungan karbon lebih tinggi daripada spesies yang lebih kecil, yang mencerminkan meningkatnya kadar penyerapan karbon dari laut, dengan itu mengurangkan bajet karbon lautan. Selain itu, ia menyediakan maklumat yang diperlukan mengenai saiz spesies yang merupakan kunci bagi kajian menyimpan karbon pada masa hadapan di rantau ini.*

Kata kunci: Atas permukaan tanah; bawah permukaan tanah; enapan; karbon organik; rumpai laut

INTRODUCTION

Seagrass species are one of the highest productive ecosystems of the world with the global net productivity of 400 Tg/yr (Duarte et al. 2005). Most of their primary production (80%) is not consumed (Duarte et al. 2013) but it is exported to adjacent ecosystems, (24%; Duarte & Cebrian 1996) or it is buried in the sediment (30-50%; Duarte et al. 2005). The estimated carbon burial in the seagrass meadows is 48.0-112 Tg per year (Duarte et al. 2013), while the total ocean carbon burial is 243.6 Tg/yr (Duarte et al. 2005). With these rates of carbon burial seagrass meadows are responsible for 50% of the global carbon sequestration in the marine sediment despite occupying 0.2% of the ocean surface (Duarte et al. 2013). These ecosystems act as a carbon sink (Duarte et al. 2005; Mcleod et al. 2011), where carbon can be trapped for a long period of time (centuries and millennia) (Duarte et al. 2005; Macreadie et al. 2014; Rozaimi et al. 2016), hence contributing the mitigation of anthropogenic CO_2 emissions (Fourqurean et al. 2012a). The destruction and/or loss of the vegetation triggers many negative effects on the ecosystem, of which the important one is erosion of already trapped carbon and lack of carbon sequestration ability (Marbà et al. 2015). One possible pathway of liberated carbon is to exit water column and pass into the atmosphere and to contribute to the atmospheric CO_2 (Macreadie et al. 2014), increasing the atmospheric carbon budget.

The ability of carbon sequestration of the seagrasses lies in their high productivity, canopy structure as well as lower nitrogen and phosphorus content in tissues and low concentrations of the oxygen in the sediment, ensuring low decomposition rates and incomplete remineralization (Duarte et al. 1998). The high below ground production have direct influence on the carbon sequestration, as more than 70% of carbon is contributed to the total carbon stock (Supriadi et al. 2014) and 45% of total rhizome production is directly placed in the sediments (Duarte et al. 1998). The seagrass species of South-east Asia have various ranges of sizes, from small *Halophila ovalis* to the largest seagrass species *Enhalus acoroides* (Duarte 1991). Their difference in the size, growth, productivity of leaves, roots and rhizomes (Duarte et al. 2010, 1998; Vermaat et al. 1995), as well as the age of the shoots (Vermaat et al. 1995) influence the rate of the carbon storage.

The aim of this study was to investigate carbon content in living parts as well as in the sediment among the species of different size in a healthy seagrass meadow.

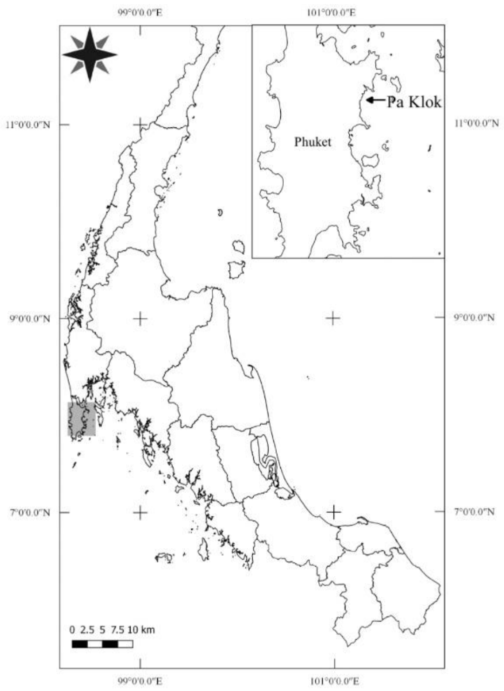

FIGURE 1. Map of the study area

MATERIALS AND METHODS

STUDY SITE

The research was conducted in Phuket province at Pa Khlok Bay in 2015. Pa Khlok Bay is located on Phuket Island (Figure 1) and it has one of the largest seagrass meadows in the province. The seagrass meadow covers an area of 284.8 hectare, with a rich diversity and high density throughout the meadow, good indicator of a healthy seagrass meadow. The samples were collected during summer period in March of 2015.

SAMPLING AND LABORATORY ANALYSIS

Three monospecific seagrass patches were located, *Enhalus acoroides* as a large species patch, *Thalassia hemprichii* as a medium size and *Halophila ovalis* as a small size species patch. These three species were selected as the good representatives of three size groups (Table 1). Distance among the patches was at least 100 m and 4 replications of biomass and one replication of sediment samples were collected per patch.

Biomass was collected from 50×50 cm^2 quadrats, which were randomly placed in the high density areas of each patch (50-75%). All the living vegetation from a quadrat was collected and placed in bags. In the laboratory, samples from each species were separated into above (leaves) and below ground (roots and rhizomes) parts, leaf blades were manually scraped to remove epiphytes and cleaned material was dried in the oven on 60°C until it reached constant weight. The dry weight of the above and below ground parts was recorded and total biomass for each species was calculated as well as for each vegetative part. Small subsamples were crushed into powder and 20 mg of subsamples were sent for percentage of organic carbon analysis to Laboratory of Forest Soils, Department

TABLE 1. Size comparison of three seagrass species

Species	Diameter of below ground (mm)		Leaf size (mm)	
	Rhizome	Root	Length	Width
Enhalus acoroides	13.2[a]	3.5[a]	500.8±1.82[b]	15.7±0.04[b]
Thalassia hemprichii	3.43[a]	1.7[a]	86.8±0.53[b]	8±0.04[b]
Halophila ovalis	1.09[a]	0.57[a]	15.4±0.09[b]	8.5±0.08[b]

[a]From Duarte et al. 1998; [b]From Vermaat et al. 1995

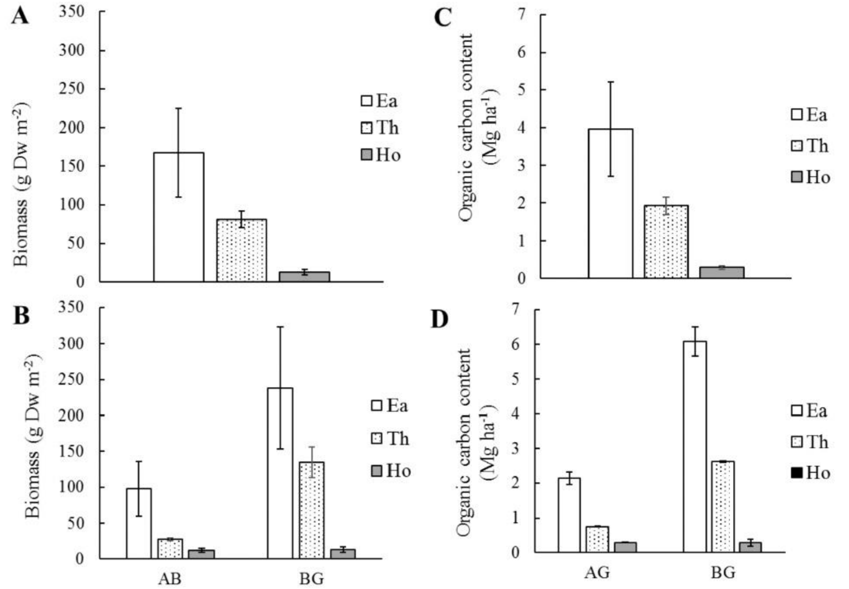

FIGURE 2. A-B: Biomass (g Dw m^{-2}) and C-D: organic carbon content (Mg ha^{-1}) of all seagrass species[a] and their living parts[b]

[a] Ea – *Enhalus acoroides*, Th – *Thalassia hemprichii*, Ho – *Halophila ovalis*. [b] AB – above ground biomass, BG – below ground biomass

TABLE 2. Average of biomass and carbon content in vegetative parts of three different seagrass species. The values with the same letter in the same column do not differ significantly (p<0.05)

Species	Biomass (g Dw m^{-1})			Carbon content (Mg ha^{-1})		
	Total	Above ground	Below ground	Total	Above ground	Below ground
Enhalus acoroides	167.105±57.35^{A}	97.68±37.87^{A}	238.10±85.07^{A}	8.15±2.5^{A}	3.13±0.8^{A}	6±1.93^{A}
Thalassia hemprichii	81±10.59^{A}	27.17±1.95^{B}	134±21.55^{B}	3.37±0.29^{B}	0.76±0.06^{B}	2.61±0.29^{B}
Halophila ovalis	12.62±3.35^{B}	11.76±2.85^{C}	13.48±3.92^{C}	0.56±0.09^{C}	0.28±0.05^{C}	0.28±0.05^{C}

Total organic carbon content highly varied (Figure 2(c)), with significant difference (p<0.05, Table 2) between the species, where highest values were recorded in the bigger species and lowest values in the smaller species of 3.97±1.25 mega gram of carbon per hectare (Mg C ha^{-1}) in *E. acoroides*, followed by *T. hemprichii* and *H. ovalis* (Table 2). The bigger and medium size species had higher carbon content in the below ground, while smaller size species had higher carbon content in the above ground parts (Figure 2(d)). Carbon content in above as well as in below ground parts varied significantly between the species (p<0.05, Table 2). The highest organic carbon content was recorded in *E. acoroides*, following by *T. hemprichii* and *H. ovalis* (Table 1). The average worldwide organic carbon content of the living seagrass biomass is 2.52±0.48 Mg C ha^{-1} (Fourqurean et al. 2012b), wherein the results of our study suggest 3.2 and 1.3-fold increase for bigger seagrass and medium size species, 4.5-fold decrease for small size species. In Southeast Asian region, our study suggested much higher carbon content in the above and below ground parts than reported by Phang et al. (2015) and Prathep (2012), while Supriadi et al. (2014) reported much higher values. The variations of the carbon pool are based on the species size, as the bigger species have longer-lived vegetation parts and lower leaf production rates. The shoots of *E. acoroides* and *T. hemprichii* live longer, with average age of 787±125 and 668±27 days, than the *H. ovalis* shoots, 27±4.2 days (Vermaat et al. 1995). Their older age increases the rate of the carbon sequestration and accumulation per day. The high leaf production rates of *H. ovalis*, 2.10±0.10 days per leaf pair (Kaewsrikhaw et al. 2016), allows this species to grow much faster, which in turn decreases the ability of this species to, accumulate carbon. On the other hand, bigger and medium size species have fewer shoots production, 3.86±0.02 leaves $shoot^{-1}$ per year for *E. acoroides* (Rattanachot & Prathep 2011), which allows them to occupy the space more permanently and to retain resources for extended periods of time (Vermaat et al. 1995).

The results of the performed linear regression analysis of all three seagrass species showed significant relationship of Silvaculture, Faculty of Forestry, Kasetsart University, Bangkok. Carbon content for above and below ground parts for each species was calculated as in (1):

$$\text{Carbon content (mg)} = \text{Carbon (\%)*weight of the sample (mg)} \quad (1)$$

The carbon stored in the sediment was estimated by extracting the sediment using stainless steel cores. There was one sample set of the sediment collection per species meadow in high density areas (same percentage as for biomass sampling), as this was preliminary study. The core had diameter of 5 cm and along 1 m length core a strip of 3 cm width was drilled in order to ease subsample collection. The strip was covered with duct tape during the sampling, so leakage thorough the strip and oxygen intrusion was limited. Immediately after the core was pulled from the bed, sediment top and bottom parts were covered to limit oxygen intrusion in the deepest parts of the sediment. The subsamples were taken at the interval of 3 cm (Fourqurean et al. 2012b) by cutting the duct tape from top to bottom in the cores with a minimal compaction. Each subsample was packed in pre-labeled bags and kept at 4°C from 24 h of collection. In the laboratory, samples were dried in the oven on 60°C until constant weight. In order to correct the core compression, compaction correction factor was calculated for each species (2) and the depth of the samples was then rescaled:

$$\text{Correction factor} = \text{Length of the recovered sample (cm)/depth that core reached (cm)} \quad (2)$$

For further analysis of the organic carbon content, each subsample ~ 5 grams were ground into powder and 20 mg of the grounded subsamples were sent for total carbon analysis in Bangkok. From the rest of the ground samples, 1-2 grams were used for analysis of inorganic carbon by acidification with 1N hydrochloric acid (HCl) and inorganic content of the sample was calculated (3):

$$\text{Inorganic carbon (\%)} = \text{((Dry mass before acid (mg) – dry mass after acid (mg))* } 0.12^{1}\text{/ dry mass before acid (mg))*100} \quad (3)$$

[1] = weight of the carbon in molecular calcium carbonate

Organic carbon in the subsamples was calculated as a difference of values of total and inorganic carbon. As the species have different root penetration depth in the sediment, the samples of the organic carbon in sediment were grouped into the three layers: top (<10 cm), medium (11-40 cm) and bottom layer (>41 cm).

STATISTICAL ANALYSIS

As all biomass, carbon in living parts and sediment samples didn't meet the assumptions of normality, non-parametric analysis was employed, Kruskal-Wallis analysis of variance and Wilcoxon sign-ranked test (R Studio 2015). In order to better understand the relationship between organic carbon and biomass, linear regression analysis was done (R Studio 2015).

RESULTS AND DISCUSSION

BIOMASS AND CARBON STORAGE IN THE LIVING PARTS

Total biomass highly varied among species ($p<0.05$, Table 2, Figure 2(a)) with the highest values in *E. acoroides* species of 167.1±57.35 gram of dry weight per meter squared (g Dw m^{-2}), followed by *T. hemprichii* and *H. ovalis* (Table 2). The same pattern as biomass, was recorded in each living vegetative part of the plant (above and below ground), with significant difference among all the species ($p<0.05$, Table 2) and higher values of biomass in below ground part than in above ground part (Figure 2(b)). The highest biomass of above and below ground parts was found in the bigger species *E. acoroides* with 97.68±37.87 g Dw m^{-2} for above and 238.1±85.07 g Dw m^{-2} for below ground, following by *T. hemprichii* and *H. ovalis* (Table 1). The average above ground biomass measured in this study was much higher than reported by Duarte and Chiscano (1999), while average below ground biomass was higher than reported by Vermaat et al. (1995) and less than stated by Duarte and Chiscano (1999). In our study as well as in Poovachiranon and Chasang (1994), Prathep et al. (2010), Rattanachot and Prathep (2015) and Vichkovitten (1998), below ground biomass exceeded above ground biomass, especially in *E. acoroides* and *T. hemprichii*. High biomass of these two species suggest bigger values of the excess biomass and larger CO_2 sinks, as threshold of excess 41 g Dw m^{-2} is necessary for a meadow to acts as a net CO_2 sink (Duarte et al. 2010). On the other hand, in our study *H. ovalis* had slightly higher below ground biomass than biomass above ground, while in the study of Duarte and Chiscano (1999) and Prathep (2012) had much higher above ground biomass than below ground. This might be due to specificity of *H. ovalis* roots which are very thin, but they branch to increase the surface, thus increasing below ground biomass (Duarte et al. 1998). The difference in the biomass between the species supports the roles of the species in the ecosystem. Smaller species support high grazing pressure and need to be able to transfer their production to the food webs, fast growing vegetation parts of *H. ovalis,* 2.10±0.10 days per leaf pair and rhizome elongation rate of 9.06±1.02 mm per day (Kaewsrikhaw et al. 2016) are capable to colonize new areas in a short period of time. On the contrary, the bigger species are considered more constant species, with longer life span, low mortality rates and long lived shoots (Vermaat et al. 1995). This allows them to allocate their production into below ground and contribute more than 70% of total carbon stock (Supriadi et al. 2014).

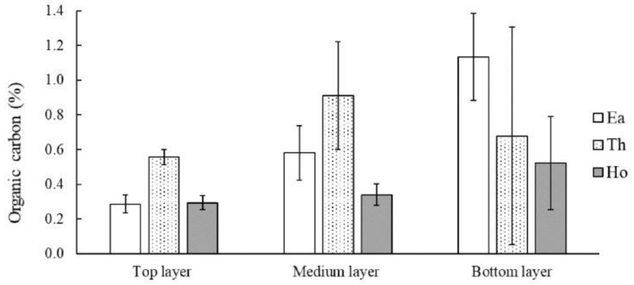

FIGURE 4. Average carbon content per sample for all three species[a] in different depth layers

[a]Ea–*Enhalus acoroides*, Th–*Thalassia hemprichii*, Ho–*Halophila ovalis*

species *H. ovalis,* could penetrate only in the first few cm of the top sediment layer, up to 5-7 cm depth (Marbà et al. 2010), which is highly influenced by the wave action and is considered short term carbon pool. Also the roots of the *H. ovalis* have less fibrous tissues therefore they decompose faster (Duarte et al. 1998). The high carbon content of the sediment in this species patch could be from algal production or from terrestrial inputs as this species occupies depositional environments (Lavery et al. 2013).

CONCLUSION

These preliminary results suggested that bigger size species have better ability to store carbon in the plants as well as in the sediment. It also proposed the positive relationship between biomass and organic carbon in the plants. However, more studies are necessary to distinguish if this relationship is species specific.

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Appendix 2 – Paper 2

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Model-based approach for estimating biomass and organic carbon in tropical seagrass ecosystems

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ABSTRACT: Seagrass ecosystems play a vital role in climate change mitigation as they are globally significant carbon sinks and are responsible for 18% of marine carbon sequestration. However, their increasingly high rates of loss and degradation over the last decade have necessitated the development of effective and non-destructive ways to estimate biomass and, consequentially, stored organic carbon. In this study, we explore cost-effective ways to estimate total organic carbon storage in monospecific (*Enhalus acoroides*) and mixed (*E. acoroides* and *Thalassia hemprichii* or *Cymodocea serrulata*) seagrass ecosystems of Southeast Asia using a modeling approach. The model can be divided into 3 units: (1) biomass prediction, (2) carbon in living vegetation prediction, and (3) carbon in sediment prediction. A series of linear regression relationships linking the units, in which the results of the previous unit represent the predictor for the subsequent unit, was used to obtain information about seagrass biomass (above- and belowground), organic carbon in the living vegetation, and organic carbon in the sediment. All of the modeling units of monospecific patches had higher and more significant correlations between the predictor and response variables compared to those of mixed patches. Following the linked units, the predicted organic carbon on a landscape scale had a small margin of error for both monospecific and mixed patches. Although the models are applicable only for certain species, they improve the cost effectiveness of the data collection and can be easily applied over a larger spatial scale. The models provide the essential knowledge required to better understand and manage seagrass ecosystems and to more effectively address climate change.

KEY WORDS: Blue carbon · Carbon sink · Stepwise structural model · Marine vegetation · Non-destructive method

INTRODUCTION

Seagrass meadows provide a variety of ecosystem services, including a high capacity to store organic carbon in their sediments (Fourqurean et al. 2012a). The estimated carbon burial in seagrass meadows is 48.0–112 Mt yr^{-1} (Duarte et al. 2013a), making them responsible for 20% of marine carbon sequestration despite occupying less than 0.2% of the ocean surface (Kennedy et al. 2010, Duarte et al. 2013a). The trapped carbon can be stored for centuries and millennia (Duarte et al. 2005, Macreadie et al. 2014, Rozaimi et al. 2016); however, degradation and/or loss of meadows triggers the release of the trapped carbon (Marbà et al. 2015) and its re-emission into the atmosphere (Macreadie et al. 2014), thereby increasing the atmospheric inorganic carbon concentration. The 7% loss of global seagrass meadows since 1990 (Orth et al. 2006, Waycott et al. 2009) is mainly due to increased river runoff from coastal development (Halpern et al. 2007),

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while in the Indo-Pacific region, overexploitation of fisheries was identified as a major threat (Fortes 1990, Tomascik et al. 1997, Nordlund 2007). The high loss of these ecosystems and their important role in climate change mitigation necessitate the development of non-destructive, rapid ways of estimating carbon over a range of meadow types, especially in the high-diversity areas of Southeast Asia.

Organic carbon in seagrass ecosystems is stored in living and dead above- and belowground seagrass vegetation, as well as in the sediment. To assess total carbon storage, it is necessary to develop approaches of estimating above- and belowground biomass of the living seagrass vegetation and to quantify stored carbon. Traditional measurements of the seagrass biomass include destructive, time-consuming, physical removal of the seagrass material from the field, which is undesirable (Downing & Anderson 1985, Duarte & Kirkman 2001). Thus, more efficient and non-destructive methods have been developed using visual techniques (Mellors 1991, Mumby et al. 1997a), photographs (Long et al. 1994, Kutser et al. 2007), percentage of seagrass cover (Heidelbaugh & Nelson 1996, Carstensen et al. 2016), and a combination of remote sensing and percentage of seagrass cover correlations (Armstrong 1993, Mumby et al. 1997b, Phinn et al. 2008, Knudby & Nordlund 2011, Lyons et al. 2015). Only the last approach can be applied over a large areal extent, using the generated relationship between percentage of seagrass cover and aboveground biomass and applying it over the whole area of the seagrass meadow. The problem with this approach is the low accuracy of biomass prediction within the meadows of several seagrass species (Knudby & Nordlund 2011). On the other hand, estimations of belowground biomass have been limited, with the few successful estimations using a correlation with blade counts (Heidelbaugh & Nelson 1996) and the strong positive relationship between above- and belowground biomass on a global scale (Duarte & Chiscano 1999). While the prediction from aboveground biomass using a linear model was not suitable for temperate species in Australia (Lyons et al. 2015) and tropical species in Kenya (Githaiga et al. 2017), belowground biomass predictions with low prediction error have been made for mangrove tree species (Njana et al. 2015) using an allometric modeling technique. Therefore, novel models should be tested on seagrass meadows.

To quantify the carbon stored in living vegetation, similar methods as those used for sediment have been suggested, including a C, H, N elemental analyzer and loss on ignition (LOI) (Fourqurean et al. 2014). However, if the budget is limited and no extra equipment is available, the estimation of the carbon content can be performed using a carbon conversion value of 0.34 (Duarte 1990). This conversion value is the average of the carbon content of the leaves of 27 seagrass species on a global extent (Duarte 1990), with a few replications for the tropical Indo-Pacific species (*Cymodocea serrulata*, *Enhalus acoroides*, *Halodule uninervis*, *Halophila ovalis*, *Halophila stipulacea*, *Syringodium isoetifolium*, *Thalassia hemprichii*). However, the average values of the carbon in above- and belowground living vegetation for tropical species is lower than the global average for most species (Supriadi et al. 2014, Phang et al. 2015). Recently, Stankovic et al. (2017) indicated a significant correlation ($p < 0.01$, $R^2 = 0.9763$) between the aboveground biomass and carbon content of 3 tropical species using a simple linear model. Therefore, novel approaches are required that can link non-destructive, time efficient ways of data collection for several types of seagrass meadows and the carbon storage within the ecosystem.

In contrast to mangrove and terrestrial ecosystems, which store half of the carbon in living biomass (Fourqurean et al. 2012a), most of the organic carbon in seagrass ecosystems is stored in the sediment within the meadow, with twice the amount of organic carbon storage per hectare compared to terrestrial soils (Duarte et al. 2005, Kennedy & Björk 2009, Fourqurean et al. 2012a). The average estimates of global stocks of organic carbon in the sediment are 9.8 to 19.8 Pg C (Fourqurean et al. 2012a), which is roughly equal to the combined amount of organic carbon stored in marine tidal marshes and mangrove forests (Fourqurean et al. 2012a). Many factors influence the amount of stored organic carbon in the sediment of seagrass ecosystems (Mateo et al. 2006, Mcleod et al. 2011). Samper-Villarreal et al. (2016) suggested that higher structural canopy complexity, higher turbidity, and shallower and lower wave action sites have higher carbon content, which corresponds with the significant but weak correlation of canopy complexity and organic matter in Tang Khen Bay, Phuket (J. Panyawai unpubl. data). Ricart et al. (2017) determined that sedimentary organic carbon is influenced by the landscape configuration as well due to its greater capacity to retain autochthonous carbon and to accumulate higher portions of finer sediments (Miyajima et al. 2017).

To predict organic carbon content in seagrass sediment, several methods have been attempted. Githaiga et al. (2017) determined that aboveground biomass is not a suitable proxy for organic carbon in the sediment prediction. Armitage & Fourqurean (2016) reported that sedimentary organic carbon can be successfully estimated from above- and below-ground carbon in *T. testudinum* tissues as the link between plants' productivity and soil carbon storage is already established in terrestrial ecosystems (Kirwan & Mudd 2012). Serrano et al. (2016) and Dahl et al. (2016) found that grain size was associated with the organic carbon content, where finer-size particles, <16 µm fractions (Secrieru & Oaie 2009) and <0.074 mm (Dahl et al. 2016), could be used to predict total organic carbon (%); however, Gillis et al. (2017) and Samper-Villarreal et al. (2016) did not find any correlation. Serrano et al. (2016) also concluded that mud content (<63 µm) is a good predictor for organic carbon for smaller species such as *Halodule*, *Halophila*, and *Zostera* spp., while it was a poor predictor for larger, long-living seagrass species, suggesting that the size of the species and its biomass has a positive correlation with organic carbon in the sediment. Gullström et al. (2018) found that organic carbon was strongly negatively linked to sediment density, where higher storage is found in the less compacted sediments due to microbial activity, which can be suppressed by the lack of oxygen (Belshe et al. 2017). Furthermore, Fourqurean et al. (2012b) reported that organic carbon (%) in the sediment has a positive relationship with the organic matter from LOI, and they developed a model for predicting sedimentary organic carbon on a global set of data with high R^2. However, R^2 of this model varies regionally (Fourqurean et al. 2012b, Phang et al. 2015, Samper-Villarreal et al. 2016), as the meadow structure and sediment in ecosystems have different properties.

Our objective in this study was to explore a rapid, non-destructive approach to predict carbon storage in the seagrass ecosystem with limited resources, which can help to estimate blue carbon. This can be achieved by a series of linked equations, in a stepwise structure, where the predictor for the first unit (% coverage of the plant) is necessary and the output is used as the predictor for the next unit.

MATERIALS AND METHODS

Study site

The study was conducted along the west coast of southern Thailand in Phuket, Trang and Krabi Provinces (Fig. 1). In total, 5 of the largest seagrass meadows (>2.5 km^2) with the highest seagrass diversity were located and selected as study areas. In each study area, the type of patch was distinguished as monospecific (*Enhalus acoroides*) and mixed species (*E. acoroides* and *Thalassia hemprichii* or *Cymodocea serrulata*). These species were selected, as Stankovic et al. (2017) found that large (*E. acoroides*) and medium-sized (*T. hemprichii* and *C. serrulata*) species store more carbon in the plants as well as in the sediment, compared to smaller species. In total, we sampled 48 patches (6 replicates per patch type from each study area). Field collection was carried out from April 2015 to December 2016 to cover 2 seasons, which led to 96 samples in total. The south of Thailand has 2 seasons, rainy (May–October) and summer (December–April), that are based on the southwest monsoon occurrence (from mid-May to mid-October) (Thai Meteorological Department, https://www.tmd.go.th/en/).

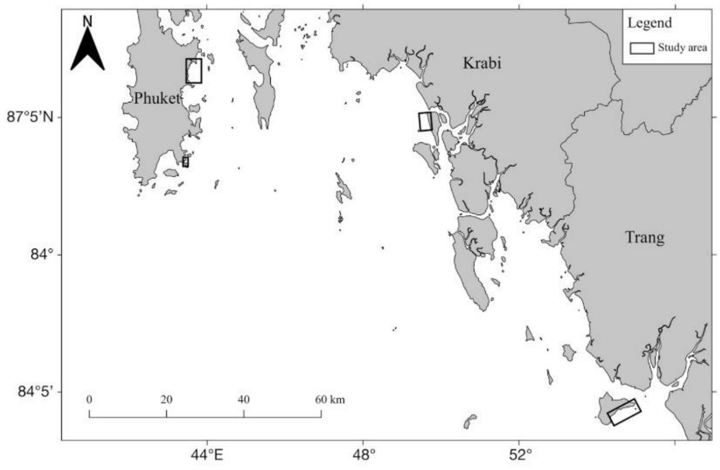

Fig. 1. Study sites along the west coast of Thailand

Field collection

In each study area, 6 replicates per patch type of biomass and sediment samples were taken. Quadrats (50 × 50 cm^2) were randomly placed in each replicate, with a distance of at least 100 m. The percent coverage within the quadrats was recorded following McKenzie & Campbell (2002). All living vegetation from a quadrat was collected and placed in pre-labeled bags and kept at 4°C until a laboratory was reached. Sediment samples were collected using stainless steel cores (5 cm diameter × 1 m length), which were placed in the same area of the quadrats. Cores were covered with duct tape before being hammered into the sediment. As a core was removed from the sediment, the bottom and top parts of the core were covered using rubber stoppers so that the oxygen intrusion to the deepest layers was minimal. Sediment samples were cut off at 3 cm intervals (Fourqurean et al. 2012b) by peeling duct tape from top to bottom (n = 2679 sediment subsamples). Each subsample was packed in pre-labeled bags and kept at 4°C until a laboratory was reached.

Laboratory study

Biomass samples from each patch type were separated into above- (leaves) and belowground (roots and rhizomes) parts (n = 288). Leaf blades were manually scraped to remove epiphytes, and cleaned material was dried in an oven at 60°C until a constant weight was achieved. The dry weights of the above- and belowground parts were recorded. Since there is little variation in organic carbon content in living vegetation (Duarte 1990), only a small number of samples (n = 48), including roots, rhizomes, and leaves, were used for organic carbon analysis. Between 20 and 30 mg of each vegetative part was crushed into powder using a mortar and pestle, and 10 mg of subsamples were used for carbon analysis (% carbon) as determined by a CHNS/O Analyzer (Thermo Quest, Flash EA 1112 Series) at the Central Equipment Division, Faculty of Science, Prince of Songkla University (PSU). Carbon content, as particulate organic carbon from above- and belowground parts for each patch type, was calculated as:

$$\text{Carbon content (g)} = \text{carbon (\%)} \times \text{dry weight of sample (g)} \quad (1)$$

Sediment subsamples were oven-dried at 60°C until their weights were constant. Approximately 15 g from each subsample (n = 240) was ground into fine powder, and 20 mg of the ground subsample was used for organic carbon (C_{org}) analysis, which was performed using the same method mentioned above for plant parts. Particulate organic carbon content (g) in each sediment subsample was calculated using Eq. (1). Inorganic carbon analysis was performed with ~5 g of fine ground powder, using acidification with 1 N HCl. The rest of the fine ground subsample powder was weighed and used for %LOI analysis. The samples were heated in a furnace at 450°C and kept for 4–8 h (Heiri et al. 2001). %LOI was calculated as:

$$\%\text{LOI} = [(\text{dry mass before combustion} - \text{dry mass after combustion}) / \text{dry mass before combustion}] \times 100 \quad (2)$$

Model structure and analyses

To predict carbon estimates in the seagrass ecosystem, the whole model is divided into 3 units: (1) biomass prediction, (2) carbon in the living vegetation prediction, and (3) carbon in the sediment prediction (Fig. 2). Both monospecific and mixed patch types were explored separately. All statistical analyses were performed using the open source language R (R Studio Team 2015). All relationship models between 2 variables were tested using linear regression analysis. For each model, both untransformed and transformed data (log and square-root transformations) were tested. The model with the lowest Akaike's information criterion (AIC) value was selected. When several models had ΔAIC <2, the simpler model was chosen as a prediction model.

In the first unit, biomass values (for both above- and belowground, 'AG' and 'BG') were predicted using 2 models: 'cover-AG' and 'AG-BG' models (Fig. 2). In the first model (cover-AG), aboveground biomass (in g dry weight [DW] m^{-2}) was predicted from seagrass coverage (i.e. cover, %). In the second model (AG-BG), belowground biomass (g DW m^{-2}) was predicted from aboveground biomass. For both models, data from 45 quadrats per patch type were tested.

For the second unit, carbon in the living vegetation was predicted from the biomass value. Two methods were tested using 20 samples per patch type (Fig. 2). The first method created a conversion factor following procedures described in detail by Howard et al. (2014). Average values of organic carbon for above- and belowground biomass for each patch type were calculated separately and used as the conversion factor. The second method was the model to predict carbon in the living vegetation (Mg ha^{-1}) from total biomass (g DW m^{-2}) ('biomass-carbon' model).

In the last unit, organic carbon in sediment (C_{org}) was predicted. Two models were tested: 'LOI-C_{org}' and 'plant-C_{org}': (Fig. 2). The first model (LOI-C_{org}) predicted organic carbon in sediment per sample based on organic matter from the LOI technique from 100 sediment samples per patch type. The results of C_{org} (%) from the C, H, N analyzer and the LOI (%)

Table 1. Summary table for all of the selected models. For all models, $p < 0.01$. Cover: plant coverage (%); AG (BG): aboveground (belowground) biomass (g dry weight [DW] m^{-2}); biomass: AG + BG biomass (g DW m^{-2}); carbon: carbon content in plants (Mg ha^{-1}); LOI: loss on ignition (g cm^{-2}): C_{org}: organic C in sediment (g cm^{-2})

Model	Equation	95% CI	R^2 (%)	Overall RMSE
Cover-AG	Monospecific: AG = 1.90157 + 1.02125 × cover	0.8715–1.1710	83	10.99
	Mixed: AG = 9.033 + 0.771 × cover	0.5709–0.9711	60	20.29
AG-BG	Monospecific: BG = 29.419 + 5.125 × AG	4.5568–5.7461	89	20.86
	Mixed: BG = 26.5542 + 2.8491 × AG	1.8899–3.8083	45	27.00
Biomass-Carbon	Monospecific: Carbon = −0.1016756 + 0.0144978 × Biomass	0.0137–0.0153	99	1.59
	Mixed: Carbon = −0.0606922 + 0.0139800 × Biomass	0.0134–0.0145	99	1.83
LOI-C_{org}	Monospecific: C_{org} = 10.1740 + 0.1714 × LOI	0.1276–0.2151	41	1.95
	Mixed: C_{org} = 10.21697 + 0.13441 × LOI	0.0804–0.1884	32	8.79
Plant[a]- C_{org}	Monospecific: C_{org} = −139.53 + 122.96 × log(BG)	122.85–123.06	87	22.81
	Mixed: C_{org} = −112.46 + 102.28 × log(BG)	102.37–112.36	79	22.50

[a]Various plant attributes

respectively, suggesting conversion factors of 0.34 and 0.32. Similarly to the first unit, a linear model with untransformed data was chosen as the model predictor for both patch types in the biomass-carbon unit (Table S1e,f). The predicted equations for both patch types are shown in Table 1.

For the sedimentary carbon prediction unit, similarly to the first 2 units, a linear model with untransformed data was chosen for the LOI-C_{org} model as the model predictor for both patch types (Table S1g,h). In contrast, for the plant-C_{org} model, a linear model with log-transformed data was chosen as the model predictor for both patch types (Table S1i,j). All predicted equations are shown in Table 1.

Model performance and evaluation

Models of monospecific patches with R^2 values of 83, 89, 41, and 87 had higher R^2 values than models of mixed patches, with R^2 values of 60, 45, 32, and 79 for cover-AG, AG-BG, LOI-C_{org}, and plant-C_{org} models, respectively (Table 1). However, R^2 values had the same value (99%) in both patch types for the biomass-carbon model. The overall RMSE of monospecific patch models was lower than that for mixed patches for cover-AG, AG-BG, biomass-carbon, and LOI-C_{org} models as well, while it was higher for monospecific conversion factor and plant-C_{org} models (Table 1).

On the landscape scale (at Tha Rai Island), coverage of the seagrass varied between 10 and 65% in monospecific meadows and between 50 and 80% in mixed meadows. Collected sedimentary organic carbon was 65.39 and 66.29 Mg ha^{-1} in monospecific and mixed species meadows, respectively. When carbon was extrapolated to 1 m depth, carbon estimations were 130.78 Mg ha^{-1} in monospecific and 132.58 Mg ha^{-1} in mixed species meadows. Following a stepwise structure of the models (Fig. 3), predicted average organic carbon in sediment was (mean ± SD) 149.95 ± 21.68 and 124.32 ± 5.38 Mg ha^{-1} in monospecific and mixed species meadows, respectively. Overall RMSE was 27.91 in monospecific and 6.31 in mixed meadows.

DISCUSSION

Biomass prediction (cover-AG and AG-BG models)

The biomass prediction unit was built up on the already established knowledge of the relationships between coverage and above- and belowground biomass (Armstrong 1993, Heidelbaugh & Nelson 1996, Mumby et al. 1997b, Duarte & Chiscano 1999). In the case of the cover-AG model, the relationship between plant coverage and the aboveground biomass has been established for several years (Armstrong 1993, Heidelbaugh & Nelson 1996, Mumby et al. 1997b, Fonseca et al. 2002, Knudby & Nordlund 2011, Lyons et al. 2015, Carstensen et al. 2016). However, our model, which separates monospecific species from the mixed-species patches, has higher R^2 values and smaller marginal error values, while the other models of total biomass (Phinn et al. 2008, Knudby & Nordlund 2011, Lyons et al. 2015) reported medium and low R^2 values with an overall RMSE > 26.

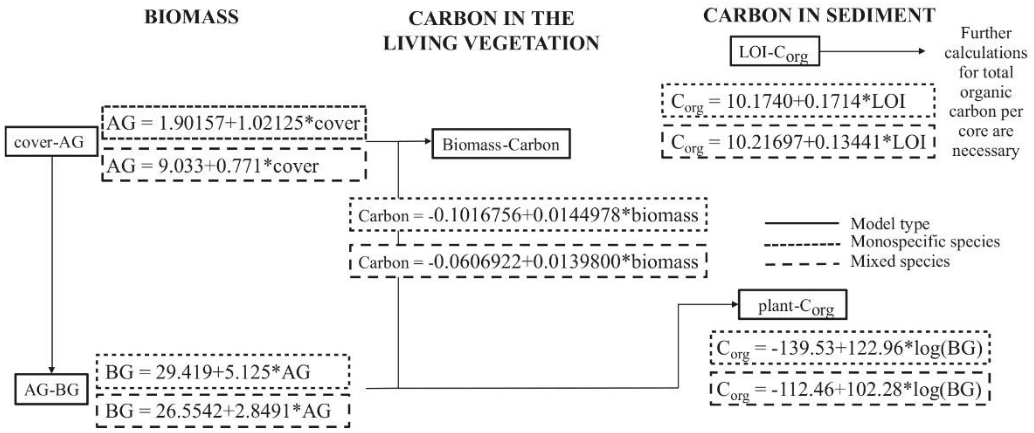

Fig. 3. Model structure with results for all 3 units: biomass prediction, carbon in living vegetation prediction, carbon in sediment prediction. See Table 1 for abbreviations

The second biomass model, AG-BG, is the model that successfully and with a small margin of error predicted belowground biomass from the aboveground biomass. This result is supported by the model of Githaiga et al. (2017) that also successfully predicted belowground biomass from aboveground biomass (only for *Enhalus acoroides* meadows). Likewise, Congdon et al. (2017) successfully predicted belowground biomass from coverage of the plants for *Thalassia testudinum*, *Halodule wrightii*, and *Syringodium filiforme*. However, Lyons et al. (2015) suggested that the prediction is not appropriate using a simple linear model, due to the plants' variability in phenology (Maxwell et al. 2014).

The existing relationship between above- and belowground biomass (Duarte & Chiscano 1999) was based on the global data set, with monospecific and mixed species pooled together, resulting in a high variation of the above- and belowground ratio (0.005–8.56), and thus a lower correlation. Similarly, our results in both models (cover-AG and AG-BG) resulted in better performance of monospecific species models than for mixed species. These same patterns of lower model performance in the mixed species patch might suggest that mixed species patches are more complex and that more input information for the model is necessary. Since Lyons et al. (2015) observed a reduction in the margin of error of the aboveground biomass prediction in the 'species' and 'dominant species' models in the mixed patches, it could be suggested that each species component of the biomass should be separated for future modeling.

Carbon in the living vegetation prediction (conversion factor and biomass-carbon model)

We suggested 2 methods of predicting organic carbon within the seagrass tissues. The first included creating conversion factors, while the second tested the relationship between organic carbon and biomass. While the global average value of organic carbon is assumed to be approx. 35% (Duarte 1990, Fourqurean et al. 2012a), the average value of the Southeast Asian region was lower at 27.5% (Phang et al. 2015). The difference of the average carbon content in seagrass tissues between global averages and the Southeast Asian region created the need for a specific carbon conversion factor for the region.

Although the conversion factor is very useful in carbon calculations, the linear regression model between organic carbon within the plants and biomass (biomass-carbon model) provides better results with a very strong correlation and a low error margin. The results from Stankovic et al. (2017) showed a very strong correlation ($p < 0.01$) as well, which suggests a linear increase in carbon within the tissues of the plants based on their structural components, form, and role in the ecosystem (Duarte 1990, Wirachwong & Holmer 2010, Rustam et al. 2017). However, when the data are separated between patch types, results show smaller errors and stronger relationships. Since both methods provided satisfactory results, in our study we can conclude that the relationship between biomass and organic carbon within the plants is not species-specific and is not influenced by the type and structure of the seagrass patch.

Carbon in the sediment prediction ($LOI\text{-}C_{org}$ and $plant\text{-}C_{org}$ models)

The $LOI\text{-}C_{org}$ model is a moderately good predictor of organic carbon in sediment, corresponding to the results of Phang et al. (2015). On the other hand, studies from temperate zones have reported much stronger relationships, with $R^2 \geq 0.80$ (Fourqurean et al. 2012a,b, Samper-Villarreal et al. 2016). Because results differ regionally, it is possible that sediments in tropical seagrass meadows experience mass loss during the LOI process even with no organic carbon present in the sediment, which could be due to the structural water and/or soluble salts in the sediment (EPA 1990).

The second model ($plant\text{-}C_{org}$) showed that the belowground biomass of the plants could be a moderately good predictor of organic carbon in the sediment. The large belowground biomass of the longer-living species such as *E. acoroides* and *T. hemprichii* (Duarte et al. 1998) produces a significant contribution to the total carbon pool (Supriadi et al. 2014), suggesting that belowground biomass has a positive correlation with organic carbon in the sediment (Serrano et al. 2016). While monospecific patches consist of a long-living single species, mixed patches consist of 2 species and are more structurally complex with 2 layers of canopy and roots. Rattanachot & Prathep (2015) reported that the redox potential and the organic carbon in the sediment were not different between monospecific and mixed-species patches, suggesting that root complexity has little influence on organic carbon in the sediment. However, Stankovic et al. (2017) concluded that monospecific patches of larger-sized species store more carbon within their sediments than smaller species. Samper-Villarreal et al. (2016) proposed that seagrass structural complexity of the canopy is the key driver in non-turbid waters that correlates with the organic carbon in the sediment, suggesting that carbon in the seagrass sediments increases as structural complexity increases. Canopy complexity is an important factor in water flow attenuation, as it limits resuspension of the organic particles to the water column (Koch 2001, Hendriks et al. 2008). The trapped carbon from external sources via canopy complexity is added to the overall carbon accumulation in the sediment (Kennedy et al. 2010, Duarte et al. 2013b). These results suggest that both patch types demonstrate a high possibility of carbon sequestration and accumulation in the sediment via larger biomass sizes in monospecific or via canopy complexity in mixed species patches. Further investigation of the correlation of the belowground biomass and structural complexity and organic carbon in the sediment should be made for more precise conclusions and more accurate models.

Landscape-scale model and its advantages

The stepwise structural model proposed in this study is the first model that can predict the organic carbon pool in seagrass ecosystems using only the coverage of plants. The lower values of the error margin on the landscape scale show that the series of the proposed linked relationships can successfully predict organic carbon, which can have several advantages compared to other approaches. Time and cost for the research can be greatly decreased. Field work for data collection can be reduced (for collecting information about species coverage), and post-field data processing in the laboratory (e.g. for organic carbon analysis) is not required. Time and cost can even be less if remote sensing imagery is applied, as field trips can be limited to ground-truth data collection. This advantage is especially important for many countries in Southeast Asia where research budgets are limited. Another key advantage is its applicability over a large area. Finally, although the model-based approach is assumed to provide less accurate results than visual/destructive sampling methods, the subjective estimates and human error during sampling cannot be quantified, while the model error is repeatable and quantifiable.

The models proposed in this study should be used with caution, as they are applicable only to a few species. Users should be aware of model errors and limitations and should apply mixed-species patches separately from monospecific species patches. Our proposed models address only autochthonous organic carbon sources, but in the seagrass ecosystems, allochthonous sources play important roles (Fourqurean et al. 2012a), so their contributions should not be neglected.

Although the models have certain limitations, they can be used in various situations. Managers can use them as a tool to promote and enhance seagrass health, conservation, and restoration, and to set conservation priorities. They can also be used by local people or government officers who want to promote seagrass meadows within national greenhouse gas schemes via carbon credits. As seagrass ecosystems contribute to climate change mitigation, the proposed models can be used for modeling of seagrass distribution in future climates and to develop efficient climate change mitigation strategies. However, it is necessary to continue to test the relationships between coverage, biomass and organic carbon—especially in mixed-species patches—so that biomass and carbon storage can be as successfully predicted as in monospecific patches, and to improve the prediction of sedimentary organic carbon. We hope that this approach can be used as a stepping stone for future research studies within the SE Asian region, as this region is failing to match the pace of current blue carbon studies.

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Model-based approach for estimating biomass and organic carbon in tropical seagrass ecosystems

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Table S1.

(a) Model fit results for the aboveground biomass (AG) prediction from seagrass coverage (cover) for monospecific species patches

Formula form	n	AIC	Delta AIC	AIC weight
AG=a+b*cover+c*cover^2	45	**373.2**	0	0.568
AG=a+b*cover	45	**373.8**	0.6	0.421
AG=a+b*sqrt(cover)	45	381.1	7.91	0.011
AG=a+b*log(cover)	45	392.6	19.46	0
Null model	45	435.3	62.10	0

(b) Model fit results for the aboveground biomass (AG) prediction from seagrass coverage (cover) for mixed species patches

Formula form	n	AIC	Delta AIC	AIC weight
AG=a+b*cover	45	**397.1**	0	0.543
AG=a+b*cover+c*cover^2	45	398.6	1.52	0.254
AG =a+b*sqrt(cover)	45	399.3	2.26	0.175
AG =a+b*log(cover)	45	403	5.96	0.028
Null model	45	428.3	31.29	0

(c) Model fit results for the belowground biomass (BG) prediction from aboveground biomass (AG) for monospecific species patches

Formula form	n	AIC	Delta AIC	AIC weight
BG=a+b*sqrt(AG)	45	**516.5**	0	0.393
BG=a+b*AG	45	**516.5**	0.05	0.383
BG=a+b*AG+c*AG	45	517.6	1.16	0.220
BG=a+b*log(AG)	45	525.9	9.41	0.004
Null model	45	591.6	75.14	0

(d) Model fit results for the belowground biomass (BG) prediction from aboveground biomass (AG) for mixed species patches

Formula form	n	AIC	Delta AIC	AIC weight
BG=a+b*AG	45	**600**	0	0.471
BG=a+b*sqrt(AG)	45	**600.9**	0.89	0.302
BG=a+b*AG+c*AG^2	45	602.4	2.37	0.144
BG=a+b*sqrt(AG)	45	603.5	3.49	0.082
Null model	45	616.9	16.82	0

(e) Model fit results for the organic carbon within living vegetation (Carbon) prediction for monospecific species patches

Formula form	n	AIC	Delta AIC	AIC weight
Carbon=a+b*biomass	20	**-5.9**	0	1
Carbon=a+b*sqrt(biomass)	20	28.6	34.48	0
Carbon=a+b*log(biomass)	20	51.8	57.75	0
Null model	20	73.1	78.97	0

(f) Model fit results for the organic carbon within living vegetation (Carbon) prediction for mixed species patches

Formula form	n	AIC	Delta AIC	AIC weight
Carbon=a+b*biomass	20	**-20.1**	0	1
Carbon=a+b*sqrt(biomass)	20	25.6	45.78	0
Carbon=a+b*log(biomass)	20	48.5	68.48	0
Null model	20	71.4	91.57	0

(g) Model fit results for the organic carbon prediction in sediment (C_{org}) from LOI for monospecific species patches

Formula form	n	AIC	Delta AIC	AIC weight
C_{org}=a+b*LOI	100	**551.1**	0	0.992
C_{org}=a+b*sqrt(LOI)	100	560.8	9.70	0.008
C_{org} =a+b*log(LOI)	100	573.9	22.78	0
Null model	100	596.2	45.07	0

(h) Model fit results for the organic carbon prediction in sediment (C_{org}) from LOI for mixed species patches

Formula form	n	AIC	Delta AIC	AIC weight
C_{org}=a+b*sqrt(LOI)	100	**348.8**	0	0.386
C_{org}=a+b*LOI	100	**349.1**	0.29	0.334
C_{org}=a+b*log(LOI)	100	349.4	0.64	0.280
Null model	100	368	19.23	0

(i) Model fit results for the organic carbon prediction in sediment (C_{org}) from various plant attributes for monospecific species patches

Formula form	n	AIC	Delta AIC	AIC weight
C_{org} =a+b*log(BG)	45	**421.4**	0	0.559
C_{org} =a+b*sqrt(BG)	45	**421.9**	0.48	0.440
C_{org} =a+b*BG	45	425.4	12.96	0.001
C_{org} =a+b*cover	45	432.6	20.21	0
C_{org} =a+b*sqrt(cover)	45	439.0	26.64	0
C_{org} =a+b*sqrt(AG)	45	445.6	33.18	0
C_{org} =a+b*AG	45	447.8	35.44	0
C_{org} =a+b*log(AG)	45	449.3	36.92	0
C_{org} =a+b*log(cover)	45	450.6	38.15	0
Null model	45	508.3	95.90	0

(j) Model fit results for the organic carbon prediction in sediment (C_{org}) from various plant attributes for mixed species patches

Formula form	n	AIC	Delta AIC	AIC weight
C_{org}=a+b*log(BG)	45	**419.5**	0	0.854
C_{org}=a+b*sqrt(BG)	45	423.0	3.57	0.143
C_{org}=a+b*BG	45	431.2	11.72	0.002
C_{org}=a+b*sqrt(AG)	45	458.8	39.37	0
C_{org}=a+b*AG	45	459.8	40.29	0
C_{org}=a+b*log(AG)	45	460.9	41.46	0
C_{org}=a+b*cover	45	487.4	67.92	0
C_{org}=a+b*sqrt(cover)	45	487.7	68.83	0
C_{org}=a+b*log(cover)	45	488.3	68.83	0
Null model	45	493.7	74.20	0

Title page

Carbon storage in seagrass ecosystems along the Andaman coast of Thailand

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Abstract page

Abstract

Seagrass ecosystems are important contributors to mitigation of climate change, since they are responsible for large carbon sinks. However, there is limited knowledge regarding the importance of variability of carbon storage in various ecosystems. In this study, we estimated carbon storage in several structurally different seagrass meadows along the west coast of Thailand and determined whether geomorphological factors, disturbance, and meadow type influenced carbon storage within these meadows. Carbon content within the living vegetation was on average 3 ± 2.7 Mg ha^{-1}, whilst average storage of carbon in the sediment was 122 ± 35.3 Mg ha^{-1}. Meadow type and disturbance had significant influence on total carbon storage in the ecosystem, while geomorphology of the bay did not show great difference. Uniform meadows had higher average of total carbon storage than mixed meadows (133 ± 36.2 and 110 ± 41.3 Mg ha^{-1}, respectively). Undisturbed meadows had higher average of total carbon storage than disturbed one (140 ± 36.5 and 103 ± 34.8 Mg ha^{-1}, respectively). Obtained results contribute towards our understanding of carbon storage on an ecosystems scale and can provide a baseline for proper management, conservation, and climate change studies in the region.

Keywords: blue carbon; carbon sink; marine vegetation; Southeast Asia.

List of non-standard abbreviations: C_{org} – organic carbon, LOI – loss on ignition

Introduction

The importance and benefits of the seagrass ecosystem services are essential for human well-being, global diversity, adaptation to climate change and resilience. In addition, these ecosystems capture and store huge amounts of organic carbon, and their proper management and conservation could play a key role in the climate change mitigation (Kennedy et al. 2010; McLeod et al. 2011; Fourqureanet al. 2012a; Lavery et al. 2013). Unlike in terrestrial ecosystems, carbon in seagrass systems is mainly stored in the sediment that can be trapped for centuries and/or millennia (Duarte et al. 2005; Macreadie et al. 2014). When ecosystems are degraded and/or lost (Marbà et al. 2015), stored carbon is at risk of being eroded and released back into the atmosphere (Macreadie et al. 2014). Despite occupying less than 0.2% of the ocean surface (Duarte et al. 2013), they are responsible for 10 – 18% of carbon storage in the marine ecosystems (Laffoley and Grimsditch 2009; Kennedy et al. 2010). On the global scale, these ecosystems provide a carbon sink of 194.2 ± 20.2 MgC ha^{-1} in a top meter of soil (Fourqureanet al. 2012a), while just in Indo-Pacific region they store 23.6 ± 8.3 MgC ha^{-1}(Fourqurean et al. 2012a).

Seagrass meadows are experiencing a global decline at the rate of 1.5% yr^{-1} (Pendleton et al. 2012), with at least one-third of the meadows having been lost over the last 140 years (Waycott et al. 2009). Various human activities have put pressure on tropical seagrass beds and rapid coastal development, overexploitation of fisheries and increased sediment input have been identified as major threats to them (Fortes 1990; Halpern et al. 2007; Tomascik 1997; Nordlund 2006). Although the highest diversity of seagrass has been recorded in Southeast Asian region (Ooi et al. 2014), our knowledge concerning the carbon storage within seagrasses is still very limited and only few studies exist with regards to it in Thailand

(Wirachwong and Holmer 2010; Miyajima et al. 2015; Rattanachot and Prathep 2015; Quak et al. 2016; Gillis et al. 2017; Stankovic et al. 2017~~a~~; Panyawai 2017), Malaysia (Rozaimi et al. 2017), Indonesia (Supriadi et al. 2014; Alongi et al. 2016) and Singapore (Phang et al. 2015). Even though the number of studies has been increasing over the past couple of years, they mostly reported carbon storages of specific area, without demonstrating the importance of the variability of carbon storage. Today there are still gaps in our knowledge regarding the factors which influence the variation of carbon storage within the seagrass meadows. These answers can provide a better understanding of seagrasses contribution to mitigation of climate change.

The aims of this study are (1) to provide a regional overview of the carbon storage in several types of the seagrass meadows along the west coast of southern Thailand; and (2) to determine whether geomorphological factors, disturbance and meadow type influence carbon storage within these meadows.

Materials and methods

Study sites

This study was conducted along the west coast of southern Thailand in Phuket, Krabi and Trang Provinces (Fig. 1). In total, eight survey areas from the five largest size (>5 ha) lower intertidal seagrass meadows were selected and classified based on disturbance, geomorphology and meadow type (Table 1). Seagrass meadows were divided into two classes based on anthropogenic influence within the meadow. Undisturbed meadows were within a National Park area, while disturbed were within tourist and residential areas and enclosed by aquaculture, hotels or agricultural fields. Meadows were divided into two types based on the geomorphology of the bay (sheltered and exposed) based on the wind and wave direction and strength. Sheltered meadows were facing toward the land or were not directly exposed to the sea and the direction of winds (SW 1–6 mph) waves (W 0.1–0.4 m); while exposed meadows were facing the open sea and were on the direct influence of the winds (SW 1–11 mph) and waves (W 0.3–0.6 m) (Thai Marine Meteorological Center 2018). Based on the meadow type, seagrass meadows were separated into uniform (with only *Enhalus acoroides* (Linnaeus f.) Royle present) and mixed (with two species: *E. acoroides* and *Thalassia hemprichii* (Ehrenberg) Ascherson or *Cymodocea serrulata* (R. Brown) Asherson & Magnus or *Cymodocea rotundata* Asch. & Schweinf.). Field collection was carried out from April 2015 to December 2016, with one sampling per season of each survey location (Table 1). Southwest monsoons of Thailand start in mid–May and end in mid–October (Thai Meteorological Department 2017) dividing the south of Thailand into two seasons: rainy (May – October) and summer (December – April).

Field sampling and laboratory study

The seagrass meadows were further separated into high (>50% of species coverage) and low (<50% of species coverage) density areas according to the seagrass coverage. The percentage of coverage was recorded according to Mckenzie and Campbell (2002). Using the combinations of the factors (disturbance, geomorphology, meadow type, density), there were 16 treatments in each season (Table 1). In each treatment, three replications of biomass and sediment were collected (n=6 in both seasons), with at least 100 m distance between them.

Biomass was collected from randomly placed 50x50 cm^2 quadrats. All living vegetation was removed and packed in pre-labeled bags where it was kept at 4 °C until reaching the laboratory. Each biomass sample was separated into three vegetation parts: roots, rhizomes and leaves. Leaf blades were manually scraped to remove epiphytes, and cleaned material was oven dried at 60 ˚C until reaching a constant weight. Organic carbon within each vegetation part was calculated using linear regression equation between biomass and organic carbon within seagrass tissues produced in "Biomass-Carbon" model (Stankovic et al. 2018).

Sediment samples were collected with stainless steel cores that were placed around the quadrats. Core was 5 cm in diameter, 1.5 m long and a rectangle (3 cm width and 1 m length) was cut off along the core's side. Before coring process commenced, a rectangle was covered with duct tape, and after process completion the top and bottom parts of the core were closed, thus limiting leakage and oxygen intrusion. In order to correct core compression, the compaction correction factor (Fourqurean et al. 2014) was calculated for each core and the depth of the samples was then rescaled. A duct tape, covering the rectangle hole, was cut from top to bottom and samples were taken at 3 cm intervals (Fourqurean et al. 2012b). They were kept at a temperature of 4 °C, 24 hr from time of collection until the time they reached the laboratory, only to be dried at 60 ˚C until reaching a constant weight. Each subsample was homogenized using pestle and mortar, and between 5 – 10 grams was used for calculating organic matter (through loss of percentage upon ignition analysis). Samples were placed in a furnace; heated until reaching a combustion point (at 450 ˚C); and kept for 4 – 8 hr after which the content of their organic matter was calculated. As the sediment of tropical ecosystems experience the loss of mass during ignition process without organic carbon present in sediment (Phang et al. 2015), organic carbon (C_{org}) in the sediment was calculated using our linear regression correlation between organic matter and organic carbon produced in "LOI-C_{org} model" (Stankovic et al. 2018).

In the interest of distinguishing factors that could influence C_{org} in the sediment, average C_{org} per layer was calculated. Three layers were separated (top layer <21 cm, middle layer 21 – 51, and bottom layer >51 cm), as each layer was affected by different root lengths and abiotic and anthropogenic activities.

Data analysis

Analysis of variance (ANOVA) was used to examine patterns in biomass and carbon content present in the living vegetation as well as in the sediment of seagrass meadows for different survey areas. As correlation between biomass and density of seagrass exists, biomass and carbon in the vegetation was analyzed using only four factors (disturbance, season, geomorphology and meadow type), while carbon in the sediment was examined using all five factors (disturbance, season, geomorphology, meadow type and density). Each individual factor and interaction between factors were examined. Underlying assumptions of ANOVA were checked for violations using residual plots. All statistical calculations were done in R statistical software (R Studio2015).

Total carbon storage (Mg ha^{-1}) was calculated by adding two carbon pools: carbon in the living vegetation and carbon in the sediment. Total areas of all seagrass meadows included in this study (Table 1) were multiplied by the estimated carbon present in the living vegetation (Mg ha^{-1}) or carbon present in the sediment (Mg ha^{-1}) in order to comprehend carbon storage that is present in the west coast of southern Thailand.

Results

Biomass

Total recorded biomass of the uniform meadows was 39.1 – 840.4 g Dw m^{-2} (median, $\tilde{x}$ = 290.2 g Dw m^{-2}) and in the mixed meadows was 36 – 605.6 g Dw m^{-2} ($\tilde{x}$ = 199.8 g Dw m^{-2}; Fig. 2A). Root biomass varied between 1.2 and 157.6 and between 3.2 and 119.6 g Dw m^{-2} ($\tilde{x}$ = 35 and 31.6 g Dw m^{-2}) in uniform and mixed, respectively (Fig. 2B). Rhizome biomass in uniform meadows varied between 18.8 and 662 g Dw m^{-2} ($\tilde{x}$ = 195.6 g Dw m^{-2}) and it was lower in mixed meadows at 15.2 – 427.2 g Dw m^{-2} ($\tilde{x}$ = 119.6 g Dw m^{-2}; Fig. 2C). Leaf biomass of uniform meadows varied between 7.2 and 157.6 g Dw m^{-2} ($\tilde{x}$ = 45.2 g Dw m^{-2}), and in mixed meadows between 8.4 and 141.6 g Dw m^{-2} ($\tilde{x}$ = 49.4 g Dw m^{-2}) (Fig. 2D). The variation of total biomass among surveyed areas are provided in supplementary material (Table S1).

There was no significant difference in total, root, rhizome and leaf biomass between the seasons, but the interaction between disturbance and geomorphology had a significant effect ($p<0.05$; Table 2) with undisturbed sheltered meadows having a higher biomass than other seagrass meadows. Total biomass was also significantly influenced by the meadow type ($p<0.05$; Table 2) of which uniform meadows have a higher biomass than mixed. Rhizome biomass was significantly influenced by both disturbance and meadow type ($p<0.05$ and $p<0.01$, respectively; Table 2), while leaf biomass was higher in the meadows in exposed areas ($p<0.05$; Table 2).

Carbon in the living vegetation

Total carbon in living vegetation of uniform meadows varied between 0.26 and 11.87 Mg ha^{-1} ($\tilde{x}$ = 3.9 Mg ha^{-1}), while in mixed meadows varied between 0.30 and 8.28 Mg ha^{-1} ($\tilde{x}$ = 2.6 Mg ha^{-1}; Fig. 3A). Carbon in the roots of uniform meadows varied between 0.002 and 2.1 Mg ha^{-1} ($\tilde{x}$ = 0.45 Mg ha^{-1}), while in mixed meadows it varied between 0.006 and 1.61

of average sedimentary carbon amongst surveyed areas are provided in supplementary material (Table S1).

There was no significant difference of total carbon and in three layers of sediment between seasons and density, but disturbance, meadow type, disturbance-geomorphology interactions, and meadow type-geomorphology interactions showed extremely significant difference between them ($p<0.001$; Table 4). However, the results of F-statistics revealed higher values for disturbance than for the disturbance-geomorphology interaction. Total carbon within the sediment was also significantly influenced by the interaction between season and meadow type ($p<0.05$; Table 4) with uniform meadows in summer storing more carbon within their sediment.

Total carbon storage

Total carbon in the living vegetation was on average 3 ± 2.7 Mg ha^{-1} while in the sediment was on average 122 ± 35.3 Mg ha^{-1}, suggesting that more than 98% of the carbon storage in these ecosystems is actually stored in the sediment. Uniform meadows support higher total carbon storage than mixed (133 ± 36.2 and 110 ± 41.3 Mg ha^{-1}, respectively), while undisturbed meadows stored higher amounts of total carbon than disturbed meadows (110 ± 41.3 and 103 ± 34.8 Mg ha^{-1}, respectively). However, total carbon storage in sheltered and exposed bays were similar (121 ± 50.9 and 123 ± 24.3 Mg ha^{-1}, respectively).

Carbon storage in west coast of southern Thailand

Carbon in the vegetation, in the sediment and total carbon in the ecosystem varied substantially from one surveyed area to another (Table 5). A similar trend existed in highest and lowest amounts, with the highest being in the mixed undisturbed exposed meadows (in

Mg ha^{-1} ($\tilde{x}$ = 0.3 Mg ha^{-1}) (Fig. 3B). Carbon in the rhizomes in the uniform meadows varied between 0.11 and 9.49 Mg ha^{-1} ($\tilde{x}$ = 2.7 Mg ha^{-1}), while in the mixed meadows it was 0.15 – 5.91 Mg ha^{-1} ($\tilde{x}$ = 1.4 Mg ha^{-1}; Fig. 3C). Carbon in the leaves was in a range of 0.06 – 2.18 Mg ha^{-1} ($\tilde{x}$ = 0.5 Mg ha^{-1}) and of 0.05 – 1.91 Mg ha^{-1} ($\tilde{x}$ = 0.5 Mg ha^{-1}) in uniform and mixed meadows, respectively (Fig. 3D). The variation of average carbon within living vegetation between surveyed areas are provided in supplementary material (Table S1).

Total carbon as well as that in roots, rhizomes and leaves was not influenced by the seasons and geomorphology; however, interaction between disturbance and geomorphology of the bay had significant effect ($p<0.05$; Table 3) with undisturbed sheltered meadows having a higher carbon content in the vegetation. Total carbon in the vegetation, carbon in the rhizomes and carbon in the leaves was also significantly different ($p<0.05$) amongst meadow types, with higher carbon values being in the uniform meadow (Table 3). Carbon in roots was significantly influenced ($p<0.05$) by the interaction between meadow type and bay geomorphology with sheltered uniform meadows having a higher carbon content in the roots (Table 3).

Carbon in the sediment

Carbon stored in the top meter of sediment varied from 45.6 to 234.4 Mg ha^{-1} ($\tilde{x}$ = 122.5 Mg ha^{-1}) in uniform and from 38.3 to 197.9 Mg ha^{-1} ($\tilde{x}$ = 113.9 Mg ha^{-1}) in mixed meadows (Fig. 4). Uniform undisturbed sheltered meadows had the highest average carbon storage of 162 ± 13.3 Mg ha^{-1}, followed by mixed undisturbed sheltered meadows of 138 ± 6.5 Mg ha^{-1} and uniform undisturbed exposed meadows of 123 ± 14.6 Mg ha^{-1}, while mixed disturbed sheltered meadows had the lowest average carbon storage (50 ± 5.8 Mg ha^{-1}). The variation living vegetation 460 ± 2.8 MgC and in sediment 12,215 ± 15.4 MgC), and the lowest in the mixed disturbed sheltered (9 ± 0.8 and 281 ± 5.8 MgC in living vegetation and in the sediment, respectively). Highest recorded total carbon storage was in the mixed undisturbed exposed meadows (12,572 ± 17.8 MgC) followed by uniform undisturbed sheltered meadows (2,605 ± 16.0 MgC) and mixed disturbed sheltered ones (290 ± 6.6 MgC).

Discussion

Biomass

Although, biomass in this study varied significantly among surveyed areas, root and rhizome biomass in uniform meadows both fell within the same range as stated by Vermaat et al. (1995), Duarte and Chiscano (1999) and Stankovic et al. (2017~~a~~), while leaf biomass was lower than it was stated by Stankovic et al. (2017~~a~~) and higher than both Vermaat et al. (1995) and Duarte and Chiscano (1999). On the other hand, biomass of roots, rhizomes and leaves in mixed meadows had similar values as in the study performed by Rattanachot and Prathep (2015); higher than in the study performed by Koedsin et al. (2016); and much lower than reported by Prathep and others (2010). Difference in biomass could be explained by a different number of study sites i.e. some studies were done on a local while others on a global scale. Additionally, different species composition in the mixed meadows may result in different biomass values, as small and medium size species have a much lower biomass than larger size ones do (Vermaat et al. 1995; Duarte and Chiscano 1999).

Meadow type strongly influenced total and rhizome biomass i.e. it was higher in uniform meadows than it was in the mixed ones. Uniform meadows consisted only of *E. acoroides*, which is considered to be a larger and more constant species with longer life span, lower mortality rates, longer living shoots and higher productivity (Vermaat et al. 1995). On the other hand, meadows that consist of *E. acoroides* and one medium size species had shorter life span, higher mortality rates, shorter living shoots and lower productivity (Vermaat et al. 1995; Duarte and Chiscano 1999). Difference in seagrass structure demonstrates a direct influence of the species on the biomass and productivity of the seagrass meadow. As root system and leaves in the mixed meadows consist of two layers and is more complex, roots and leaves are not influenced by the meadow type. Medium size species such as *T. hemprichii* have dense and long root hairs and form root-like nets (Rattanachot and Prathep 2015) thus increasing their biomass. Moreover, in terms of resource requirements *T. hemprichii* is the dominant species (Duarte 2000) and without accompanied species, it would increase its extent and biomass.

Seasons did not influence the biomass, which is in contradiction to the results obtained by Prathep et al. (2010) and Rattanachot and Prathep (2015). Reason for such contradiction might be in the fact that Rattanachot and Prathep (2015) had included into their study only small and medium size species which had to develop a longer root and rhizomes (Kaewsrikhaw and Prathep 2014; Rattanachot and Prathep 2015) in order to withstand the wave action during the rainy season. Although it was expected that geomorphology would influence the biomass, results of this study indicate that bays' geomorphology only influenced biomass of the leaves. Exposed bays are under higher influence of waves, currents and winds, which can in turn increase leaves' biomass so that the wave action can be attenuated. The results of total, root and rhizome biomasses showed that they depend on the disturbance of the seagrass meadows. This suggests that meadows which are protected from high winds and waves and on which there is limited human activity have higher biomass than other meadows.

Carbon in vegetation

In this study average carbon content of roots, rhizomes and leaves for both uniform and mixed meadows fall within the global estimates (0.001 – 5.548 for above, and 0.001 – 17.835 for below ground) (Pendleton et al. 2012). On the other hand, reported carbon for above and below ground was two and 1.5 times higher than in Indonesia (Alongi et al. 2016), more than seven times higher than in Singapore (Phang et al. 2015), and twice as high as in Micronesia (Kauffman et al. 2011). Higher values of carbon in this study suggest that seagrasses in Thailand not only have a higher carbon uptake, but also a better assimilation that can in turn provide higher carbon storage in the ecosystems.

Influence of meadow type on carbon in the living vegetation is the same as it is on the biomass, with a strong influence on total carbon in vegetation and rhizomes. As carbon in the living vegetation positively correlates to the biomass (Stankovic et al. 2018), we expected to see similar pattern of variation. Species in the uniform meadows not only live longer and have an average life of 787 ± 125 days (Vermaat et al. 1995), but they also have fewer shoots produced per year (3.86 ± 0.02 leaves shoot^{-1}) (Rattanachot and Prathep 2011) which allows them both to retain resources for an extended period of time, and to increase the rate of carbon accumulation and sequestration. On the other hand, roots were not influenced by the type of the meadow as their structural complexity could compensate for variations within different meadows.

Carbon storage in sediment

Results of this study indicated that average carbon storage in sediment was at least 1.8 times lower than the global estimates (194.2 ± 20.2 Mg ha^{-1}) and five times higher than Indo-Pacific estimates, 23.6 ± 8.3 Mg ha^{-1} (Fourqureanet al. 2012a). Results of the studies in the Southeast Asian region, Indonesia (Alongi et al. 2016) and Singapore (Phang et al. 2015) showed similar amounts of carbon in the sediment as did results of this study, whilst reported results in Malaysia (Rozaimi et al. 2017) and Micronesia (Kauffman et al. 2011) depicted lower levels of carbon storage. However, these meadows are highly affected by construction and dredging (Rozaimi et al. 2017), which supports the results obtained in this study which stipulate that less carbon is stored in sediment found in disturbed meadows than in undisturbed. Overall results obtained from other studies regarding carbon storage in Thailand were 16.3±21.1 Mg ha^{-1} in Haad Chao Mai National Park (Rattanachot and Prathep 2015) and 29.27 Mg ha^{-1} at Tang Khen Bay Phuket (Panyawai 2017) which is much lower than those obtained in this study. These reports showed lower carbon storage as the data was gathered from seagrass meadows that contained only few smaller to medium sized species.

Factors influencing carbon storage

Overall, meadow type, with different species composition, highly influenced carbon storage. Panyawai (2017) reported higher carbon storage in mixed meadows, which would suggest that structurally complex meadows have increased carbon storage (Samper-Villarreal et al. 2016). On the other hand, Gillis et al. (2017) reported lower carbon content in the sediments of mixed meadows, while Rattanachot and Prathep (2015) reported similar levels in mixed and uniform meadows. This suggests that structure, morphology of the species (Rozaimi et al. 2013) and species composition (Gillis et al. 2017; Stankovic et al. 2017~~a~~) in the meadows are important factors which influence carbon storage in the ecosystem. Disturbance-geomorphology strongly influenced carbon storage in the seagrass meadows with undisturbed sheltered meadows supporting higher production and better ability to trap sediment. These meadows are under less influence of abiotic factors such as strong currents, waves and winds, and they together with limited human activity provide a suitable habitat for seagrass meadows. Anthropogenic disturbances are generally known to have a negative impact on the ecosystem health and services, thus reducing carbon sequestration and storage capacity in seagrass meadows (Rozaimi et al. 2017). However, as carbon storage in the sediment was strongly influenced by disturbance alone, we propose that in the sheltered meadows some portion of carbon might be transferred to the adjacent ecosystems and thus similar carbon storage in the sediment with the exposed meadows. On the other hand, seagrass density did not influence carbon storage within the meadows which was unexpected. The areas of lower seagrass density have higher patchiness and more meadow edges, which should lower the trapping and accumulating ability (Ricart et al. 2015, 2017; Gullstrom et al. 2017; Oreska et al. 2017), comparing with the area of high seagrass density (Githaiga et al. 2017; Ricart et al. 2017; Mazarresa et al. 2018).

Carbon storage in west coast of southern Thailand

The total carbon storage in the investigated seagrass ecosystems varied between 290.53 and 12,683.78 MgC depending on the type of the meadow. However, this was underestimated as it included only five large seagrass meadows, excluding the meadows on the east coast and other meadows along the west coast. More precise estimates of total carbon storage can be obtained using seagrass species and their areal coverage, so further studies are necessary. Although, this study included only few representatives of the seagrass meadows in Thailand, total carbon stock in them is comparable to other tropical meadows. It is at least four times higher than it is in the meadows in tropical Australia (Lavery et al. 2013) and at least five times higher than it is in Indonesia (Supriadi et al. 2014). Although few studied meadows are similar in size i.e. in Singapore, meadows in this study stored more carbon (2,605.182 and 2,280.16 MgC in uniform and mixed, respectively) than in Chek Jawa (1,949 MgC) (Phang et al. 2015).

In Thailand, Rattanachot and Prathep (2015) estimated total carbon storage in Haad Chao Mai National Park (one of the largest seagrass meadow in Thailand, Green and Short 2003) at 19,340 MgC, which is 1.5 times higher than the highest reported storage in this study. However, the reported values of carbon storage might have been underestimated since only three seagrass species were studied (Rattanachot and Prathep 2015) and there is a lack of information on *E. acoroides,* which is the largest species in the tropics and stores higher amounts of carbon than do smaller size species (Stankovic et al. 2017~~a~~). On the other hand, Panyawai (2017) estimated 162.15 MgC in the seagrass meadows at Than Khen Bay, Phuket which is two times lower than the one reported in this study. In her study Panyawai (2017) had included and investigated only two species of seagrass and had excluded *C. serrulata* which dominates mid to lower intertidal area of the bay. Although the total carbon storage in the meadows of the west coast of Thailand is higher than that reported in the region, it is still considerably lower than the global records of 4.2 – 8.4 PgC (Fourqureanet al. 2012a).

Since this study covered only a small portion of the seagrass area in Thailand, further studies are necessary to estimate the whole carbon budget of seagrass meadows in Thailand. This study provided necessary baseline knowledge on the regional scale regarding various seagrass meadows and factors which influence carbon storage. The findings can be as well used for adequate management of the anthropogenic activities within the meadows, such as use of destructive fishing gear. Moreover, appropriate conservation can be established via carbon zoning of the meadows, which can contribute to the national greenhouse gas schemes via carbon credits. As the stored carbon contributes to climate change mitigation, this study provides stepping stone for various future studies of climate change in the region.

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Table and Figures

Table 1. List of all surveyed areas of the seagrass meadows: site, location (lat/long), seagrass area (ha), time of data collection (Summer/Rainy), species composition (Ea: *Enhalus acoroides*, Cs: *Cymodocea serrulata*, Th: *Thalassia hemprichii*, Cr: *Cymodocea rotundata*), and average percentage of seagrass coverage (C). In surveyed areas where two species are occupying the plot, the portions of both species are equal.

Survey areas	Study site	Location (lat/long)	Seagrass area	Time of collection	Species composition & average seagrass coverage (%)
Uniform disturbed exposed high density	Krabi, Sriboya island	N7°54'10.8" E98°58'14.8"	20.84	April 2016/October 2016	Ea C=74±13.6 %
Uniform disturbed exposed low density	Krabi, Sriboya island	N7°54'10.8" E98°58'14.8"	20.84	April 2016/October 2016	Ea C=23±8.8 %
Mixed disturbed exposed high density	Krabi, Sriboya island	N7°54'46.08" E98°58'9.12"	15.70	April 2016/October 2016	Ea, Cs C=76±10.7 %
Mixed disturbed exposed low density	Krabi, Sriboya island	N7°54'46.08" E98°58'9.12"	15.70	April 2016/October 2016	Ea, Cs C=30±7.7 %
Uniform disturbed sheltered high density	Phuket, Pa Klok	N8°1'12" E98°24'50.4"	11.82	March 2016/August 2016	Ea C=81±5.8 %
Uniform disturbed sheltered low density	Phuket, Pa Klok	N8°1'12" E98°24'50.4"	11.82	March 2016/August 2016	Ea C=17±6.8 %
Mixed disturbed sheltered high density	Phuket, Tang Khen Bay	N7°48'43.56" E98°24'15.48''	5.54	April 2015/August 2015	Cs, Cr C=77±7.5 %
Mixed disturbed sheltered low density	Phuket, Tang Khen Bay	N7°48'43.56" E98°24'15.48''	5.54	April 2015/August 2015	Cs, Cr C=24±7.4 %
Uniform undisturbed exposed high density	Trang, Libong island site 1	N7°14'11.4" E98°26'39.11''	17.84	December 2016/June 2016	Ea C=78±12.1 %
Uniform undisturbed exposed low density	Trang, Libong island site 1	N7°14'11.4" E98°26'39.11''	17.84	December 2016/June 2016	Ea C=23±11.7 %
Mixed undisturbed exposed high density	Trang, Libong island site 1	N7°14'19.32' E98°26'45.23''	101.56	December 2016/June 2016	Ea, Th C=76±16.6 %
Mixed undisturbed exposed low density	Trang, Libong island site 1	N7°14'19.32' E98°26'45.23''	101.56	December 2016/June 2016	Ea, Th C=32±11.7 %
Uniform undisturbed sheltered high density	Trang, Libong island site 2	N7°14'7.8' E98°25'16.68''	13.10	December 2016/June 2016	Ea C=64±11.6 %
Uniform undisturbed sheltered low density	Trang, Libong island site 2	N7°14'7.8' E98°25'16.68''	13.10	December 2016/June 2016	Ea C=23±10.8 %
Mixed undisturbed sheltered high density	Trang, Libong island site 2	N7°14'4.56' E98°25'1.91"	17.84	December 2016/June 2016	Ea, Cs C=65±18.2 %
Mixed undisturbed sheltered low density	Trang, Libong island site 2	N7°14'4.56' E98°25'1.91"	17.84	December 2016/June 2016	Ea, Cs C=19±4.9 %

Table 2. Summary of statistical analysis (F statistics) from ANOVA on seagrass biomass

Source of variation	Biomass			
	Total	Roots	Rhizomes	Leaves
Disturbance	3.38	0.83	**4.28***	0.0017
Season	0.96	0.54	1.11	0.40
Geomorphology	0.32	0.02	0.29	**4.17***
Meadow type	**6.13***	1.02	**8.29****	0.01
Disturbance*geomorphology	**6.10***	**9.91****	**5.33***	**7.1476****
Disturbance*meadow type	1.52	0.0049	1.12	2.48
Disturbance*season	0.48	0.20	1.79	0.02
Season*meadow type	1.13	0.43	0.97	0.04
Season*geomorphology	0.37	0.11	0.60	0.28
Meadow type*geomorphology	2.03	2.62	0.92	1.86

Note: Significant differences at *, p<0.05; **, p<0.01; ***, p<0.001. All the rest are non-significant.

Table 3. Summary of statistical analysis (F statistics) from ANOVA on carbon in living vegetation.

Source of variation	Carbon in living vegetation			
	Total	Roots	Rhizomes	Leaves
Disturbance	3.12	2.03	**4.73***	0.05
Season	0.89	1.66	1.37	0.14
Geomorphology	0.89	0.06	0.50	0.08
Meadow type	**6.64***	2.30	**10.02****	**5.17***
Disturbance*geomorphology	**5.89***	**5.90***	**4.80***	**5.61***
Disturbance*meadow type	1.28	0.009	1.33	3.36
Disturbance*season	0.51	0.20	1.36	0.02
Season*meadow type	0.97	0.41	1.21	0.27
Season*geomorphology	0.41	0.08	0.82	0.06
Meadow type*geomorphology	2.10	**4.66***	1.18	2.68

Note: Significant differences at *, p<0.05; **, p<0.01; ***, p<0.001. All the rest are non-significant.

Table 4. Summary of statistical analysis (F statistics) from ANOVA on carbon in sediment.

Source of variation	Carbon in sediment			
	Total	Top layer	Middle layer	Bottom layer
Disturbance	**52.86*****	**52.06*****	**84.83*****	**31.66*****
Season	3.12	0.70	0.02	0.52
Geomorphology	0.26	**7.82****	0.39	**4.62***
Meadow type	**17.62*****	**39.96*****	**32.52*****	**31.76*****
Density	1.23	0.52	0.0006	0.08
Disturbance*geomorphology	**36.66*****	**31.86*****	**66.13*****	**24.57*****
Disturbance*meadow type	1.44	**18.26*****	**15.98*****	**10.09****
Disturbance*season	1.75	0.98	0.88	3.07
Disturbance*density	0.08	1.53	0.09	0.08
Season*meadow type	**4.23***	1.31	0.02	0.62
Season*geomorphology	0.18	1.37	9.77	0.66
Season*density	0.04	0.03	0.04	0.17
Meadow type*geomorphology	**19.40*****	**21.75*****	**20.55*****	**15.13*****
Meadow type*density	1.08	**5.31***	0.56	0.41
Geomorphology*density	1.00	1.13	0.58	1.40

Note: Significant differences at *, p<0.05; **, p<0.01; ***, p<0.001. All the rest are non-significant.

Table 5. Average organic carbon in vegetation, in sediment and total carbon in area on ecosystem scale.

Survey areas			Carbon in vegetation (MgC)	Carbon in sediment (MgC)	Total carbon per area (MgC)
Uniform	disturbed	exposed	47.48 ± 2.24	2,015.34 ± 10.81	2,062.82 ± 13.05
		sheltered	68.85 ± 3.4	1,352.69 ± 11.17	1,421.54 ± 14.57
	undisturbed	exposed	105.71 ± 3.42	2,174.44 ± 14.60	2,266.21 ± 17.51
		sheltered	55.10 ± 2.64	2,550.07 ± 13.35	2,605.18 ± 16.04
Mixed	disturbed	exposed	62.25 ± 2.38	2,534 ± 8.50	2,583.69 ± 10.52
		sheltered	9.00 ± 0.84	281.53 ± 5.83	290.53 ± 6.67
	undisturbed	exposed	460.84 ± 2.80	12,215.95 ± 15.43	12,572.73 ± 17.84
		sheltered	43.55 ± 1.80	1,809.23 ± 6.51	1,846.482 ± 8.34

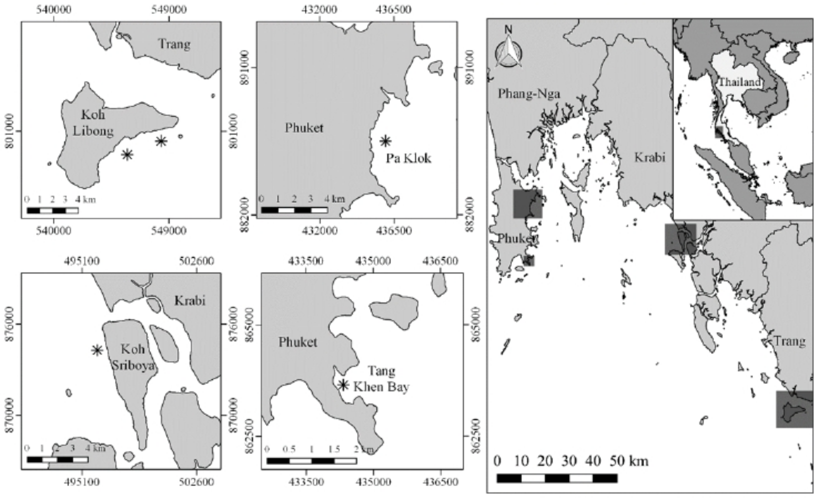

Figure 1. Map of the study sites: ■ locations of the sites, ✱ location of sampling.

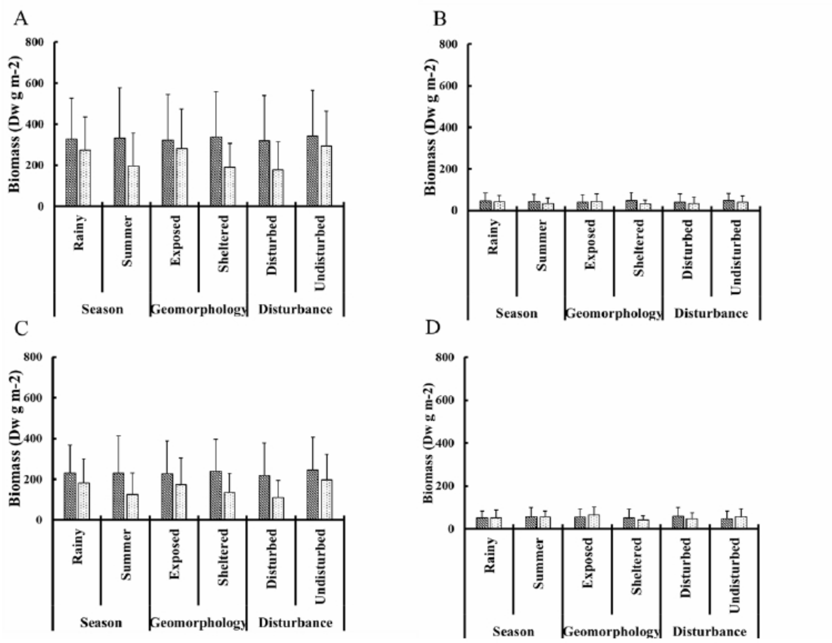

Figure 2. Average values of biomass from each treatment for ▧ uniform and ⊡ mixed meadows separated by each factor (season, geomorphology and disturbance): A-total biomass, B-root biomass; C-rhizome biomass; D-leaves biomass.

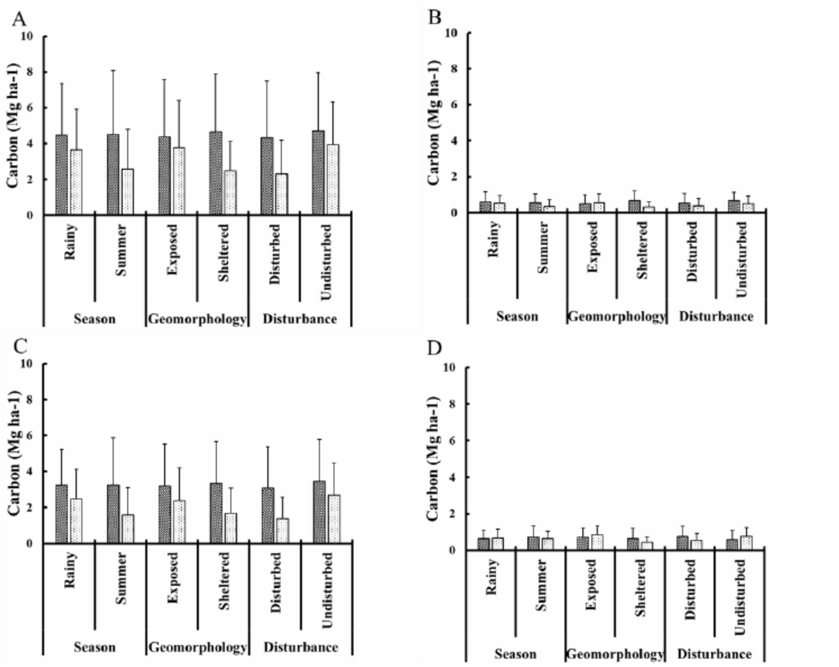

Figure 3. Average values of the carbon content in living vegetations from each treatment for uniform and mixed meadows separated by each factor (season, geomorphology and disturbance): A-total carbon in living vegetation; B-carbon in roots; C-carbon in rhizomes; D-carbon in leaves.

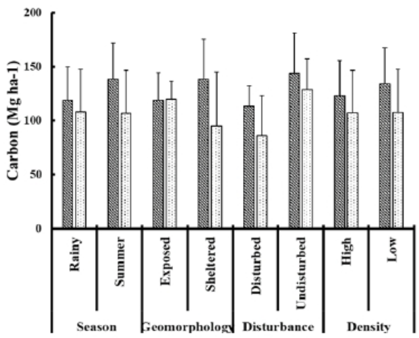

Figure 4. Average values of the total carbon in the top meter sediment in uniform and mixed meadows separated by factors (season, geomorphology, disturbance and density).

Legends of the figures

Figure 1.

■ Location of the study sites

✳ Location of the sampling

Figures 2. – 4.

▧ Uniform meadows

⊡ Mixed meadows

Supplementary materials

Table S1. Average values of total biomass, total organic carbon in living vegetation and in sediment in each surveyed area.

Survey areas				Average values of total biomass (g Dw m^{-2})	Average values of total C_{org} in living vegetation (Mg ha^{-1})	Average values of total sedimentary C_{org} (Mg ha^{-1})
Uniform	disturbed	exposed	high density	324 ± 137.3	4 ± 2.0	125 ± 27.9
			low density	103 ± 37.6	1 ± 0.6	100 ± 7.6
		sheltered	high density	614 ± 162.9	9 ± 2.4	118 ± 13.9
			low density	231 ± 83.6	3 ± 1.2	110 ± 14.8
	undisturbed	exposed	high density	633 ± 112.5	9 ± 1.6	138 ± 28.6
			low density	225 ± 105.9	3 ± 1.5	112 ± 19.7
		sheltered	high density	398 ± 121.5	6 ± 1.7	163 ± 47.2
			low density	109 ± 63.0	1 ± 0.9	162 ± 29.6
Mixed	disturbed	exposed	high density	368 ± 117.0	5 ± 1.6	121 ± 17.0
			low density	83 ± 47.4	1 ± 0.6	120 ± 15.7
		sheltered	high density	167 ± 53.4	2 ± 0.7	53 ± 10.1
			low density	91 ± 41.2	1 ± 0.6	52 ± 6.6
	undisturbed	exposed	high density	491 ± 155.4	7 ± 2.2	123 ± 26.2
			low density	184 ± 90.3	2 ± 1.3	116 ± 5.3
		sheltered	high density	323 ± 118.9	4 ± 1.7	142 ± 40.7
			low density	178 ± 101.7	2 ± 1.4	134 ± 30.7

Appendix 4 – Manuscript 1

(draft version)

Change of seagrass distribution in future climate change scenarios

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Abstract

Seagrass meadows are one of the most important carbon sinks in the marine ecosystem, annually trapping 1.01 – 66.5 t km^{-2} y^{-1} of organic carbon. However, seagrass ecosystems are declining globally at a rate of 12.8% y^{-1}, due to anthropogenic threats and climate change. In this study, we developed models predicting the distribution of uniform and mixed Southeast Asian seagrass meadows under selected climate change scenarios. Using generalized additive models (GAM) and two predictors (mean sea level and sea surface temperature), we developed models to predict seagrass occurrence in uniform and mixed meadows in the next 75 years. Mixed seagrass meadows increased their probable extent in every scenario, whereas uniform meadows expanded in area up until 2025 then started to decline or completely disappear thereafter. This study assessed the distribution of the seagrass meadow, which can provide sufficient knowledge for the management and conservation of the meadows in the present time.

Key words: marine vegetation, GAM, species distribution, habitat modeling, tropical seagrass

Introduction

Seagrass meadows provide various important ecosystem services (Campagne et al. 2014; Cullen-Unsworth et al. 2014; Nordlund et al. 2016), among which is the sequestration and storage of organic carbon (Fourqurean et al. 2012). Seagrasses alone are responsible for more than 18% of marine carbon sequestration (Kennedy et al. 2010). As the stored organic carbon in the sediment of seagrass meadows is trapped for centuries and millennia (Duarte et al. 2005; Macreadie et al. 2014), these ecosystems play a vital role in the mitigation of the climate change. The estimated global capacity of seagrass meadows to act as a sink is 0.08 – 0.22 Pg C yr^{-1} (Duarte et al. 2013), which is equal to the 0.6 – 2% of global anthropogenic CO_2 emissions (IPCC 2014). However, there are many threats to the seagrass ecosystems (Waycott et al. 2009; Unsworth and Cullen 2010; Short et al. 2011; Nordlund et al. 2016) causing rapid disappearance and decline at an annual rate of 7% (Waycott et al. 2009). At this current rate, it is estimated that 30 – 40 % of seagrass ecosystems could be lost in the next 100 years (Pendleton et al. 2012). The degradation and/or loss of the meadows initiates a great loss associated with the loss of ecosystems services, such as stabilization of the shore (Bos et al. 2007), nutrient cycling (Costanza et al. 1997) and provision of habitats and food for fish, bird, invertebrate and mammals (Heck et al. 2003; Hughes et al. 2009). More importantly, it includes the loss of carbon sequestration ability and release of the trapped carbon (Marbà et al. 2015) and its re-emission to the atmosphere, consequently increasing the atmospheric carbon concentration. Recent estimates suggest that seagrass could release up to 299 Tg C per year to the atmosphere, which accounts for 10% of all CO_2 emissions caused by anthropogenic land use changes (Fourqurean et al. 2012). Thus, the potential emissions from the seagrass loss could have global impact on climate and significant economic consequences.

Global economic and population growth is identified as the most important driver of increasing CO_2 emissions (IPCC 2014). In the last decade, despite green house gas (GHG) policies, annual emissions grew at average rate of by 1.0 Gt CO_2 per year (IPCC 2014). The changes of the average surface temperature by 0.78 °C is highly caused by the increase of GHG, land use and from aerosols (IPCC 2014). The increase of the atmospheric temperature causes the melting of the of snow and ice, with the rate of 1.6% and 3.5 – 4.1 % per decade, respectively (IPCC 2014). The newly melted freshwater input is increasing the mean sea level of oceans, with an average rate of increase by 3.2 mm yr^{-1}. Continued GHG emissions will cause further warming of the atmosphere and oceans, which will have long lasting consequences and irreversible impacts on the ecosystems and human life. Projections of the CO_2 concentrations suggest that by 2100 it will rise from 430 to more than 1000 ppm depending on the representative concentration pathways (RCP), which is more than 2 times higher than in present time.

The increasing rate of atmospheric temperature will have large impacts on the oceans and will have both direct and indirect effects on seagrass ecosystems. The increase of sea water temperature will mainly alter growth rates and other physiological functions of the plants (Short and Neckles 1999), while distributions of several species might be affected as well, through the heat stress induced flowering (Diaz-Almela, Marbà, and Duarte 2007; Ruiz et al. 2017) and limited seed germination at higher temperatures (Abe, Kurashima, and Maegawa 2008; Xu et al. 2016) . The sea level rise will cause increase of depth and reduced light, which will modify the depth threshold of plant growth, therefore directly affecting the seagrass distribution (Short and Neckles 1999). The impacts of the increase of CO_2 in the oceans could alter seagrass photosynthesis and productivity (Short and Neckles 1999). Seagrass ecosystems provide a variety of valuable of ecosystem services, and climate change induced changes in the these ecosystems will not only be perceived as changes to the distribution of seagrasses, but it will cause change to the distribution and biodiversity of many fishes and marine animals, increase coastal erosion, migration of the marine animals and loss of the adjacent habitats, which will have vast impacts on the fisheries, livelihoods of the people and global economy.

The aim of this study was to explore the probable change of distribution of tropical seagrass meadows in the future climates following the most likely climate change scenarios.

Materials and methods

Study site

The study was conducted along the west southern coast of Thailand, in Phuket, Krabi and Trang provinces (Fig 1). In each province the largest seagrass meadows (>5 ha) were selected and were defined as either uniform (with only *Enhalus acorides* present) or mixed (with *E.acorides* and one medium size species – *Thalassia hemprichii, Cymodocea serrulata* or *Cymodocea rotundata*). These species were selected because of their size (Duarte et al. 1998; Vermaat et al. 1995), since larger species are easily identified and recorded during the mapping of the meadows. Data was collected during summer season in 2016.

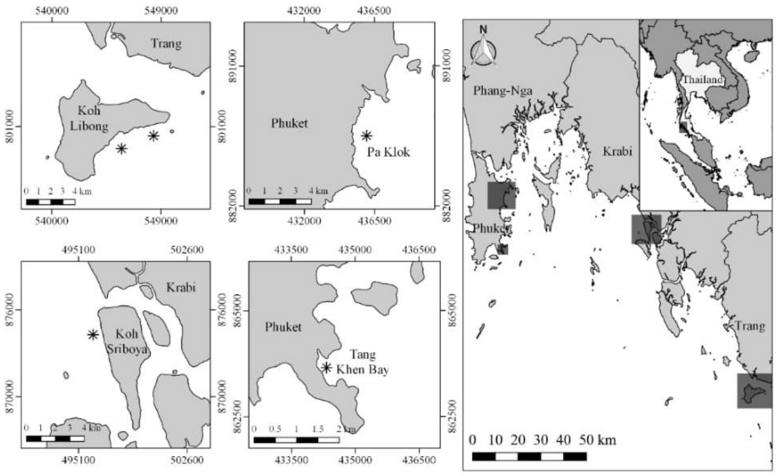

Figure 1. Map of the study areas and location seagrass meadows

Mapping and image processing of the seagrass meadows

Small unmanned aerial vehicle (UAVs), commonly known as drone, was used to map the seagrass meadows at each study area. The high-resolution images were taken with DJI Phantom 3. Autonomous flight was selected, as the drone is flying automatically over selected area and no manual operation of the drone is necessary. Grid flight planning was used to cover the specified area. The images were acquired with a visible RGB camera at the lowest tide at an altitude of 300 m with in flight speed of 10 – 15 m/s. Images were taken so that there was an 80% and 60% overlap on front and side imagery. The digital camera attached to the UAVs (DJI model FC300S) had a resolution of 4000x3000 pixel and focal length of 4 mm.

To distinguish seagrass area, a supervised classification algorithm analysis with spectral information was used. Maximum likelihood classification was chosen as it has overall accuracy of more than 70% (Knudby and Nordlund 2011; Meyer and Pu 2012; Koedsin et al. 2016), with a supervisor providing objects of the same class (training areas). Training areas were selected by classified random stratification and there were 25 areas per class. The land and 5 m from the land was masked out as the land layer, while the rest was used for classification of the two classes: 1. seagrass area; 2. barren substrate.

Modeling

The species distribution model (SDM) for seagrass meadows was fitted using generalized additive models (GAM, Hastie and Tibshirani 1990). GAMs are semi parametric extensions of generalized linear models (Guisan et al. 2002) and they are widely used to describe non-linear relationships between predictors and response (Yee and Mitchell 1991; Downie et al. 2013). GAM models are fitted using smoothing splines, where the function and degree of smoothness have broad categories. Compared to alternative modeling approaches, GAM often outperforms them, suggesting that this model can use extra information available from absence records (Chefaoui et al. 2016), which is an advantage in defining distribution of the species.

Model fitting was done on the data set from the 2016 survey, while for the prediction, two climate change representative concentration pathways (RCP) were selected: RCP 4.5 and RCP 8.5. These pathways represent greenhouse gas concentration trajectories based on the IPCC Climate Change 5th Assessment Report (AR5) in 2014. The trajectories are named by the probable range in 2100 of radiative forcing (measure of the influence a factor has in altering the balance of incoming and outgoing energy in the Earth-atmosphere system, IPCC) relative to pre-industrial values. The pathways are based on different assumptions of population growth, economy, energy consumption and sources and land use over the time. We selected two pathways (4.5 and 8.5) as a representative of the moderate and nightmare scenarios. Their characteristics, features and predictions are presented in Appendix 1.

Data collection

Species presence/absence was recorded from the previously mapped areas. In each area, 2000 points were randomly selected from within the seagrass area (recorded as presence) and barren substrate (recorded as absence).

In total, 12 environmental factors were selected assuming that these factors had an important influence on the presence and absence of seagrass (Table 2). Environmental data was obtained from freely available sources (Table 2), while the maps of the mean sea level were constructed using inverse distances weighted interpolation from the points along the west coast from Phang Nga to Satun province. The data of all environmental factors was re-scaled to a resolution of 100 meters.

Table 2. Selected environmental factors

Factors	Grid	Source
Bathymetry	1 km	MARSPEC
Chlorophyll a	4 km	Modis AQUA
Nitrate	9.2 km	Bio-Oracle
pH	9.2 km	Bio-Oracle
Phosphate	9.2 km	Bio-Oracle
Sea surface temperature	4 km	Modis AQUA
Sea surface salinity	5 km	SMOS-BEC
Mean sea level		Hydrographic Department Thai Royal Navy
Distance to shore	1 km	MARSPEC
Light	9.2 km	Bio-Oracle
Oxygen	9.2 km	Bio-Oracle
Current velocity	9.2 km	Bio-Oracle

Information regarding future values of environmental factors (sea level rise, oxygen, pH, sea surface temperature) was obtained using SimCLIM for Marine environment add-on for ArcGIS (http://www.climsystems.com), while for other variables (sea surface salinity, nitrate, phosphate, Chlorophyll a, current velocity) Bio-Oracle (http://www.bio-oracle.org) was used. Both of these sources were compatible with the selected RCPs and IPCC Climate Change strategies. On the other hand, future bathymetric data was calculated from estimates of sea level rise and distance to shore. The obtained images of the environmental variables had the resolution of 25 km and 9.2 km, so they were rescaled to the 100 m resolution. In each pathway, there were 3 selected years in the future 2025, 2050 and 2075.

Model fitting and validation

The model fitting was done on the obtained seagrass presence/absence points from mapping, calibration dataset (Fig 3). Uniform and mixed meadows were analyzed separately. Spatial dependency in each model was tested using Moren's I and to account for spatial autocorrelation, coordinates of points were included as smoothed terms using a tensor product smooth with interaction (i.e., the ti() function in the mgcv package)

To evaluate the model's performance, 1000 points were randomly sampled and overlaid with the present environmental variables (evaluation dataset, Fig 3). The model presented the results as the probability of occurrence from 0 to 1, where all the points above 0.75 were accepted as presence and less than 0.75 chance of occurrence as absence of seagrass, since we wanted to include higher probabilities of occurrence in seagrass distribution maps.

To use this model in the future predictions, 2000 new random points across the whole area were selected (prediction dataset, Fig 3), and they were overlaid with the environmental variables from both RCP (4.5 and 8.5) in 2025, 2050 and 2075.

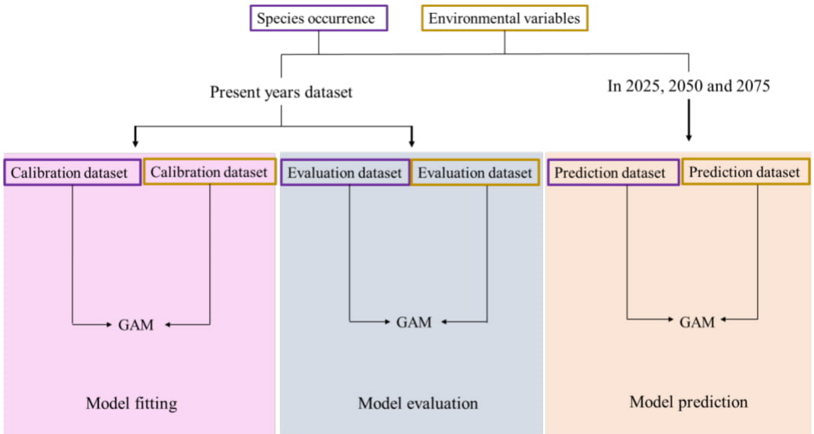

Figure 3. The structure of the modeling of the seagrass distribution

Data analysis

All the calculations of the models were done using "mgcv" package (Wood 2011) within R (R Core Team 2011), while the mapping and preparation of the maps was done in ArcGIS software (ESRI 2011). The change of area of the seagrass meadows was calculated as a difference between selected year in the future and the area in present time. Similarly, change of the seagrass area (%) was calculated, from the division of changed area and area in present.

Results

Current seagrass distribution

The seagrass distribution in each study site was successfully extracted from drone images (Fig 4). However, at the Libong study site 2, the images were too blurry and could not be used for classification, as the water was to murky and turbid. To obtain the distribution of the seagrass at this study site, information from previous studies were used (Khongkhao et al 2017). The accuracy of the maximum likelihood classification, as well as user and producer accuracy of each study site are presented in Appendix 2A.

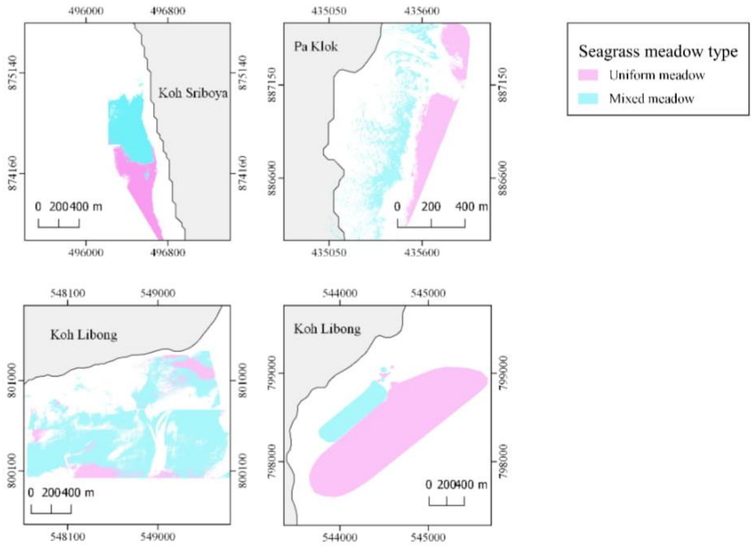

Figure 4. Seagrass meadow distribution along the coast

Total area of seagrass was highly variable, with the highest recorded at Libong site 1 and lowest at Libong site 2 (Table 3). Overall, uniform meadows had higher area of coverage than mixed meadows, except at the Libong site 1, where the trend was opposite (Table 3). The highest area of uniform meadows was recorded at Sriboya island, while the lowest was at Pa Klok. On contrary, highest recorded mixed meadow was at Libong site 1, and lowest at Pa Klok.

Table 3. Seagrass area in the present

Study site	Total area (ha)	Area of uniform meadows (ha)	Area of mixed meadows (ha)
Sriboya	45.36	25.18	20.18
Pa Klok	17.36	11.82	5.54
Libong 1	119.4	17.84	101.56
Libong 2	28.8	15.7	13.1

Model

Correlation among the environmental variables (Appendix 2B), indicated that just two factors were appropriate for modeling: sea surface temperature and mean sea level. The semi-parametric portion of the GAM included the position (longitude and latitude) of the seagrass occurrences and the basis applied was a thin-plate spline. Sea surface temperature and mean sea level were included in the GAM as parametric variables. The seagrass presence/absence was modeled with a binomial distribution and the link function applied was the logit function. The main model equation is given in Equation 1 of the appendix (Appendix 2C), while the dimension of the bases used to represent the smooth term (k) was selected for each meadow type specifically to prevent over-fitting and over-smoothing. The model in uniform meadows had higher adjusted R^2 values (0.76, 0.77, 0.80 and 0.88) and explained more deviance (75 %, 75.4 %, 77.6 % and 87.7 %; Table 3, Appendix 2C). On the other hand, models of mixed meadows had moderate adjusted R^2 values (0.46, 0.67, 0.75, 0.78) and explained 42.8 %, 67.6 %, 73.0% and 78.7 % of the deviance (Table 4, Appendix 2C). The detailed results of the fitted models for each of the study sites are presented in Appendix 2C in Table 3 and 4, for uniform and mixed meadows, respectively.

Distribution of the seagrass meadows in the future

Compared to the present day, seagrass meadows expanded their distributions inland, occupying areas which were once barren substrate. Based on the trajectories, RCP4.5 showed a moderate expansion of the seagrass meadow throughout the years (Fig 5 – 7), while RCP8.5 expressed a moderate expansion in 2025, while in the following 50 years the seagrass drastically expanded or diminished their area (Fig 8 – 10). Mixed seagrass meadows showed a clear pattern of expansions in the shallower areas, while the uniform meadows did not expand in the shallower areas (except at Pa Klok). Uniform meadows occupied the similar space as in the present time, until they completely vanished from the area.

In the future years, following both climate change trajectories, total seagrass area in all study sites increased (Table 4 and 5). The highest increase in the area, in both RCPs, was in the mixed meadows at Libong site 1, followed by mixed meadows at Sriboya and at Pa Klok. In the uniform meadows, there was increase in the area in both pathways only for the meadows at Pa Klok. The uniform seagrass meadows at Sriboya disappeared in 2050 in both RCPs, while at Libong 2 they vanished by 2075 following RCP4.5 and by 2050 following RCP8.5. The meadows at Libong 1, showed the tendency of area declining in both RCPs. The probable distribution of seagrasses in both RCPs in 2025, 2050 and 2075, is presented on the Figures 5 and 8, 6 and 9, 7 and 10, respectively.

Mixed and uniform meadows had different trends along the years, in both pathways. Following RCP4.5, in 2025 the area of the uniform meadow at Sriboya decreased by more than 50%, and it disappeared by 2050 (Table 5, Appendix 2D). On the other hand, at Libong site 1 in 2025 the area increased more than 1,000 %, and then started to decrease, but by 2075 it never reached the size of the original area (Table 5, Appendix 2D). At Libong site 2, the area of uniform meadow increased by more than 3,000% by 2025 from its original size in present day, but by 2050 the area decreased and by 2075 the whole meadow disappeared (Table 5, Appendix 2D). On contrary, at Pa Klok the trend was different, by 2025 the area of uniform meadow increased by more than 2,000% and it continued to increase in the next 50 years (Table 5, Appendix 2D). Following RCP8.5, the uniform meadows expressed similar trend, but the increases and decreases were more noticeable, with the drastic decrease of 87% of the uniform meadow at Sriboya by 2025 and its complete disappearance by 2050 (Table 6, Appendix 2D). Uniform meadows at Libong site 1 and Pa Klok had the same trend in each year, as in the RCP4.5 (Table 6, Appendix 2D). On the other hand, uniform meadow at Libong site 2, presented complete disappearance by 2050 (Table 6, Appendix 2D). On contrary, mixed seagrass meadows expressed only increase in their area in both pathways, increasing by more than 1,000% than their original area in the present (Table 6, Appendix 2D).

Table 4. The seagrass area in the selected years in the future following RCP 4.5 trajectory

Year	Seagrass area (ha)	Sriboya	Pa Klok	Libong 1	Libong 2
	Total	475.80	728.40	1,990.65	833.70
2025	Uniform	11.30	288.10	270.10	572.50
	Mixed	464.50	440.30	1,720.55	261.20
	Total	555.80	1,089.00	2,173.20	91.02
2050	Uniform	0.00	468.20	126.70	51.20
	Mixed	555.80	620.80	2,046.50	39.82
	Total	612.30	1,154.15	2,216.00	508.70
2075	Uniform	0.00	503.20	98.60	0.00
	Mixed	612.30	650.95	2,117.40	508.70

Table 5. The seagrass area in the selected years in the future following RCP 8.5 pathway

Year	Seagrass area (ha)	Sriboya	Pa Klok	Libong 1	Libong 2
	Total	488.60	811.50	1,968.10	745.60
2025	Uniform	3.10	328.40	234.30	409.20
	Mixed	485.50	483.10	1,733.80	336.40
	Total	618.70	1,242.10	2,106.80	528.80
2050	Uniform	0.00	705.10	108.20	0.00
	Mixed	618.70	537.00	1,998.60	528.80
2075	Total	643.60	1,360.70	2,200.20	664.70
	Uniform	0.00	710.80	80.10	0.00

Mixed	643.60	649.90	2,120.10	664.70

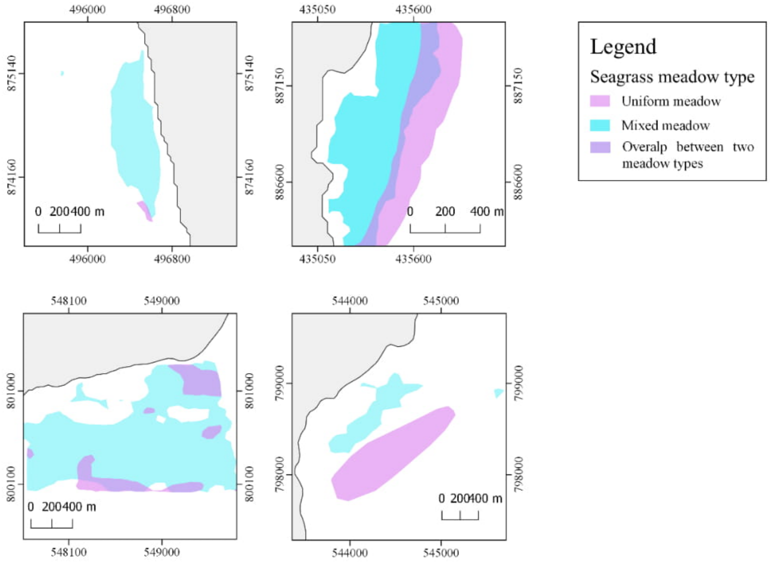

Figure 5. Seagrass meadow distribution in 2025 following RCP 4.5

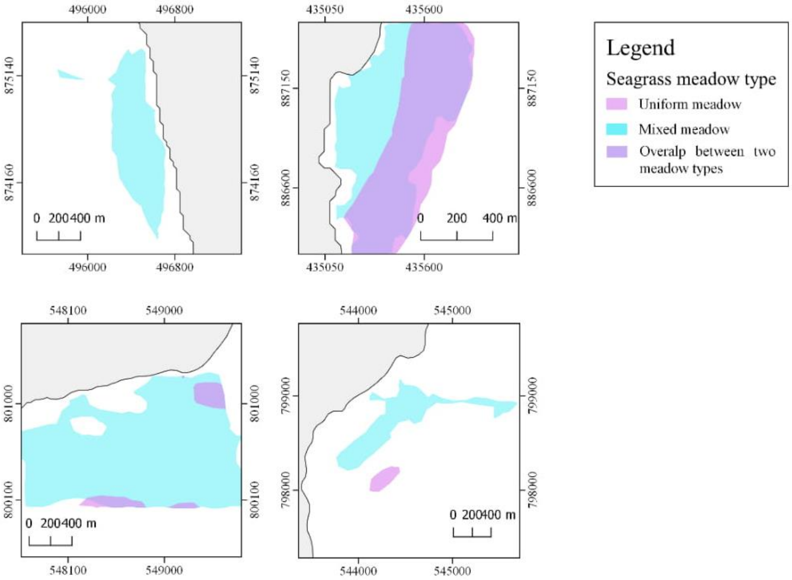

Figure 6. Seagrass meadow distribution in 2050 following RCP 4.5

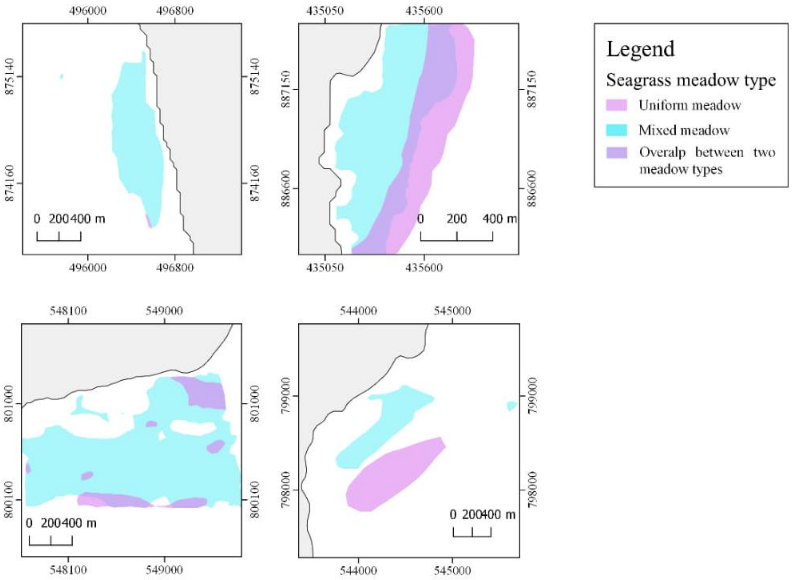

Figure 7. Seagrass meadow distribution in 2075 following RCP 4.5

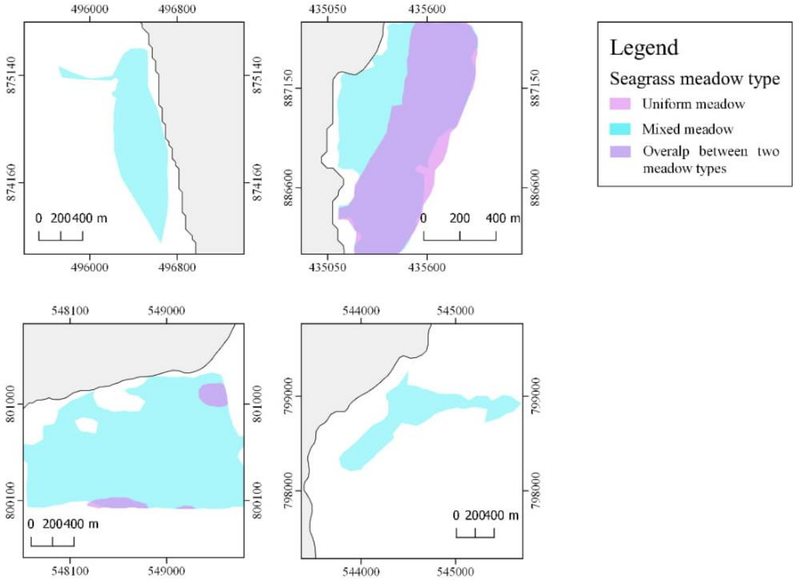

Figure 8. Seagrass meadow distribution in 2025 following RCP 8.5

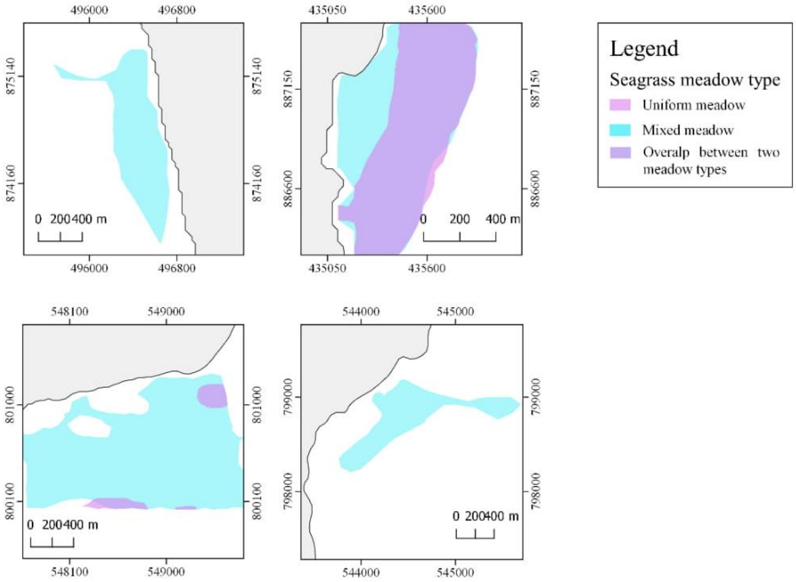

Figure 9. Seagrass meadow distribution in 2050 following RCP 8.5

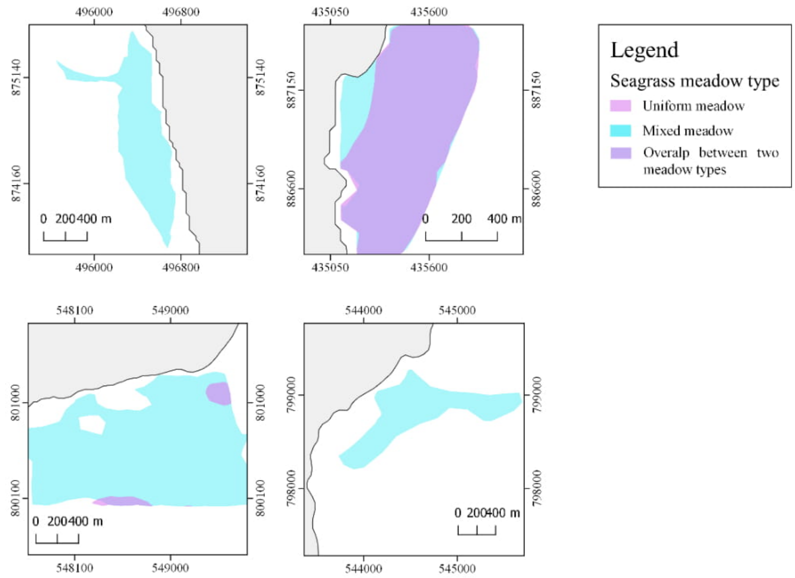

Figure 10. Seagrass meadow distribution in 2075 following RCP 8.5

Discussion

Seagrass mapping

Mapping of the seagrass meadows for monitoring purposes has been conducted using a variety of the approaches, including scuba/snorkeling surveys (Gotceitas et al. 1997), ground based sampling (Moore et al. 2000) and mapping using hovercraft (Mckenzie 2003). Remote sensing approaches are becoming widely used to estimate species coverage, biomass, species composition and quality of seagrass habitats (Koedsin et al. 2016; Lyons et al. 2015; Phinn et al. 2008; Roelfsema et al. 2014). However, the inability of satellite's measurements to capture fine scale patterns of the seagrass distribution and sparsely vegetated area, has led to the use of drones, which have been widely used in hydrology (DeBell et al. 2015), forestry (Inoue et al. 2014) and wildlife monitoring (Chabot et al. 2015; Hodgson et al. 2013). More recently, drone technology has been used to successfully map seagrass meadows (Duffy et al. 2018). As these technologies are coming more available, their use and obtained maps of the seagrass meadows should not be limited only to monitoring. In this study we presented how the seagrass maps can be used in a climate change modeling. However, the use of drone in mapping seagrass meadows is limited to intertidal areas. Lower intertidal and subtidal areas can me mapped using drone, only when the water is not turbid and murky, as in the case of Libong site 2.

Modeling

In the recent years, ecological modeling became very useful tool in showing and describing the influence of the different factors towards the species, communities and ecosystems. These models utilize associations between environmental variables and species occurrence records (Pearson et al. 2007) and then identify where suitable environments are distributed in the space and/or time. Species distribution models have been widely used in terrestrial ecosystems, while in marine environments models have been rare until last few decades (Elith and Leathwick 2009). However, most of the models have been developed on the marine animals, with only few models for seagrass ecosystems (Chefaoui et al. 2016; Downie et al. 2013; Grech and Coles 2010). In all cases, modeling approaches (GAM, GLM, RF, MARS, Maxent and Bayesian belief) were successful in predicting seagrass occurrence in spatial scale based on the species–environment relationship of *Cymodocea nodosa* (Chefaoui et al. 2016), *Zostera marina* (Downie et al. 2013) and species assemblage at Great Barrier Reef (Grech and Coles 2010) and vast range of environmental and landscape variables.

Our results demonstrate that seagrass distribution can be successfully modeled using GAM modeling approach in space and time using their occurrence and a set of environmental variables. Although, the model included only two environmental factors, both variables are highly important for the seagrass growth and well-being. Additionally, these two factors are highly associated with the climate change, where their change triggers a number of negative effects on the ecosystems (IPCC 2014). Sea surface temperature has been shown as important variable in seagrass distribution modeling (Chefaoui et al. 2016), while the effects of sea level rise indicated that the seagrass habitats would decrease due to reduced light penetration (Davis et al. 2016) or coastal squeeze (Mills et al. 2016). The studies have shown that half of the mangrove forests of Indo-Pacific will be lost by 2100 due to sea level rise (Lovelock et al. 2015) and the inability to move inland.

Changes of the seagrass distribution

The predicted seagrass distribution covered larger area than in the present time. The rise of the sea level increased habitat availability, as the areas towards the land in present time were too shallow for seagrasses to grow. The distribution and biomass seagrass species are negatively correlated with tidal exposure and amount of solar radiation (Stapel, Manuntun, and Hemminga 1997; Unsworth et al. 2012), suggesting that their upper distribution is limited by exposure duration and the availability of water during the lowest tides. The seagrass meadows expanded their distribution towards these areas, as the depth increased. The general trend of the seagrass distribution of uniform and mixed meadows was different. The mixed meadows expanded their distribution in the shallower areas, as did the mixed seagrass meadows of Solomon Islands (Albert et al. 2017). However, their lower limit of distribution in deeper parts was not reduced, as they have large depth range (Duarte 1991). The high expansion of mixed species meadows is due to the species characteristics. These meadows consist of medium size species, which are considered opportunistic, with higher recruitment rate (Vermaat et al. 1995) and shoot turnover (Kilminster et al. 2015). On the other hand, uniform meadows expanded their distribution towards shallower areas by 2025, but by the end of the century their distribution reduced, or the meadow vanished.

The sea level rise is suggested to have high influence the distribution of the uniform meadows, as *E.acoroides* has very narrow depth range (Duarte 1991). Its upper distribution limits are influenced by the exposure duration, as it is very vulnerable to the solar radiation (Unsworth et al. 2012), while the lower limits are correlated with the availability of light (Kiswara et al. 2005).

The temperature of the sea is known to have influence on the seagrass growth, production and gemination (Short and Neckles 1999). As the temperature in the future will increase by only a few degrees Celsius, its influence on tropical seagrass will be minimal. The studies showed that both meadow types have highest leaf growth (Kenyon et al. 1997) and net photosynthesis (Pedersen et al. 2016) at the temperatures around 30°C. Temperatures higher than 45°C resulted in the sharp decline of net photosynthesis and the leaf die off at 50°C (Pedersen et al. 2016), suggesting that these species have physiological resistance (Kilminster et al. 2015).

Changes of the seagrass area

Change of the seagrass area in the future was estimated based on the probable occurrence of the species. As uniform and mixed meadows were modeled separately, there were areas which were suitable for both meadow types, seen as overlapping areas on Fig 5 – 10. The mixed meadows would most probably occupy these areas, as the species are considered opportunistic, with high shoot turnover, higher growth rate, they faster reach sexual reproduction and they have rapid recovery (Kilminster et al. 2015). On the other hand, the overlapping areas also included the parts where the mixed meadows expanded their distribution into the areas where uniform meadows are in present time (Libong 1 and Pa Klok). As uniform meadows consist of climax species, which is very persistent and constant (Kilminster et al. 2015; Vermaat et al. 1995), it is highly probable that they would continue to occupy these areas.

Conclusion

This study provided the novel information how the climate change would impact the seagrass meadows in South East Asia. Although the models have certain limitations and they are as accurate as the input information, they can be used in various situations. This knowledge of distribution change of the seagrass meadow can be used by managers to promote and enhance seagrass health, conservation and to set conservation priorities. As seagrass ecosystems play important role in mitigation of climate change, these results can be used to estimate the future carbon sequestration and storage capacities in these ecosystems, as well as the CO_2 emissions of the diminishing meadows. However, it is necessary to continue the testing the modeling approaches and to include more environmental variables, so the predicted distribution of the seagrass can be as close as possible to the real-life scenario.

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List of Publication and Proceeding

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