

**MAPPING SEAGRASS HABITAT AND CHARACTERISING DUGONG
FEEDING PREFERENCES IN SIBU-TINGGI ARCHIPELAGO, JOHOR**

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**INSTITUTE FOR ADVANCED STUDIES
UNIVERSITI MALAYA
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CHARACTERISING DUGONG FEEDING
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JOHOR**

HENG WEI KHANG

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**INSTITUTE FOR ADVANCED STUDIES
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2021

Dugong dugon
LADY OF THE SEA



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**MAPPING SEAGRASS HABITAT AND CHARACTERISING DUGONG
FEEDING PREFERENCES IN SIBU-TINGGI ARCHIPELAGO, JOHOR**

ABSTRACT

The dugong (*Dugong dugon*) is a marine mega-herbivore that is a seagrass community specialist. Seagrass meadows are eminently essential to dugongs as their main feeding grounds. The species' feeding behavioural patterns are often associated with the features of the seagrass habitat. Elucidating such behavioural patterns is vital for understanding how a designated space is used. In Malaysia, the Sibul-Tinggi Archipelago, is regarded as one of the most important habitats for dugongs, hosting a significant local population due to the presence of extensive subtidal seagrass meadows. Field surveys were conducted in 2016 – 2018, across three seasons influenced by the northeast monsoon. An underwater towed video and spatial interpolation method was used to map the meadow extent and seagrass coverage in the Sibul Archipelago, while field sampling of seagrass was conducted around both Sibul and Tinggi Islands to investigate dugong feeding habits and preferences. The mapped meadow was found to be by far the largest known seagrass bed in Malaysia with an areal size of 12.88 km². The meadows experienced a reduction of areal extent from the inter-monsoon and pre-monsoon to only 76% of the original size during the post-monsoon. Seagrass coverage similarly declined from mode 76-100% cover to mode 0-5% cover. At local scale (<10 km²), dugongs demonstrated a spatially clustered feeding pattern by maintaining a feeding patch size of 1.4 - 4.2 km² across seasons. Two feeding patterns were detected which are likely influenced by seagrass coverage; 1) dispersed feeding occurred when seagrass meadows were in low (mode 0 – 25% cover) and high (mode 76-100% cover) seagrass covers, while 2) concentrated feeding occurred when the seagrass coverage was moderate (mode 26-75% cover). Feeding hotspots were mainly distributed off the southwest of the Sibul Archipelago,

consistently between the southernmost tip of Pulau Sibul Besar and Pulau Sibul Tengah across the seasons, while feeding coldspots were mostly found around the edges of the meadow. Seagrass cover in the feeding hotspots was significantly higher than in the feeding coldspots, indicating that dugongs were strategically feeding in response to seagrass quantity. Generalized linear modelling identified the aboveground biomass and the ratios of aboveground:belowground biomass of *Halophila ovalis* as the most potential drivers of feeding area selection in the Sibul-Tinggi meadows (with combined explained deviances of 38.0% out of 56.0%), highlighting the role of the quantity of *H. ovalis* among the other factors. The proportion of silt-clay in the sediment was also selected by the model to explain the presence of dugong feeding (with explained deviances of 11.99% out of 56.0%). Although food quality parameters were absent in the final model, dugong feeding areas were associated with seagrasses with high nitrogen (0.14 - 2.13%), starch (1.53 - 3.11%) and fibre (3.02 - 14.98%) concentrations, but with low carbon (19.08 - 37.08%) and C:N ratios (15.97 - 264.84). Interspecies nutrient comparisons showed that the high starch and low fibre concentrations likely made *H. ovalis* and *Halodule uninervis* the most favoured food species, besides their fast regeneration characteristic which provides the benefit of continuous food supply to the dugongs. This in-depth study of dugong spatial and feeding ecology in subtidal seagrass meadows provides important baseline information to monitor changes in the species' core habitats and identify important areas for conservation and habitat management.

Keywords: herbivore, seagrass, subtidal, habitat use, Malaysia

PEMETAAN HABITAT RUMPUT LAUT DAN PENCIRIAN PILIHAN

MAKANAN DUGONG DI KEPULAUAN SIBU-TINGGI, JOHOR

ABSTRAK

Dugong (*Dugong dugon*) ialah sejenis herbivor mega laut yang mempunyai tabiat pemakanan khusus di kalangan ahli komuniti rumput laut. Padang rumput laut adalah penting kepada dugong sebagai kawasan makan utama mereka. Corak perilaku pemakanan species ini sering dikaitkan dengan ciri-ciri habitat rumput laut. Penjelasan terhadap corak perilaku pemakanan yang sedemikian adalah sangat penting untuk memahami bagaimana ruang habitat digunakan. Di Malaysia, Kepulauan Sibutinggi adalah salah satu habitat terpenting untuk populasi dugong, yang mempunyai populasi tempatan yang signifikan kerana terdapatnya padang rumput laut yang luas. Kerja lapangan telah dijalankan dari tahun 2016 – 2018, merentas tiga tempoh yang dipengaruhi oleh monsun timur laut. Kaedah video tunda bawah laut dan kaedah interpolasi digunakan untuk memeta keluasan dan liputan rumput laut di Kepulauan Sibutinggi, manakala kerja persampelan rumput laut pula dijalankan di perairan Pulau Sibutinggi and Pulau Tinggi untuk menyiasat faktor pemilihan makanan dugong. Padang rumput laut di Pulau Sibutinggi didapati mempunyai keluasan rumput laut yang terbesar di Malaysia dengan ukuran seluas 12.88 km². Keluasan padang rumput laut tersebut menurun dari musim ‘antara monsun’ dan ‘pra monsun’ ke hanya 76% daripada keluasan asal semasa musim ‘pasca monsun’. Liputan rumput laut turut menurun dari mod 76-100% ke mod 0-5%. Pada resolusi berskala tempatan (<10 km²), dugong menunjukkan corak pemakanan berkelompok dengan saiz ruang makan seluas 1.4 - 4.2 km² di sepanjang tiga musim. Terdapat dua corak pemakanan dugong yang dikesan dalam kajian ini yang berkemungkinan dipengaruhi oleh liputan rumput laut: 1) pemakanan secara tersebar, ketika liputan rumput laut pada tahap rendah (mod 0 - 25%) dan tinggi (mod 76-100%), dan 2) pemakanan

secara bertumpu, ketika liputan rumput laut pada tahap sederhana (mod 26-75%). Di sepanjang tiga musim, kawasan *hotspot* kebanyakan terletak di sebelah barat daya Kepulauan Sibul, iaitu di antara hujung selatan Pulau Sibul Besar dengan Pulau Sibul Tengah, sementara kawasan *coldspot* kebanyakan terletak di pinggir padang rumput laut. Liputan rumput laut di kawasan *hotspot* adalah jauh lebih tinggi daripada kawasan *coldspot*, menunjukkan bahawa dugong memakan secara berstrategi yang mana dipengaruhi oleh kuantiti rumput laut. Biojisim rumput laut di atas permukaan tanah dan nisbah biojisim rumput laut di atas permukaan tanah: biojisim rumput laut di bawah permukaan tanah bagi *Halophila ovalis* telah dikenal pasti oleh *Generalized Linear Model* sebagai faktor-faktor yang paling berpengaruh dalam pemilihan tempat makan dugong di Kepulauan Sibul-Tinggi (jumlah *explained deviances* ialah 38.0% daripada 56.0%). Ini menonjolkan peranan kuantiti rumput laut *H. ovalis* di antara faktor-faktor lain. Perkadaran nisbah tanah *silt-clay* dalam sedimen juga dipilih oleh model sebagai salah satu faktor yang mempengaruhi pemilihan tempat makan dugong (jumlah *explained deviances* ialah 11.99% daripada 56.0%). Walaupun parameter kualiti makanan tidak termasuk dalam model terakhir, namun tempat makan dugong didapati berkait rapat dengan rumput laut yang mempunyai kandungan nitrogen (0.14 – 2.13%), kanji (1.53 – 3.11%) dan serat (3.02 – 14.98%) yang tinggi, serta rumput laut yang mempunyai kandungan karbon (19.08 – 37.08%) dan nisbah C:N (15.97 – 264.84) yang rendah. Selain mempunyai ciri pertumbuhan semula yang cepat serta kemampuan membekalkan sumber makanan yang berterusan kepada dugong, perbandingan nutrien antara species telah menunjukkan bahawa kandungan kanji yang tinggi dan serat yang rendah pada *H. ovalis* dan *Halodule uninervis* berkemungkinan menjadikan kedua-dua species tersebut sebagai makanan yang paling digemari oleh dugong. Kajian terperinci ini mengenai ekologi ruang dan pemakanan dugong di habitat rumput laut subpasang surut telah mengumpulkan

maklumat asas bagi membantu pemantauan perubahan pada habitat utama haiwan dan penentuan kawasan penting untuk pemuliharaan dan pengurusan habitat tersebut.

Kata kunci: herbivor, rumput laut, subpasang surut, penggunaan habitat, Malaysia

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LIST OF SYMBOLS AND ABBREVIATIONS

DM	:	Dry matter
g DW m ⁻²	:	Gram dry weight per square metre
km ²	:	Square kilometre
HO	:	<i>Halophila ovalis</i>
HU	:	<i>Halodule uninervis</i>
CS	:	<i>Cymodocea serrulata</i>
SI	:	<i>Syringodium isoetifolium</i>
AG	:	Aboveground
BG	:	Belowground
C	:	Carbon
N	:	Nitrogen
P	:	Phosphorus
S	:	Starch
TDF	:	Total dietary fibre
DFT	:	Dugong feeding trails
FA	:	Feeding areas
NFA	:	Non-feeding areas
h	:	Hour
GLM	:	Generalized linear model

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CHAPTER 1: GENERAL INTRODUCTION

1.1 The dugong

The dugong (*Dugong dugon*) is the one and only mammalian herbivore that is strictly marine and feeds on seagrass throughout its lifespan, from a calf a few weeks after birth until the average age of 70 years in the wild (Heinsohn & Birch, 1972; Marsh et al., 1982). The dugong is the only living species in the Family Dugongidae (Order Sirenia), sharing an ancestral lineage with the Steller's sea cow (*Hydrodamalis gigas*) which went extinct in the 18th century, and another closer modern day relative in the Family Trichechidae (Order Sirenia) – the manatee (Domning, 1994).

The dugong normally occupies shallow water ecosystems along the tropical and subtropical coasts and islands of the Indo-West Pacific Ocean, from East Africa to the Solomon Islands and Vanuatu, which coincides with the distribution of its food plants (Marsh et al., 2002). Spanning across at least 48 states (countries and territories that exercise jurisdiction over any part of the range of the species) in its range, most of the dugong population nowadays is considerably reduced in comparison to historical records, resulting in small, isolated and scattered populations separated by large areas of seas and continents. Moreover, population status data is scarce and high threat exposures have been an issue to many of the developing countries that comprise the majority of the dugong's range (Hines et al., 2012). Among the recognised threats to dugongs include direct take for their meat and parts such as oil and tusks, habitat destruction or modification, incidental capture as bycatch, injury or mortality caused by boats or fishing practices such as dynamite and cyanide, and pollution (Marsh et al., 2002). Given those threats, the dugong is classified as 'Vulnerable to Extinction' on the IUCN Red List of Threatened Species, and is especially vulnerable in areas with small populations such as Eastern Africa, the India sub-continent and Andaman and Nicobar Islands, and Southeast Asia (Marsh & Sobotzick, 2015).

In Malaysia, the dugong is categorised as an endangered marine species in the Fisheries (Control of Endangered Species) Regulation 1999 and is fully protected under the Fisheries Act 1985 (Part VI, Aquatic Mammals) (in Peninsular Malaysia), the Wildlife Conservation Enactment 1997 (in Sabah) and the Wildlife Protection Ordinance 1998 (in Sarawak). Dugong sightings within the country encompass historical records, anecdotal reports, stranding records, interview surveys, boat-based surveys and aerial surveys, all of which suggest that the species occurs in low numbers locally (Nadarajah, 2000; Marsh et al., 2002; Jaaman & Lah-Anyi, 2003; Perrin et al., 2005; Rajamani, 2013; Ponnampalam et al., 2015). In present times, dugongs still occur in the Johor Strait, Johor east coast islands, Brunei Bay, Labuan, Pulau Banggi (*pulau* = island), Pulau Jambongan, Kudat, Sandakan and Pulau Mantanani, as depicted in **Figure 1.1** (Mansor et al., 2000; Affendi et al., 2005; Zulkifli Poh, 2009; Rajamani & Marsh, 2010; Ponnampalam et al., 2015).



Figure 1.1 Major locations of dugong sightings in Malaysia

In Peninsular Malaysia, the Johor east coast islands of Sibul and Tinggi are host to a significant population of dugongs whereby a maximum daily count of 20 individuals and 4 mother-calf pairs were recorded during an aerial survey in 2010, covering nearly 3,000 km of search area (Ponnampalam et al., 2015). The presence of this small but viable population, which is mainly distributed off the southwest of Pulau Sibul, reinforced the previous findings of Mansor et al. (2000) and Affendi et al. (2005). The population is believed to be a resident attributable to the existence of an extensive seagrass meadow in this area (Ooi et al., 2008). While those aforementioned threats for dugongs still exist in Malaysia, it is exacerbated by the increasing loss of seagrass habitats and insufficient knowledge of its ecology (see next section).

1.2 Seagrass

Seagrasses, which comprise the main diet of dugongs, are not true grasses even though they resemble terrestrial grasslands. Seagrasses are the only vascular flowering plants (angiosperms) that are adapted to fully submerged life in marine waters. They form dense meadows on the seafloor along shallow coastal waters of all the world's continents, except in Antarctica (Green & Short, 2003). There are 70 recognised species classified in 13 genera within six families of seagrasses worldwide (Cymodoceaceae, Hydrocharitaceae, Posidoniaceae, Zosteraceae, Ruppiaceae, Potamogetonaceae) (Larkum et al., 2018). The Indo-Pacific region has the highest record for seagrass diversity in the world, with up to 24 species (Short et al., 2001).

Seagrasses form a highly productive marine ecosystem which has long been recognised as providing multiple essential ecosystem services (Nordlund et al., 2016). Seagrass beds serve as food and nursery habitats for more than 1,000 species of fish and shellfish, including commercially important fisheries species such as penaeid shrimps, Atlantic cod and white-spotted spinefoot, especially during their juvenile stage (Ho et al.,

2018; Unsworth et al., 2019). It is also a critical habitat for many threatened and charismatic species such as dugongs, manatees, sea turtles and seahorses (Bjorndal, 1980; Marsh et al., 2005; Castelblanco-Martínez et al., 2009; Vincent et al., 2011). Additionally, seagrasses also largely contribute to biogeochemical cycling, improve water quality by filtering suspended sediments, recycling nutrients, dissipate wave impacts, and stabilise bottom sediment (Orth et al., 2006; Christianen et al., 2013). By accounting for 10% of the ocean's capacity to store carbon, seagrasses help to mitigate the rapid threat of global warming (Fourqurean et al., 2012; Duarte et al., 2013).

Unfortunately, there has been a global decline of seagrass meadows due to multiple natural and anthropogenic stressors (Waycott et al., 2009). This habitat loss is considered to have contributed to the decline, and even extinction, of many seagrass-associated species, especially dugongs (Preen & Marsh, 1995; Carlton et al., 1991; Christianen et al., 2014; Harasti, 2016). It is now known that herbivory by grazers such as dugongs and green turtles in the seagrass meadow is desirable for sustaining the delivery of its ecosystem services by altering biomass, productivity and species assemblages (Jackson et al., 2001; Christianen et al., 2018; López et al., 2019). Therefore, knowledge of the complex interactions between plants and herbivores, e.g., top-down and bottom-up responses of seagrass and dugong, are crucial for effective management of the species' habitats in order to achieve a balanced ecosystem that well delivers its services (Scott et al., 2018).

Seagrasses are one of the most overlooked coastal ecosystems in terms of knowledge and protection (Unsworth et al., 2019). Southeast Asia is one example of a region that has very little information of seagrass from the published literature, and has been facing challenges in the conservation and management of seagrass resources (Ooi et al., 2011b). Despite having high species diversity and providing numerous ecosystem services, seagrasses in Malaysia are largely understudied and underdocumented, with only 0.02%

of known meadow extent in relative to the size of the country's territorial sea (Ooi et al., 2011b; Fortes et al., 2018). Increasing human use of coastal areas with concomitant land reclamation for urban development or agriculture, pollution and sedimentation, has led to the degradation of seagrasses in Malaysian waters (Kamarruddin, 2008). Lack of local baseline information especially on spatial extent of seagrass meadows, species composition and abundance, is limiting our understanding of the ecological interactions between a seagrass habitat and the herbivores that depend on it. In this case, the paucity of information on the distribution of seagrass meadows within the dugong habitat is hampering progress in identifying dugong feeding grounds and their feeding behaviours, which in turn are impeding the protection and management of endangered dugong populations and their critical habitats in Malaysia.

1.3 Dugong spatial foraging ecology

1.3.1 Spatial ecology

Spatial ecology aims to understand how spatial arrangement of organisms, populations and landscapes influence ecological dynamics (Fletcher et al., 2018). Ecological dynamics, in a broad sense, is related to the interactions of each ecological entity within an individual organism (e.g., movement, dispersal, migration), within and across species (e.g., competition, facilitation, trophic level), as well as the responses of organisms to environmental features that are established in space (habitat heterogeneity) (Holyoak et al., 2005). In the end, it is the combined action and feedback of these processes that result in the spatial patterns that are observed at the population or community levels.

The approach of spatial foraging ecology is to look at how space affects both the spatial structure of the foraging habitat and foragers' distributions, and how foragers respond to spatially structured foraging habitats (**Figure 1.2**). Ecological processes such as dispersal

or interactions tend to operate with an inherent link-effect with nearby locations, creating autocorrelation in foragers abundance. Foragers respond to the variations of the environmental conditions in the habitat, which themselves are inherently structured in space, inducing spatial dependence with more complex patterns (i.e., linear or non-linear interactions) at a specific scale. However, studying foraging in spatially complex landscapes that have patchy resource distribution is especially challenging because there are multiple processes at play across the space, each of which are themselves shaped by environmental changes.

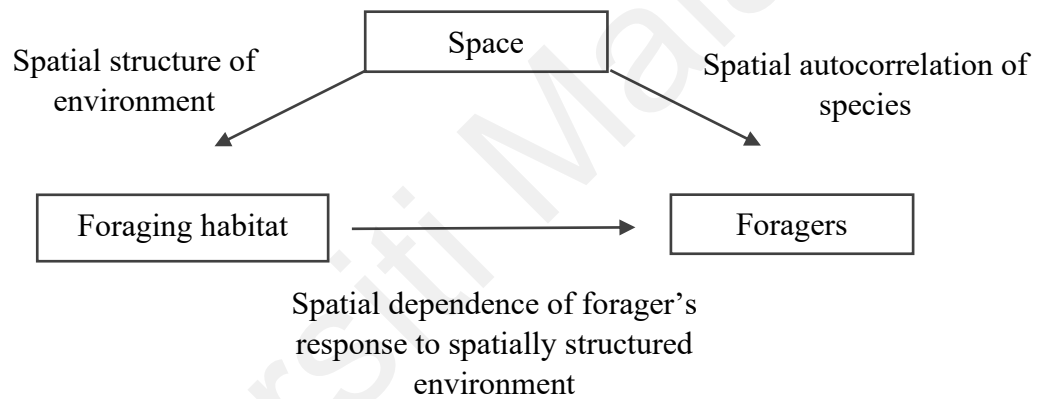


Figure 1.2 The effect of space to the habitat (environment) and foragers (species) distribution. (adapted from Wagner & Fortin, 2005).

1.3.2 Dugong habitat use in spatiotemporally complex seagrass meadows

Like terrestrial grasslands, seagrass meadows are usually spatially heterogenous (patchy) habitats from fine spatial scales to landscape scales (Larkum et al., 2018). Each of the patches have different vegetation structure which vary in species composition, abundance and nutritive value (Preen & Marsh, 1995). These variations are often driven by compounding factors of plant life strategies, physiochemical and biological properties of both water and sediments, in addition to anthropogenic impacts such as nutrient influx and pollution (Hemminga & Duarte, 2000). As a result, the wide variation of nutritive

quality across seagrass patches forms spatiotemporally complex carrying capacity of a habitat for dugongs and has a remarkable influence on their feeding behaviour and habitat use (Gross et al., 1995).

The habitat use behaviour of dugongs is not yet fully understood. Dugongs have been observed to select certain types of seagrass beds as their foraging ground and avoid others at a range of spatial scales (Heinsohn & Birch, 1972; Preen, 1995b; Sheppard et al., 2007; Sheppard et al., 2010; D'Souza et al., 2015). Yet, the external factors that drive feeding area selection of dugongs are still not well established as they appear to differ between locations (Tol et al., 2016). Feeding behaviour, which greatly influences the decisions in selecting feeding area, is difficult to be confirmed in the wild as food choices are not consistent across all locations and times (Marsh et al., 2011). For instance, dugongs were observed to feed deliberately on ascidians and polychaetes in the subtropical Moreton Bay and Shark Bay, Australia, but dugongs in the tropics were rather ingesting them incidentally with seagrass, possibly because seagrass species in the tropics is more diverse and less seasonally variable in terms of nitrogen availability (Anderson, 1989; Preen, 1995a). In fact, the diet of the dugong's closest relative, i.e., the manatee, has also shown variations with regard to location (Mignucci-Giannoni & Beck, 1998; Castelblanco-Martínez et al., 2009; Alves-Stanley et al., 2010).

While identifying key habitats is one of the most important initiatives for the conservation of dugongs, knowledge of habitat use by dugongs has been very limited outside of Australian waters particularly in the Malaysian region, due to the lack of information needed to predict the behavioural response of the animals towards heterogeneous seagrass landscapes (Briscoe et al., 2014). At present, there are only two studies, i.e., Briscoe et al. (2014) and Hashim et al. (2017), that have been conducted in Malaysia to examine the relationship between dugong presence and the habitat characteristics. However, both studies were limited by either the availability of primary

data collected on the environment of the dugong habitats or high-resolution spatial information of dugong presence-absence, and therefore might not have fully captured the behaviour and habitat use patterns that would help to predict habitat choices by dugongs across multiple scales. With regard to this, Sheppard (2008) addressed the information that is required to determine spatial habitat use of dugongs, which included: (i) the characteristics (i.e., species composition, meadow structure, nutrient quality, substrate type) of the seagrass patches that dugongs select or avoid when foraging at local scales ($< 10 \text{ km}^2$), (ii) the characteristics of the seagrass meadow that dugongs use to forage at landscape-scales ($10 - 10\,000 \text{ km}^2$), and (iii) the movement patterns of dugongs when foraging between core habitats at regional-scales ($> 10\,000 \text{ km}^2$).

1.4 Dugong feeding ecology

1.4.1 Feeding behaviours

Dugongs, like other sirenians, forage for food in the seagrass meadow in two different ways (Heinsohn & Birch, 1972). The more common feeding mode is “excavating” by uprooting the whole plant including both above-ground (leaves and shoots) and below-ground parts (rhizomes and roots), which disturbs the sediment and creates sediment plumes. Such feeding method enables the dugong to obtain adequate energy and nutritional value from the whole plant, to best support the growth of their large body size and lifetime reproductive success. Another feeding mode of the dugong is “cropping”, which removes the above-ground plant parts only, and is employed when feeding on tall-growing seagrass species such as *Amphibolis antartica* or *Enhalus acoroides* (Anderson, 1982; Nakanishi et al., 2008) or in seagrass patches with compacted sediment (Aragones, 1996). Cropping has been suggested as a safer tactic for dugongs to remain vigilant of its predators (Wirsing et al., 2007a). Feeding scars, also known as feeding trails due to their track-like appearance on the bottom sediment, are left behind by the dugongs after

excavating the seagrass, and are used as indicators for their feeding activity (Preen, 1992; Nakanishi et al., 2006; Tol et al., 2016).

Dugongs typically feed in the seagrass meadows in small (three to five animals) to large herds (more than five and up to 15 animals in each), or sometimes solitarily (Anderson & Birtles, 1978). They have been observed to enter shallower intertidal areas during an ascending tide and move to deeper areas or outside of the seagrass meadow as the tide recedes (Anderson & Birtles, 1978; Sheppard et al., 2009). Dugongs also spend most of their time (67% - 75% of all dives) in a day feeding (Anderson, 1998; Chilvers et al., 2004). It is estimated that adult dugongs can eat up to 28 to 40 kg of seagrass per day, which amounts to approximately 7 to 10% of their body weight (for a dugong sized at 350 to 400 kg) to supply energy for their metabolic and physiological use (Best, 1981; Preen, 1992; Aragonés, 1994; Goto et al., 2004).

1.4.2 Feeding preferences

Analysis of dugong stomach and mouth contents proved that dugongs consumed mainly seagrass leaves and rhizomes (Johnstone & Hudson, 1981; Marsh et al., 1982; André et al., 2005), while algae is largely consumed only under exceptional circumstances when seagrass is not available (Preen, 1995a). Seagrass species typically consumed by dugongs encompass 9 genera and 26 species that occur within their range (Green & Short, 2003). It has been inferred that dugongs show preference for 'colonising' species especially *Halophila ovalis* and *Halodule uninervis*, that are typically lower in fibre and higher in protein than 'opportunistic/persistent' genera such as *Zostera* and *Enhalus* (Lanyon, 1991; Aragonés, 1994; Preen, 1995b). Colonising species, also known as pioneer species, are characterised by faster growth rates, short life spans, and rapid recovery from disturbances. Opportunistic/ persistent species are represented by those

with slower growth rates, long live spans, and slow recovery from disturbances, with persistent species being the latest successional community (Kilminster et al., 2015).

As a seagrass specialist, dugongs exhibit similar feeding preferences as other large, terrestrial mammalian grazers, optimizing their intake of nutrients by selecting high nutritive value and/or energy food plants from within grass prairie of lower quality herbage (Sheppard et al., 2007). A definitive set of determinants for the dugong's food preferences is not clear yet (Marsh et al., 2011). This is because direct observation of diet selection by the animals is difficult in the wild due to their elusive and inconspicuous nature, in addition to availability of food choices that vary with tides and seasons (Schipper et al., 2008; Cleguer, 2015; Sheppard et al., 2007, 2010). For example, within the Australian region, dugongs in the tropical Torres Strait and Great Barrier Reef fed according to species that were present in the area with higher biomass, such as *Thalassia hemprichii*, a persistent species that is lower in nitrogen (André et al., 2005; Tol et al., 2016), in contrast to dugongs in the subtropical Moreton Bay which prefer *H. ovalis* and *H. uninervis* (Preen, 1992). Meanwhile, food selection of dugongs in the intertidal mixed-species seagrass bed at subtropical Hervey Bay was influenced by the tides, as the availability of certain species of foods is restricted during certain periods of the day (Sheppard et al., 2010). Due to the complexity of feeding preferences as reported in the literature (see sub-section 2.1), it is important for research to investigate the habitat characteristics of a dugong population on a site-by-site basis.

1.4.3 Plant-herbivore interactions

As dugongs consume about 7% of their body weight per day, herbivory by dugongs which graze directly on the entire plant of seagrass (i.e., including roots and rhizomes) can remove substantial quantities of seagrass biomass from the meadows. It was estimated that each individual dugong would disturb about 300 to 800 m² of seagrass per

day, with a daily consumption of 3.2 – 4.5 kg dry matter (Marsh et al., 2005). Moreover, dugongs often form small or large herds that graze over a vast stretch of meadow landscapes which could induce intensive grazing disturbance at some sites where dugong densities are high. McMahon (2005) estimated a monthly average of 23% removal of seagrass from *Halophila ovalis* meadow by a population of 50 – 150 dugongs in Moreton Bay, Australia. Masini et al. (2001) estimated that the dugong population removed more than 50% of seagrass production from the meadows in Shark Bay, Western Australia. While in the Andaman and Nicobar Archipelago, India, the shoot density of seagrass was reduced by half with a moderate level of dugong grazing (D'Souza et al., 2015).

Meadows that undergo intensive dugong grazing are not heavily altered in terms of productivity, but also community structure and nutrient composition of the plants especially at the local scale (Aragones & Marsh, 2000). Simulated grazing experiments showed that the composition of seagrass communities could be altered by favouring the growth of fast-growing genera of seagrass such as *Halophila* and *Halodule* at the expense of slower-growing species such as *Zostera capricorni* (Preen, 1995b; Aragones & Marsh, 2000). The chemical composition of the seagrass plants also showed changes after a year – increases in nitrogen concentration in new foliage and reduction in starch for preferred species, i.e., *H. ovalis* and *H. uninervis* (Aragones et al., 2006). Over time, regular feeding by sizable numbers of dugongs may have significant positive effects on grazed meadows by providing better quality food to the herbivore compared to ungrazed or minimally grazed areas, via enhanced nutrient recycling within the sediment column (Lanyon et al., 1989; Aragones, 1996; Perry & Dennison, 1999). This grazing optimisation practice known as “cultivation grazing”, has been suggested as a foraging strategy that provides long-term benefits to the dugongs which feed in large herds such as those in Moreton Bay, Australia (Preen, 1995b) and also dugongs which feed in small assemblages such as those in the tropics (de Iongh et al., 1995; D'Souza et al., 2015).

Another type of positive feedback mechanism is that intermediate levels of dugong grazing would increase the seagrass clonal richness in a meadow by facilitating recruitment of new genets (a single individual comprised of several ramets) into the population, which subsequently increase the seagrass' resilience to disturbance and greater genetic diversity (McMahon et al., 2017). Dugongs also play a role in seagrass seed dispersal by transporting seeds from one population to another (Kendrick et al., 2012; McMahon et al., 2014; Tol et al., 2017), and the faeces of dugongs probably promote the growth of seagrass in areas of deposition (McMahon, 2005).

1.5 Research objectives and hypotheses

1.5.1 Primary research aims

The purpose of this study was to investigate the spatial feeding patterns of dugongs in the Sibuluan Archipelago in Johor, and to ascertain factors driving their feeding preferences and feeding strategies in a subtidal meadow (**Figure 1.3**). First, I aimed to map and characterise the distribution of the seagrass meadow. Using the data, I then aimed to determine whether dugongs are strategic or opportunistic feeders in the seagrass meadows and how their feeding strategies change with seagrass variability across space and time. I also aimed to identify a set of potential factors that competently drive their feeding preferences. This study served as the first in-depth study on dugong feeding behaviour in Malaysia by blending elements of spatial ecology, landscape ecology and nutritional ecology.

Specifically, the objectives of this study were:

- 1) to determine the spatial distribution pattern of seagrass habitats, focusing on the Sibuluan group of islands;
- 2) to elucidate the spatial and temporal distribution of dugong feeding trails in the subtidal seagrass meadow; and

- 3) to ascertain the diversity, vegetative qualities (i.e., abundance, nutrient composition) of seagrass consumed by dugongs and selection factors driving dugong feeding preferences.

1.5.2 Central research hypotheses

My general hypotheses were as follows:

- 1) dugongs are strategic feeders by feeding in a spatially structured pattern;
- 2) dugongs modify their feeding strategies according to food quantity by selecting patches which maximise their net intake (feeding efficiency); and
- 3) site preferences for feeding are influenced by the quantity (abundance) and quality (nutrient) of the seagrass community as a whole, instead of individual species.

1.6 Thesis structure

In *Chapter 2: Literature Review*, I reviewed our current knowledge of the feeding preferences and habitat use behaviour of dugongs and how they are driven by food quality, food quantity and meadow conditions in seagrass habitats. I also summarised the foraging challenges encountered by dugongs and potential coping mechanisms for better understanding the feeding strategies of dugongs in diet and habitat selection.

In view of the absence of spatial information in describing dugong habitats in the Sibuluan Archipelago, an underwater towed video survey was conducted for mapping the seagrass meadow's extent and distribution in order to characterise the spatiotemporal variability of dugong habitat landscape in this area. In *Chapter 3: Spatial and Temporal Distribution Patterns of Seagrass Habitats*, I explained the underwater towed video

method used to conduct a systematic seagrass transect survey to obtain fine-scale biogeographical information of the meadow.

Information of “where” in the meadow they use to feed is key to understanding “how” dugongs use their seagrass habitat by identifying their spatial feeding patterns. In *Chapter 4: Spatial and Temporal Distribution Patterns of Dugong Feeding Trails*, I used spatial analysis to quantify the feeding patterns of dugongs and relate the observed patterns with the spatial dynamics of seagrass cover.

The ultimate understanding in dugong feeding ecology is in knowing “why” they exhibit specific behaviours or strategies when subjected to certain constraints. In *Chapter 5: What Drives Dugong Feeding Preferences*, I examined the biochemical attributes of each food species and physical environmental properties that were present in dugong feeding areas and non-feeding areas to elucidate dugong feeding preferences and the main factors that drive their decisions toward habitat selection.

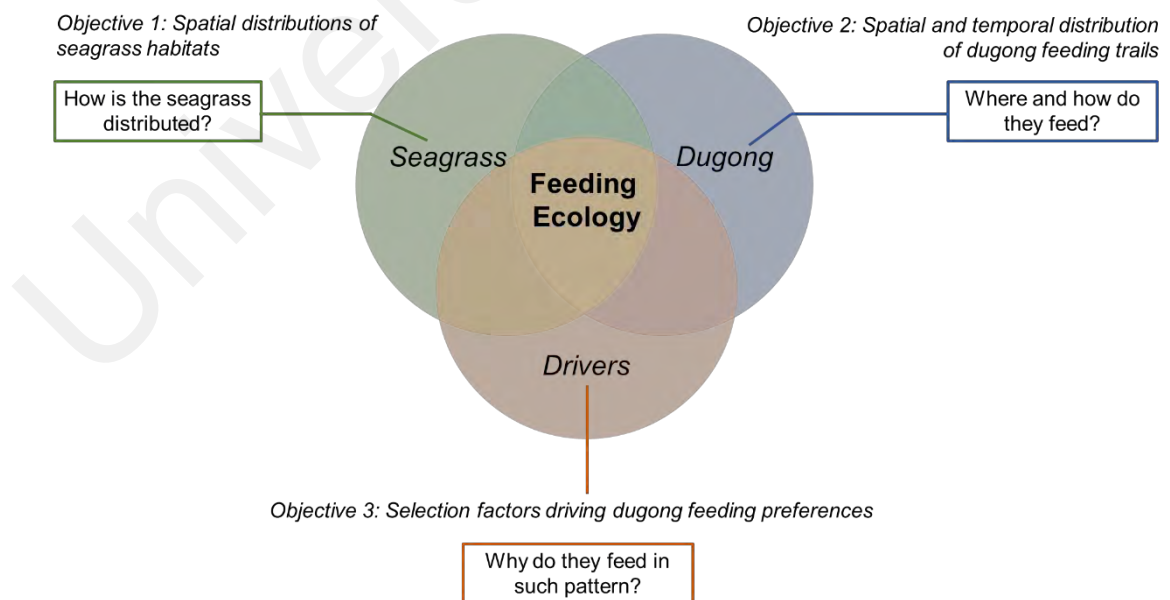


Figure 1.3 A conceptual framework for dugong feeding ecology in this study, showing the integration of three components: seagrass, dugong and drivers

CHAPTER 2: LITERATURE REVIEW

2.1 Dugong feeding preferences and habitat selections

The highly specialised diet requirements and selectivity mechanism of dugongs suggest that some seagrass meadows may be used differently than others as a foraging habitat (Preen, 1995b). There are some potential descriptors of feeding preferences that have been suggested which have been given better ideas of how dugongs use their habitat (Marsh et al., 2011). For herbivores, the nutritive quality of food is commonly known as the primary determinant of feeding preferences over the quantity of food (Owen-Smith & Novellie, 1982). Several researchers who investigated the nutritional profile of seagrasses have suggested that dugongs prefer structurally small, colonising species of seagrass especially *Halophila ovalis* and *H. uninervis*, which are higher in nitrogen and less fibrous compared to larger, persistent species such as *Zostera capricorni* which is lower in nitrogen and more fibrous (Lanyon, 1991; de Iongh et al., 1995; Yamamuro & Chirapat, 200; Sheppard et al., 2007).

Although the preference for low biomass colonising species has been generally agreed upon by dugong scientists (Preen, 1992; Aragones, 1994; Adulyanukosol, 2010; Sheppard et al., 2010; D'Souza et al., 2015), the ranking of the most preferred to least preferred food species for dugongs remains unclear and inconsistent across all locations or times. For example, within the tropical and subtropical regions of Australia, *Zostera capricorni*, *Amphibolis antarctica*, and *Thalassia hemprichii* appeared to be the most eaten seagrass by dugongs in the Shoalwater Bay, Shark Bay and Torres Strait/ North Queensland region, respectively (Anderson & Birtles, 1978; Marsh et al., 2002; Tol et al., 2016). In subtropical Hervey Bay, Australia, where meadows were dominated by low biomass seagrass species, i.e., *Halophila ovalis*, *Halodule uninervis*, *Halophila spinulosa* and *Zostera muelleri*, the selection of seagrass by dugongs was influenced by the

availability and nutrient concentrations of their food resources in different tidal zones (Sheppard et al., 2010).

Meanwhile outside of Australia, most studies support the theory of dugongs prefer to consume *Halophila ovalis* or both *Halophila ovalis* and *Halodule uninervis*. The present distribution of dugongs in the Andaman and Nicobar Archipelago, India, is largely found in *Halophila*- and *Halodule*-dominated meadows but not in fragmented meadows with low seagrass cover (D'Souza et al., 2013, 2015). *Halophila* sp. was the species that was most associated to dugong feeding trails in Davao Gulf, Philippines (Lucero, 2010). Similar observation was also reported in Thailand, covering Andaman coast and Gulf of Thailand (Nakanishi et al., 2005; 2006; Adulyanukosol, 2010), and Sungai Pulai, Malaysia (Zulkifli Poh, 2009). Whereas in East Ambon, Indonesia, de Iongh et al. (1995) suggested that dugongs prefer low biomass areas with high levels of carbon in the belowground component when they feed in the meadows dominated by *Halodule uninervis*. However, seagrass nutritional study is generally lacking to support whether dugongs' habitat selection is driven by the food quality or food quantity, and which parameters are more competent in influencing dugong feeding patterns in these regions.

2.1.1 Food quality

The nutritional quality of seagrass species as a food source for herbivores is largely determined by certain nutrients within the plant tissues that are essentially required by the animal and the digestive capability of the animal to process and absorb the nutrients (Lanyon & Marsh, 1995). For hindgut fermenters like dugongs and green turtles, they tend to maximise their intake of digestible nutrients from their relatively poor-quality diets (Bjorndal, 1980; Lanyon & Marsh, 1995) and minimise indigestible tissues or inhibitory chemical substances (i.e., fibre and phenolics) that would reduce their digestion efficiency (Aragones, 1996; Heck & Valentine, 2006). However, unlike most herbivorous

mammals and other hindgut fermenters in particular, which are usually capable of processing high fibre food with the aid of large and/or more complex dentition, dugongs have rather simple, flat-crowned teeth that wear quickly, an indication that their dentition lacks strong mechanistic pressure for grinding plants (Lanyon & Sanson, 2006a). It is, therefore, believed that dugong teeth play a secondary role in food comminution compared to the better-developed horny oral pads, which thus limits them from consuming a wider variety of plants.

Aside from relying more on soft mouthparts to break down food particles, dugongs possess much longer digesta retention times (146 – 166 h) compared to other herbivorous, hindgut fermenting mammals such as elephants and horses (22 – 26 h). This trait helps to increase the digestion of fibre, enabling them to almost completely digest low-fibre seagrasses compared to high-fibre seagrasses (Goto et al., 2004; Lanyon & Marsh, 1995). Therefore, the combination of having less efficient dentition in favour of the development of soft mouthparts, and slow passage rate in their long tubular digestive tract, have made dugongs specialised to a low-fibre seagrass diet consisting of small, fast-growing species such as *Halodule* sp. and *Halophila* sp. (Lanyon & Marsh, 1995; Lanyon & Sanson, 2006b).

Generally, most herbivores' diets are constrained by limited dietary nitrogen load, this of which is more limiting for marine herbivores as seagrasses have lower nitrogen content than terrestrial grasses (Birch, 1975; Lanyon, 1991). Therefore, dugongs may selectively forage nitrogen-rich food to maximize their rate of nitrogen intake (Westoby, 1974), and less fibrous plants resulted from less effective food comminution process with their rudimentary dentition (Thayer et al., 1984; Lanyon, 1991; Preen, 1995b; Lanyon & Sanson, 2006b). In subtropical Australia, dugongs have been observed to frequently target *Halophila ovalis* and *Halodule uninervis* because both species are high in nitrogen and digestibility (low concentration of fibre) (Preen, 1995b; Mellors et al., 2005; Sheppard et

al., 2007). The findings from those studies are consistent with the claim that nitrogen is the limiting factor for herbivorous animals. Similar dietary preference by dugongs for these two colonising species was observed in many other studies in various parts of the dugong's range (Heinsohn & Birch, 1972; Boonprakob et al., 1983; Aragonés, 1994; Adulyanukosol, 2010).

Apart from nitrogen and fibre limitations, some other studies further suggest that dugongs also seek seagrass species that are high in soluble carbohydrates (starch). de Longh et al. (1995), Anderson (1998) and Masini et al. (2001) observed that dugongs fed efficiently on *H. uninervis* in monospecific meadows as its rhizomes are rich in starch. Despite their findings that lacked relative comparisons due to the absence of other species, their studies were still in agreement that access to the energy sources (i.e., starch and carbohydrate) that are usually higher in rhizomes compared to the leaves, are more important to dugongs at some seasons at some places (Aragonés, 1996; Sheppard et al., 2007; Sheppard, 2008). By choosing to feed on low biomass species such as *H. ovalis* and *H. uninervis*, dugongs are able to extract and obtain the nutrients from the entire plant, including roots and rhizomes which usually have a greater biomass than the aboveground parts (Sheppard et al., 2010).

2.1.2 Food quantity

While the importance of food quality is said to prevail over food quantity, the food resources for herbivores are typically patchily distributed and thus herbivores are predicted to select patches or foods that maximise their intake rate (food quantity) and energy/ protein intake (food quality) over the cost of searching for and handling food (Searle, 2005; Shipley, 2007). As large mammalian herbivores, dugongs are required to forage a large amount of food biomass per day to support their metabolic cost (Marsh et al., 1982). Hence when high quality food is scarce and travelling cost, i.e., energy cost,

becomes more significant, it is likely that the spatial distribution of food becomes more important in determining their feeding behaviour and then the habitat selection (WallisDeVries, 1996), hence the relative importance of food quantity and food quality may be different from sites to sites as well.

Dugongs in other meadow compositions display preferential grazing based on the food availability in terms of biomass. In tropical north Queensland, Australia, *Thalassia hemprichii*, a large, persistent species which has relatively lower nitrogen content, appears to be the food plant that is most grazed by dugongs, compared to *Halophila ovalis* and *Halodule uninervis* which in contrast, are the most common species available and are greater in nitrogen and more digestible. As such, it was suggested that feeding is mainly influenced by the plant biomass as each species is consumed in proportion to their availability and increasing biomass (Tol et al., 2016). Similar observations have also been documented in Torres Strait, north Australia, where dugongs apparently fed on the more abundant and higher biomass *T. hemprichii* when the *H. ovalis* has relatively lower cover and distribution, despite still being present at density comparable to those in Moreton Bay where the species was preferred by dugongs (André et al., 2005).

A qualitative study of *H. ovalis* from an intertidal flat in Laem Yong Lam, Thailand showed that its carbon, nitrogen and phosphorus content in the aboveground component were distinctively lower than other slow-growing species, i.e., *Cymodocea rotundata*, *Thalassia hemprichii* and *Enhalus acoroides*, making it nutritionally poorer for dugongs (Yamamuro & Chirapart, 2005). In addition, the dugongs' access to *H. ovalis* beds in that area in Thailand were limited as they emerged completely only during low tide. Therefore, the authors reported that the dugongs in Laem Yong Lam fed exclusively on *H. ovalis* was not necessarily due to the plant's nutritional quality, but rather its fast-growing properties that were able to recover the grazed biomass in a shorter time, which made it a stable food supply. The observations in Thailand were supported by D'Souza et al.

(2015) in their study at Nicobar and Andaman Islands, India, which stressed on the quick recovery of the early successional species that allowed the meadow to support repeated grazing by dugongs, even after major production losses due to dugong grazing (i.e., moderate level of grazing can reduce 50% of the shoot density).

2.1.3 Meadow conditions

Food patches that provide constant access to the dugongs are usually more advantages and efficient for feeding as dugongs have been observed to feed throughout the day, however they have been observed to prefer feeding at shallow intertidal areas, in addition to monospecific meadows. In Talibong Island, Thailand, more feeding trails were found in intertidal monospecific *H. ovalis* beds at the shallow sites of tidelands compared to the mixed community of *H. ovalis* with other species in the deeper subtidal areas, which suggested that dugongs there prefer monospecific *H. ovalis* beds at shallower areas (Nakanishi et al., 2006). More feeding sounds of dugongs captured in intertidal seagrass beds compared to the subtidal beds added evidence that the dugongs at Talibong Island prefer to feed at the lower tide level zone of intertidal seagrass beds (Amamoto et al., 2009b). Johnstone & Hudson (1981) observed that dugongs in the Queensland, Australia, prefer to graze monospecific meadows. Meanwhile, dugongs in the Andaman and Nicobar Islands in India showed preference towards contiguous and exposed meadows over fragmented and sheltered meadows, due to a lesser food uptake efficiency in grazing in areas where foods are patchily distributed (D'Souza et al., 2015).

A comprehensive habitat selection study done by Sheppard et al. (2010) in subtropical Hervey Bay, Australia, showed that food selections by dugongs were in relation to food quality, quantity and tidal factors, but in a more interactive and complex pattern. Satellite-tracked dugongs in that study were consistently associated with high nitrogen seagrass patches, except during low tides at daytime where the access to high nitrogen (quality)

patches was limited, during which the animals then fed in high biomass (quantity) patches at deeper areas. Sheppard et al. (2010) also found that during high tides at both day and night-times where there was no restriction to any areas by water depth, dugongs were associated with seagrasses with high starch (quality) content in the intertidal areas, yet with generally low seagrass biomass. This strongly suggests that the dugong feeding preferences in Hervey Bay were influenced by many factors which worked interactively. A diet study of Amazonian manatees by using digestive tract samples found that the manatees became more selective (i.e., eating few number of species) during high water of the year when all food species were available and more abundant, and became less selective (i.e., eating more number of species) during low water of the year when food availability was lower (Colares & Colares, 2002).

2.1.4 Habitat suitability for dugongs in Malaysia

Models on habitat suitability of dugongs in Malaysia, particularly in Johor and Sabah states, predicted the most suitable dugong habitat in the two regions are mainly influenced by seagrass biomass, distance from coast and water depth (Briscoe et al., 2014; Hashim et al., 2017). Dugongs are more likely to be present in shallow water areas where seagrass biomass is high and closer to the shore, indicating their preferences in habitat selection.

2.2 Dugong foraging strategies

2.2.1 Foraging challenges

As mentioned in sub-section 2.1, plant nutritional quality plays a central role in the diet preferences of large herbivores, hence habitat selection is mainly determined by the nutritive values of each potential food resource within the habitat (Owen-Smith & Novellie, 1982; WallisDeVries, 1996). While predators generally search for spatially scattered prey of high nutritional quality, large herbivores confront a problem of low and

highly variable food quality which are widely dispersed over the landscape (Senft et al., 1987). Consequently, large herbivores such as dugongs face a series of interrelated foraging challenges, each on a different spatial and temporal scale, as summarised below:

- (1) Plants are generally poor in nutritional values and these nutrients can be bound to indigestible fibres, resulting in a bulk quantity of food intake that is required to meet nutritive requirements of herbivores (Thayer et al., 1984). In addition, dugongs, unlike typical hindgut fermenters, lack of well-developed dentition that can properly masticate high fibre seagrass but adapted to effectively masticate low fibre seagrass (Lanyon & Sanson, 2006b), in which can be almost completely digested within their long food retention time in the hindgut, i.e., 6 to 7 days (Lanyon & Marsh, 1995). Thus, feeding time, digestibility of food and rate of digestion become a constraint in the process of diet selection;
- (2) Plants are varied in their nutritional values in different parts of their structure and species. As dugongs consume up to 91-94% of the aboveground and 61-75% of the belowground seagrass biomass (de Iongh et al., 1995; Nakaoka & Aioi, 1999), they are not affected so much by the nutrient variation among different plant parts as many terrestrial herbivores do, rather, dugongs tend to be more affected by the nutrient variability both within and among seagrass species, e.g., younger leaves and fast-growing species usually have higher nutrient content and lower fibre, compared to older leaves and slow-growing species (Bjorndal, 1980; Cebrián et al., 1998); and
- (3) Plants exhibit high spatial heterogeneity in their distribution over a landscape, with disproportionate nutritional quality and densities across different patchiness, community structure, and abiotic factors such as tidal exposure (Searle et al., 2005). Hence, selecting high quality patches becomes difficult in a heterogenous environment with associated foraging cost such as energy expenditures associated

to searching time and interpatch travel time (Senft et al., 1987a; WallisDeVries et al., 1999).

These foraging challenges which encompassed digestive constraints, forage quality and patch characteristics, strongly influence the foraging decisions and feeding patterns of dugongs at multiple scales. Most studies on dugongs feeding behaviour have focused on the diet and habitat selection by exploring the effects of food attributes, e.g., biomass and nutritional values, to the selective feeding behaviour, but rarely consider the impact of the spatial distribution of those food attributes at a range of ecological scales, which can result in complex foraging and feeding patterns of dugongs within their foodscapes environment.

2.2.2 Coping mechanisms

The behavioural responses and distribution patterns of the animals provide a mechanistic view of the coping mechanisms, or foraging strategies, in response to the challenges. The response and distribution patterns may result from decisions made by the animals at different spatiotemporal scales, to ensure their efficient foraging is achieved (Bailey et al., 1996). Foraging efficiency is highest when the intake rate (nutrient and/or energy) is greatest with least effort (time and/or energy used) spent (Sheppard, 2008). To do so, dugongs must regulate their time of staying in one patch and movement between quality patches (WallisDeVries, 1996). To understand better on habitat selection, several foraging theories have been used to consider how dugongs employ optimal feeding strategies by considering trade-offs between costs and benefits (de Iongh et al., 1995; Aragonés, 1996; Sheppard et al., 2007, 2010).

One adaptive optimal foraging theory that has been regularly suggested for dugongs is 'cultivation grazing' *sensu* Preen (1992). Dugongs have been observed to have developed accurate spatial memories that remember locations of quality patches and return to feed

more frequently than less quality patches, similar to elephants, their closest land relatives (Sheppard et al., 2007; Tsalyuk et al., 2019). This cognitive ability helps the animals to use their previous experiences to decide when and where to feed, in order to save the cost of travelling and searching between patches which improves their foraging efficiency. When dugongs have such favoured foraging patches at which they repeatedly come back and graze, the abundance of food at a later time will depend on the extent of the animals' behaviour at this point of time. Group feeding has been observed in dugongs and this behaviour is believed to increase foraging efficiency by maintaining the pasture with lower seral, fast-growing species of seagrass (e.g., *Halophila ovalis* and *Halodule uninervis*) – food plants that typically more nutritious than persistent species. Speaking from a timescale, this type of optimised foraging behaviour makes sure of a sustainable food yield that would allow dugong to maximise its net rate of intake for a longer period (Preen, 1995b; Aragonés, 1996; Aragonés et al., 2006). This theory also supports the dugong's tendency in feeding on these two species (see sub-section 2.1.2.2) as both are more tolerant and adapted to disturbances due to their opportunistic life history strategies (Preen, 1992).

CHAPTER 3: SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF SEAGRASS HABITATS

3.1 Introduction

Seagrasses in Malaysia typically occur in shallow, sheltered intertidal areas such as shoals, mudflats, semi-enclosed lagoons, and also can be found in deeper, exposed subtidal areas such as coral reef flats and forereefs (areas extended seawards beyond the reef) (Japar Sidik et al., 2006). There are at least 15 species of seagrass recorded in Malaysian waters, which include *Enhalus acoroides*, *Halophila beccarii*, *Halophila decipiens*, *Halophila ovalis*, *Halophila minor*, *Halophila major*, *Halophila spinulosa*, *Halodule pinifolia*, *Halodule uninervis*, *Cymodocea rotundata*, *Cymodocea serrulata*, *Thalassia hemprichii*, *Syringodium isoetifolium*, *Ruppia maritima* and *Thalassodendron ciliatum* (Fortes et al., 2018).

The total estimated area for known seagrass beds across the 4800 km coastline of Malaysia is about 16.3 km² (Fortes et al., 2018), however this information is incomplete due to the paucity of published information on seagrass meadow extents (Ooi et al., 2011b). The review of seagrass distribution in Malaysia across available information from 1994 – 2004 revealed that there were at least 78 seagrass beds which ranged from patches of several metres diameter to several hectares, present in the coasts of Peninsular Malaysia, Sabah and Sarawak (Japar Sidik et al., 2006). Since then, from the late 2000s until now, much of the research have been focused on seagrass morphology, taxonomy, phenology, community structure, physiology, and ecosystem functions, yet areal extents of seagrass beds in most of the areas have not been updated. The paucity of information is largely due to the logistical challenges of mapping seagrass meadows, especially for subtidal ones (Fortes et al., 2018). This information gap not only is preventing ecologists and resource managers from obtaining near-true estimates of the areal extent and the health status of local seagrass resources for effective management and protection, but is

also hampering the understanding of long-term spatiotemporal dynamics of the seagrass ecosystem. Obtaining such information is especially important, given the increasing levels of anthropogenic activities and pressures in Malaysian coastal zones.

A nationwide trend of continued seagrass meadow loss and degradation has been observed due to human activities, such as sand mining, dredging and land reclamation for coastal development, yet the information on the rate of seagrass reduction and the changes in spatial coverage remains unknown, thus hindering the mitigation response for the protection of seagrass habitats (Zakaria & Bujang, 2011). To date, seagrass habitats are still the least protected of the three main marine ecosystems in Malaysia, namely coral reef, seagrass and mangrove. There are no specific legislations drafted and passed specifically for seagrass protection. Seagrass habitats are only protected if they fall within the gazetted marine parks or state parks (Japar Sidik & Muta Harah, 2003).

The ecological importance and uniqueness of seagrass meadows in the Sibutu Archipelago have been widely overlooked. The Sibutu Archipelago, which has been part of the Tinggi Island Marine Park in Malaysia since 1994, was previously (in 2005) and more recently (in 2016) proposed by the Johor state government for the establishment of a dugong sanctuary in order to protect the dugong populations and their seagrass habitats (The Star, 2005, 2016). At the time of this writing, the proposed dugong sanctuary is still pending a Federal gazette. In 2019, the area was also internationally designated by the IUCN as an Important Marine Mammal Area (IMMA). However, there is a general paucity of information on the geographical distribution and ecological conditions of the seagrasses in the Sibutu group of islands. As the use of current policies and enactments do not provide a direct safeguard on the seagrass habitats especially those that utilised by the dugongs, both information – spatial distribution of the seagrass habitats and habitat utilisation by dugongs, are imperative for strengthening conservation priorities for the seagrass meadows of the Sibutu Archipelago.

Seagrass meadows in Malaysia are commonly being assessed in the intertidal zone by field monitoring to collect data on the community structure such as species composition, cover and biomass, either by visual estimation of leaf cover and/or manual harvest of seagrass within quadrats, by means of systematic or non-systematic sampling. Remote sensing satellite data technique has been employed to record the submerged seagrass in the subtidal zone at an efficient rate of data collection over large areal coverage but its accuracy in differentiating between seagrass and non-seagrass features is subjected to depth limits and clarity of the water column (Mazlan et al., 2014; Hossain et al., 2015a,b). Underwater towed video method has been used for seafloor mapping since the 20th century (Bicknell et al., 2016) and proved to be a good method in characterising subtidal seagrass in deeper benthic zones, where it is more difficult to be mapped by physical sampling and satellite imagery (Lefebvre et al., 2009). This technique manages to produce cost-effective permanent data - high resolution video imageries, where extractive methods are unnecessary or unsuitable. Despite the growing application of advanced automatic or semi-automatic tool development in data analysis (Mohamed et al., 2018), this method, however, is remarkably less performed for seagrass mapping in Malaysia.

This chapter describes the spatial and temporal distributions of the subtidal seagrass meadow in dugong habitats, focusing on the Sibuluan group of islands (hereafter referred to as Sibuluan Archipelago) which was previously unmapped by means of comprehensive survey. Sibuluan Archipelago was also selected because the area was recorded with the most frequent sightings of dugongs around the east coast islands of Johor (Ponnampalam et al., 2015). I used the underwater towed video method to locate the meadow edges and quantify the seagrass coverage within the meadow. I aimed to obtain the meadow size of the Sibuluan Archipelago as baseline information of available foraging habitat for the dugong population and to determine the areal coverage change across three monsoon seasons.

The results of this chapter were then used in the next chapter (*Chapter 4*) to investigate the relationship between dugong feeding patterns and seagrass cover.

3.2 Literature Review

3.2.1 Geographical distribution of seagrass in Malaysia

Seagrasses are mainly distributed along both west and east coast of Peninsular Malaysia. Along the west coast, patches of mixed species community occurred on sandy mud to sand-covered corals substrates along the mainland coastline, from Langkawi, Kedah on the northern region to Port Dickson, Negeri Sembilan and Pulau Serimbun, Melaka on the central region (Phang, 2000). Intertidal seagrass was found growing on the reef platform at Teluk Kemang, Port Dickson. In the southern region, mixed species seagrass meadows occurred on sandy mud banks and calcareous sandy mud shoals at Tanjung Adang-Merambong Shoal (Japar Sidik et al., 1996; Phang, 2000). This seagrass bed was known as the largest contiguous seagrass bed in Peninsular Malaysia in the 2000s, and covered approximately 0.90 – 1.12 km² in area (Japar Sidik & Muta Harah, 2003; Hossain et al., 2015a; **Table 3.1**). It was also known to harbour the highest species diversity in Malaysia, as many as nine seagrass species compared to the number of species documented in the other regions of the country, e.g., only three species in the northern region of Peninsular Malaysia (Japar Sidik et al., 2001). However, some parts of this seagrass bed have been damaged by land reclamation for a port development project since 2014 (Hossain et al., 2015a).

In contrast, seagrasses are not usually found on the eastern coastline of Peninsular Malaysia which are mainly composed of sandy to rocky areas. The seagrasses on the east coast inhabit the sandy mud substrate in shallow sheltered coastal lagoons, from Pengkalan Nangka, Kelantan to Paka, Terengganu. Monospecific and mixed species seagrass beds are also present at the outer regions of fringing coral reefs around the

offshore islands, i.e., Pulau Redang and Pulau Perhentian, Terengganu, Pulau Tioman, Pahang, and Pulau Sibul, Pulau Tinggi, Pulau Besar, Pulau Tengah, Johor (Japar Sidik et al., 1999; Muta Harah et al., 2003; Japar Sidik et al., 2006; Muta Harah & Japar Sidik, 2013). The distribution of seagrass around the coastal islands is usually at relatively sheltered areas such as small bays, channels, or at the leeward side of the islands where the impacts of the annual northeast monsoon (November to February) such as heavy rain and strong wave action (Varikoden et al., 2011) are relatively lower. In comparison to the west coast where seagrasses normally grow in the shallow water at depths below 4 m, clearer water on the east coast allows seagrasses to extend to the deeper depths of the subtidal zone, about 5 – 7 m (Japar Sidik & Muta Harah, 2003). *Halophila decipiens* was found at a water depth of 24 m in Chagar Hutang, Pulau Redang, Terengganu (Muta Harah et al., 2003).

In Sabah, East Malaysia, mixed species seagrass beds are found in the intertidal zone, with some mixed with coral reefs, around the west and southeastern coasts. Subtidal seagrass is present on the coral rubble substrate around Pulau Maganting, Pulau Tabawan, Pulau Bohey Dulang and Pulau Sipadan at the southeastern coast (Norhadi, 1993; Japar Sidik et al., 1997; Japar Sidik et al., 1999a,b; Japar Sidik et al., 2000). In Sarawak, another state of East Malaysia, seagrasses are distributed on the subtidal and intertidal mudflats of Punang, Sari Lawas (Ahmad-Kamil et al., 2013; Hossain et al., 2015b). Based on literature, the seagrass beds at Sari Lawas were the largest seagrass bed in Malaysia, covering more than 2 km² over the estuary, an area also known as the feeding ground for dugongs (Bujang & Zakaria, 2011). The other areas in East Malaysia where seagrasses are known to be present are at Sungai Bintulu (den Hartog, 1970) and Pulau Talang-Talang, Semantan from herbarium records (Phang, 2000).

Table 3.1 Locations of known seagrass and estimated coverage in Malaysia, updated from Kamarruddin (2008).

State	Location	Area (km ²)	Reference
Kelantan	Pengkalan Nangka	>0.25	Hossain et al. (2015b)
	Kampung Baru Nelayan – Kampung Sungai Tanjung	0.27	Japar Sidik & Muta Harah (2003)
	Pantai Baru Lagoon	0.20	Japar Sidik & Muta Harah (2003)
Terengganu	Gong Batu (Setiu Lagoon)	0.05	Japar Sidik & Muta Harah (2003)
	Sungai Terengganu	0.01	Japar Sidik & Muta Harah (2003)
	Sungai Kemaman	0.17	Japar Sidik & Muta Harah (2003)
	Chukai, Kemaman	0.03	Japar Sidik & Muta Harah (2003)
	Telaga Simpul	0.28	Japar Sidik & Muta Harah (2003)
	Paka Merchang	>0.40 0.03	Hossain et al. (2015b) Japar Sidik & Muta Harah (2003)
Negeri Sembilan	Teluk Kemang	0.11	Japar Sidik & Muta Harah (2003)
Johor	Tanjung Adang-Merambong Shoal	0.90	Hossain et al. (2015a)
	Pulau Tinggi*	3.00	Ooi et al. (2011)
Pulau Pinang	Middle Bank Seagrass	1.35	Asilah (pers. comm.)
Sarawak	Punang-Sari Lawas River Estuary	>2.00	Hossain et al. (2015b)
Sabah	Pulau Banggi	4.15	Rajamani & Marsh (2015)
	Pulau Mantanani	1.12	Rajamani & Marsh (2015)

* Including surrounding islands: Pulau Mentigi, Pulau Nanga Kecil, Pulau Nanga Besar and Pulau Simbang.

3.2.2 Habitat characteristics of Sibiu-Tinggi Archipelago

The Sibiu-Tinggi Archipelago has been highlighted as an important habitat for dugong in Peninsular Malaysia (Ponnampalam et al., 2015), yet the information on the spatial distribution of the seagrass for the whole archipelago is incomplete. Comprehensive seagrass mapping was previously only conducted around Pulau Tinggi using the towed video method, which obtained a continuous spatial dataset for the subtidal seagrass (mainly 3 – 10 m) in the leeward side of the island (Ooi et al., 2011b, 2014). It was found

that seagrass meadows in the Sibutu-Tinggi Archipelago are predominantly subtidal and stretch out at the forereef zone – extends seaward and downward from the reef crest. However, similar surveys have not been conducted for those seagrass meadows around the Sibutu Archipelago to collect high spatial resolution data of the seagrass.

There were only two companion consultancy reports which aimed to document presence of dugongs and assess the extent of seagrass meadows around the coasts of Johor, Malaysia, have reported seagrass information around the Sibutu Archipelago. The first survey in 2005 estimated a total of 7.06 km² area of seagrass meadows on the western side of the Sibutu Archipelago, by using satellite images and aerial survey (Affendi et al., 2005). The seagrass meadows were comprised of two larger meadows, one was in the Sibutu Bay and another one was located west of Pulau Sibutu Tengah which extended to the depth about 8 metres, lying at the outer part of the fringing coral reefs, and two smaller meadows on the north and south sides of Pulau Sibutu Tengah (**Figure 3.1**). The second survey in 2007 revealed that *Halophila ovalis*, *Cymodocea serrulata*, *Syringodium isoetifolium* and *Halodule uninervis* were the most common species found in the Sibutu Archipelago (Ooi et al., 2008). The seagrass cover across the islands was low (mean 18.6%, range 4.79% - 23.45%) which indicated possibly highly fragmented seagrass landscapes or were perhaps under-represented by small sample size ($n = 5$) in that study. The mean dry weight biomass was 3.09 g DW m⁻² (range 5.02 ± 6.77 - 9.11 ± 10.08 g DW m⁻²) and the main biomass contributor was *H. uninervis*, although *H. ovalis* was the most widespread species. Seagrass cover and dry weight biomass reported in Ooi et al. (2008) were observed to be reduced compared to the results obtained by Affendi et al. (2005), however the reasons for the differences were unidentified.

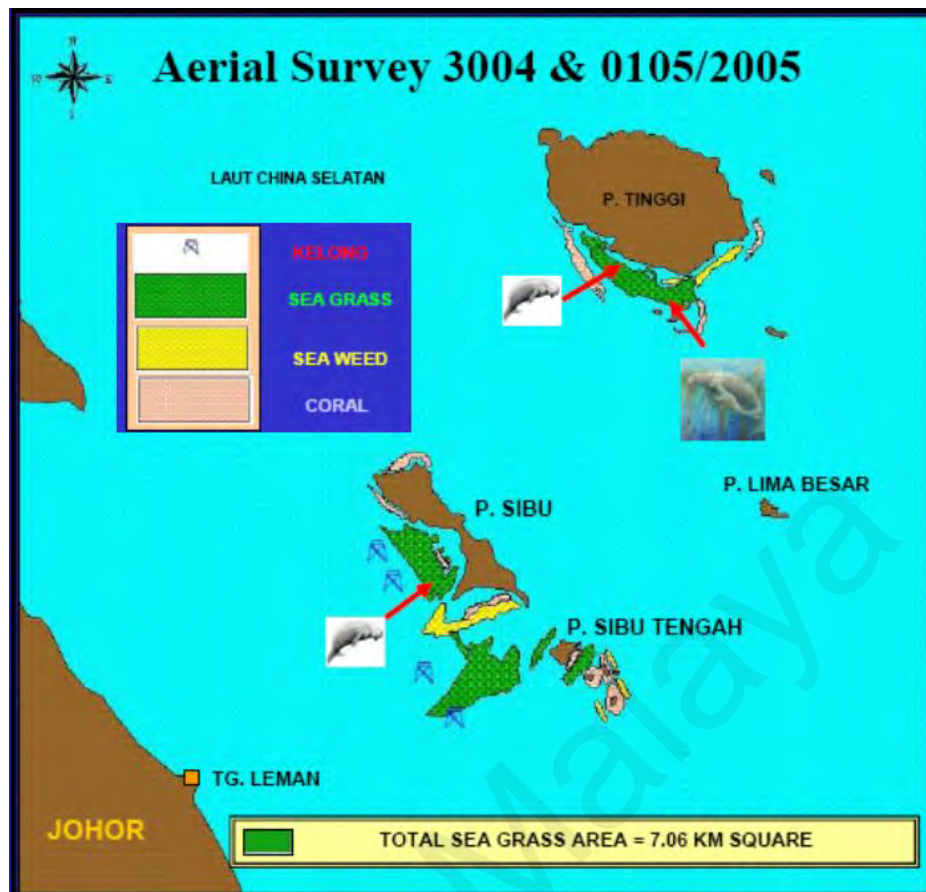


Figure 3.1 Seagrass meadows in Sibuluan Archipelago identified in 2005. Taken from Affendi et al. (2005) with permission

The seagrass meadows in Pulau Tinggi were relatively well studied compared to Sibuluan Archipelago (Ooi et al., 2011a, b). The seagrass survey in 2009 for Pulau Tinggi, including the surrounding islands of Pulau Mentigi, Pulau Nanga Kecil, Pulau Nanga Besar and Pulau Simbang, reported approximately 3 km² of subtidal seagrass meadows (Ooi et al., 2011b). A total of nine seagrass species was recorded, with *Halophila ovalis* and *Halodule uninervis* being the most widespread species, while other co-occurring species were *Cymodocea serrulata*, *Syringodium isoetifolium*, *Halophila minor*, *Halophila decipiens*, and *Halophila spinulosa*. *Cymodocea rotundata* and *Thalassia hemprichii* were found in small quantities in shallow water (<1 m deep).

3.3 Methodology

3.3.1 Study site

The Sibul Archipelago lies within the Tinggi Island Marine Park, 10 km off the southeast coast of Peninsular Malaysia (**Figure 3.2**) It consists of four islands, the main and largest one being Pulau Sibul Besar, with the three smaller islands of Pulau Sibul Tengah, Pulau Sibul Kukus and Pulau Sibul Hujung positioned in a southeasterly direction. Of these, only Pulau Sibul Besar is inhabited. The area hosts what is possibly the most significant population of dugongs in Peninsular Malaysia (Ponnampalam et al., 2015) due to its subtidal forereef seagrass meadows that extend to about 10 m depth (Ooi et al., 2011b). These islands are strongly affected by heavy rainfall, strong waves and currents on the windward side during the northeast monsoon (November to March) but have relatively calm and dry weather during the southwest monsoon (May to October).

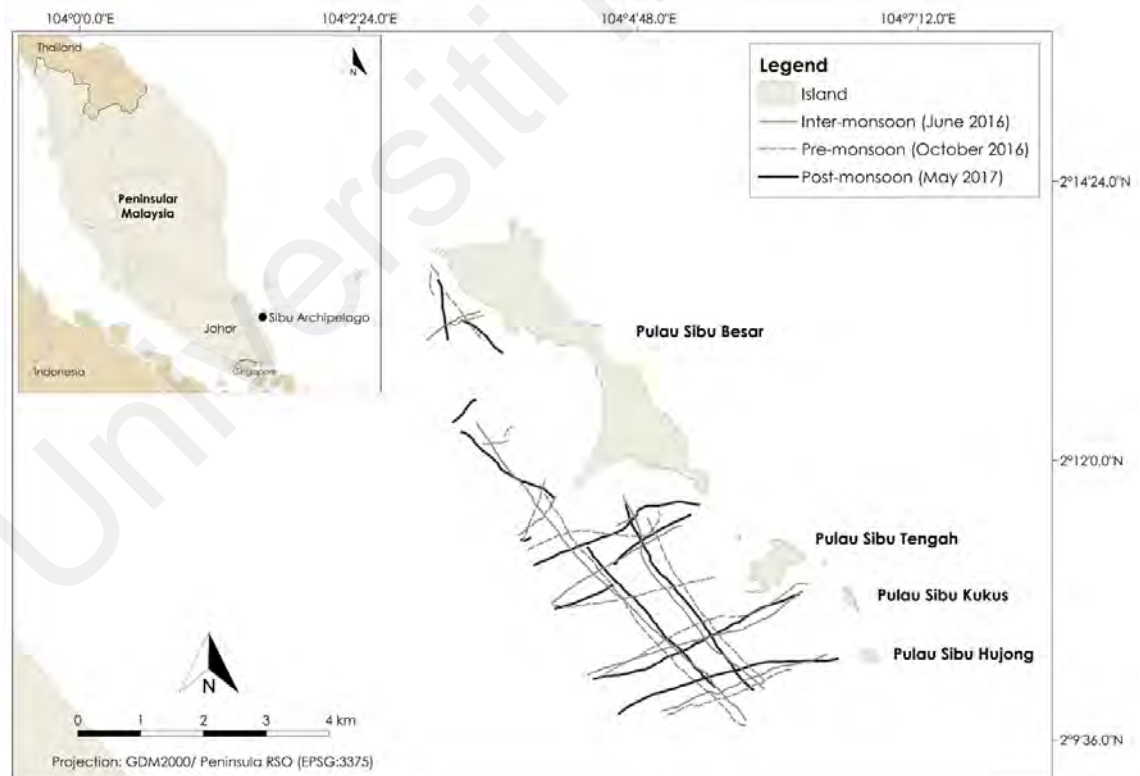


Figure 3.2 Map of Sibul Archipelago, eastern coast of Johor, Peninsular Malaysia and location of towed videos (lines comprised of all towed video points) across three sampling seasons in 2016 – 2017. Locator map of Peninsular Malaysia with Sibul Archipelago highlighted in the inset

3.3.2 Data collection

Seagrass distribution was assessed in water depths of 3-10 m using towed video surveys (Charoll et al., 2018), similar to that used to study the spatial structure of seagrass species (Ooi et al., 2014). An underwater camera mounted on a glider frame was deployed from a boat and towed along pre-determined transects (**Figure 3.2**) at a fixed speed of 1 – 2 knots to acquire continuous video of seafloor features (**Figure 3.3**). Transects crossed the full extent of seagrass meadows in the study area, but certain areas close to the islands (c. 8% of the sampling areas) could not be surveyed due to very shallow depths and presence of coral reefs. The camera was held at a height between 0.5-1.0 m above the seabed and projected to 45° below the horizontal field of view to observe seagrass coverage and dugong feeding trails. Video frames were georeferenced to the boat's locations at 3 s intervals. Environmental data, i.e., water depth, sea surface temperature (SST), salinity, pH, dissolved oxygen profiles was collected using a handheld YSI multiparameter probe at the start and end of each transect line. Data were collected thrice across three seasons relating to the northeast monsoon, from 2016 to 2017—inter-monsoon (June 2016), pre-northeast monsoon (October 2016) and post-northeast monsoon (May 2017). The northeast monsoon was used as the reference season because it strongly impacts the study site, bringing with it extreme weather conditions, i.e., heavy rainfalls, strong winds and low water temperatures.

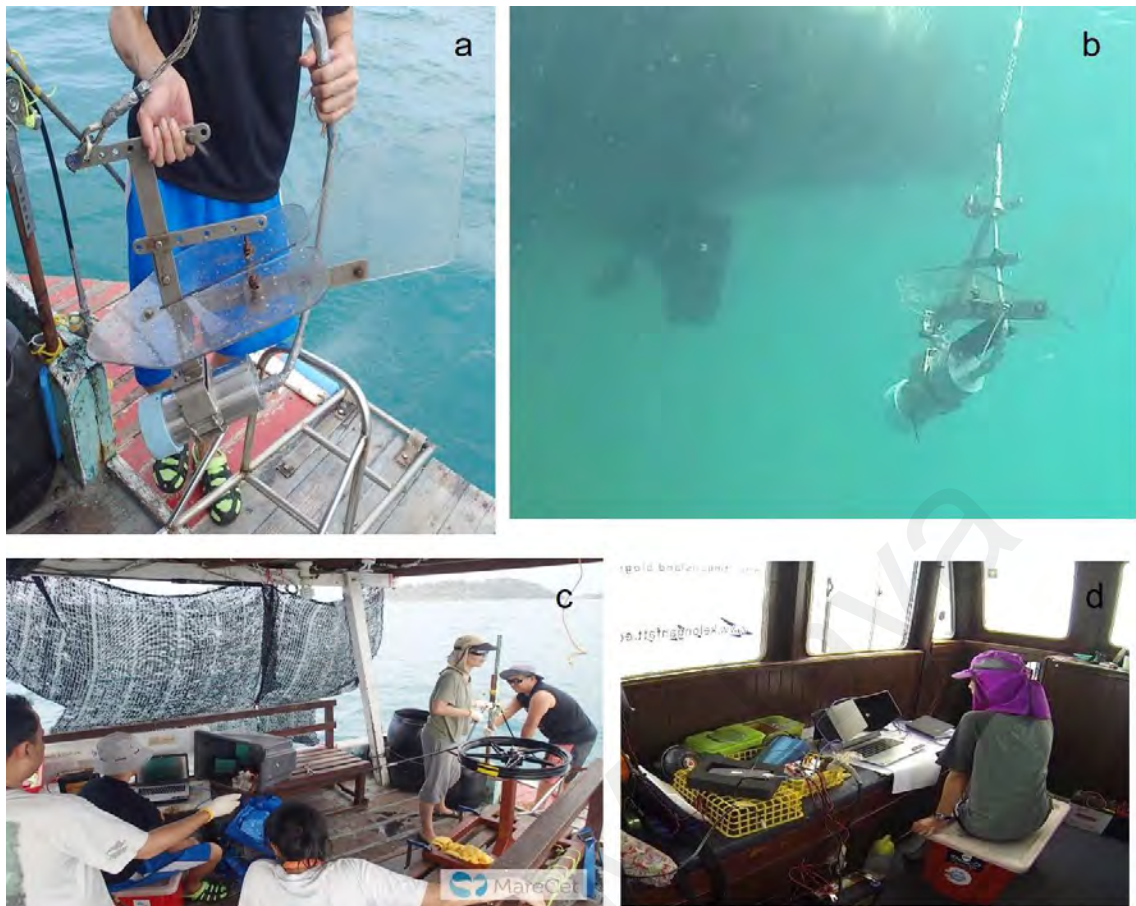


Figure 3.3 (a) Setup of underwater towed video system – a video camera enclosed in waterproof housing, attached together with its data and power cables to the metal bar, (b) A video camera towed behind the boat to record the seagrass surface cover, (c) At least three manpower needed to maintain the height of the camera in from the seabed while the boat is moving, (d) An observer was monitoring and recording the video in the cabin while towing the camera

3.3.3 Data processing and spatial analysis

Video frames were sub-sampled at 5 m intervals to record seagrass percent cover. Seagrass cover was estimated using percent cover standards from Seagrass-Watch (McKenzie, 2003) and scored based on interval categories modified from the Braun-Blanquet scale (Braun-Blanquet, 1972; **Table 3.2**), which uses fast visual index with broad categories to reduce estimation error for a broader-scale (tens of metres) seagrass meadow (Fourqurean et al., 2001). Seagrass coverage by species was not recorded because the video resolution and distance between camera and seabed were not optimal for species identification. Instead, seagrass species composition was determined via field

sample collection which was described in *Chapter 5* and reported here only to describe the meadow.

Table 3.2 Modified Braun-Blanquet (B-B) scale for seagrass cover abundance.

B-B Score	Coverage (%)	Biomass Condition
1	0-5	Poor
2	6-25	
3	26-50	Moderate
4	51-75	
5	76-100	Rich

Seagrass meadow extent was plotted from the outermost sampling points of the transects that contained seagrass (McKenzie et al., 2001). Seagrass cover maps were produced by interpolating in 10 x 10 m grids by using Inverse Distance Weighting (IDW). All geographical data layers were projected to Geodetic Datum of Malaysia 2000 in QGIS software version 3.4.2.

3.4 Results

Towed video footage was acquired across approximately 22 km of transects in each season. Seagrasses were present in 87 – 88% of sampling frames in the inter-monsoon and pre-monsoon and 54% in the post-monsoon (**Table 3.3**). The video dataset revealed a large, continuous seagrass meadow composed of mixed species on the leeward side of the Sibü Archipelago. Field collection of seagrass specimens confirmed the occurrence of four species captured in the towed video footages: the colonising species *Halophila ovalis* and *Halodule uninervis* were dominant (59.5 % and 37.6 % of total frames, respectively), and co-occurred with the opportunistic species, *Cymodocea serrulata* and *Syringodium isoetifolium* (1.49 % and 1.37 % of total frames, respectively).

Table 3.3 Summary statistics for video dataset across three sampling seasons in 2016 – 2017, Sibul Archipelago, Peninsular Malaysia.

Data	Inter-monsoon		Pre-monsoon		Post-monsoon	
	<i>n</i>	% of total frames	<i>n</i>	% of total frames	<i>n</i>	% of total frames
Total transect line distance (km)	22.38		22.31		22.07	
Total video frames scored	3485		3460		3292	
Seagrass present	3016	86.54	3032	87.63	1782	54.13
Seagrass absent	469	13.46	428	12.37	1510	45.87

The mapping of the seagrass extent revealed a teardrop-shaped seagrass bed that was estimated to cover 12.88 km² of shallow-water shelf between ~2 and 10 m depth (**Figure 3.4**). Meadow size was largest in the inter-monsoon (12.25 km²) and shrank by 7% in the pre-monsoon (11.43 km²) (**Figure 3.5**). By the post-monsoon, the meadow was about three-quarters (9.30 km²) of its original size. The highest seagrass cover also occurred in the inter-monsoon (mode 76-100% cover), and declined during both pre-monsoon (mode 26-50% cover) and post-monsoon (mode 0-5% cover).

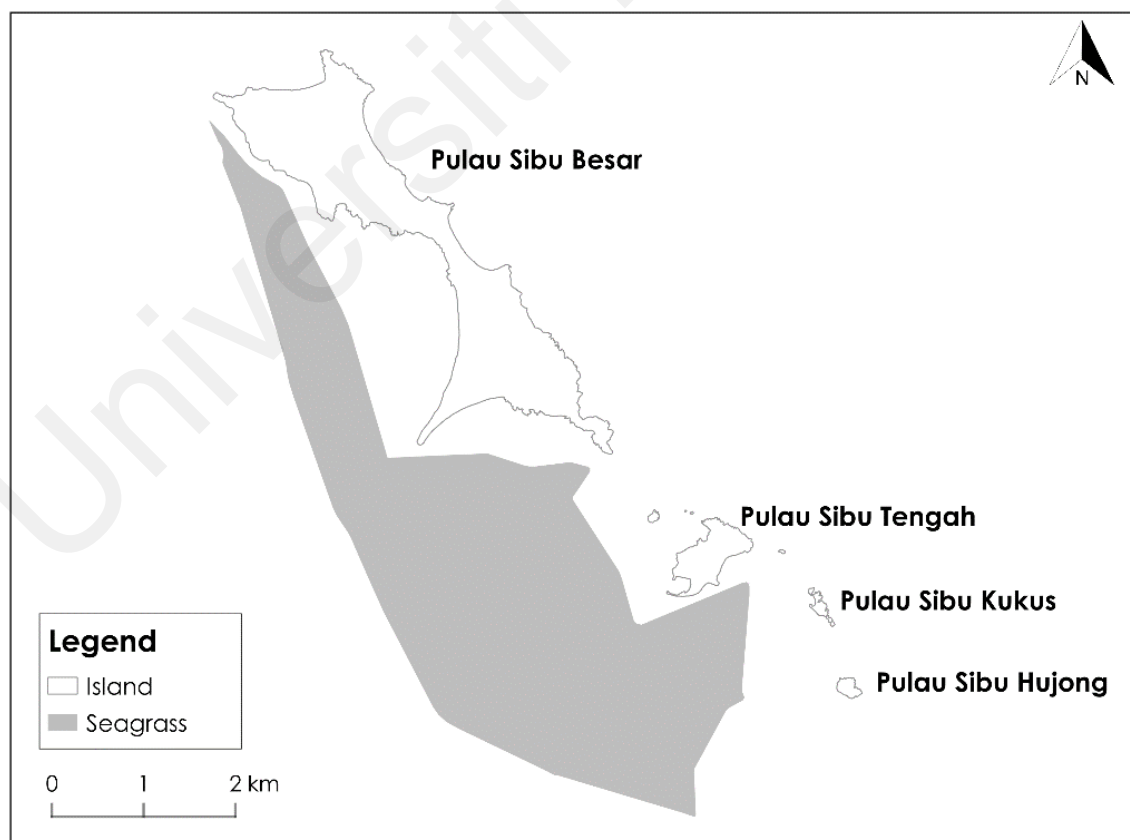


Figure 3.4 Seagrass formed a continuous meadow of 12.88 km² at the leeward side of the Sibul Archipelago, Malaysia

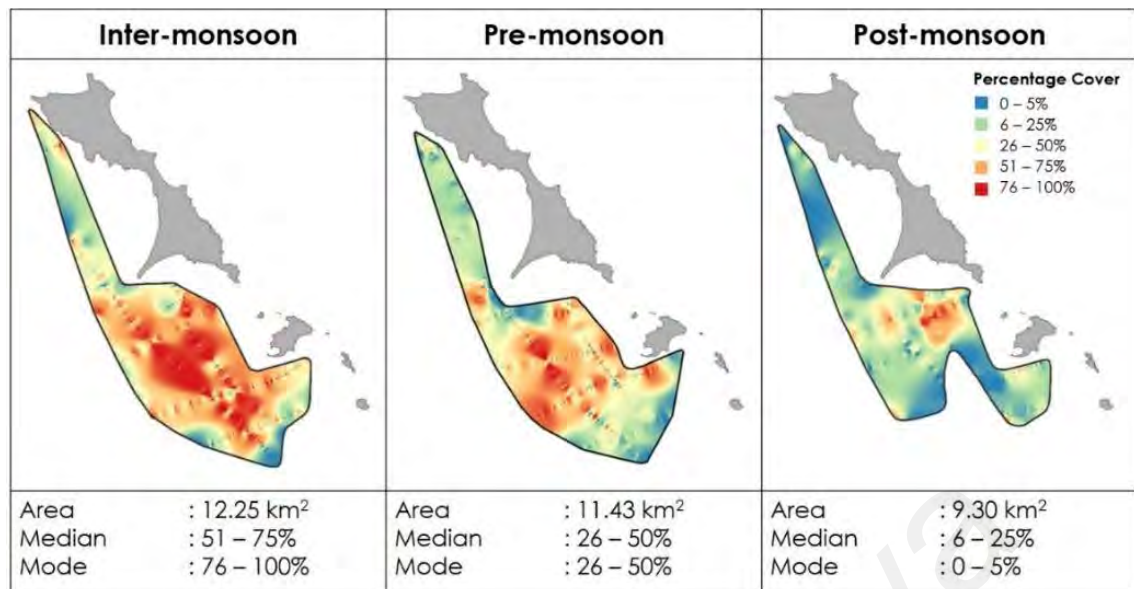


Figure 3.5 Seagrass percentage cover interpolated in 10 x 10 m grids using Inverse Distance Weighting (IDW) with weighting coefficient of 5

3.5 Discussion

The seagrass meadow in this study area is the single largest meadow recorded for Malaysia. At 12.88 km², it is far more extensive than other better-known meadows in the country. For example, the Tanjung Adang-Merambong Shoals of Sungai Pulai in southern Johor, is known as the largest seagrass meadow in Peninsular Malaysia, yet its largest recorded extent before year 2014 was ~0.9 km² (Hossain et al., 2015a). As the areal extent of an ecosystem determines the magnitude of its ecosystem function and services (Fortes et al., 2018), the sheer size of this meadow—and particularly one with high populations of dugongs—is not trivial.

The diminishing trend of seagrass cover observed during this study suggests that this meadow is exposed to high gradients of change. The northern and southern edges of the meadow were the most affected, while the meadow interior was able to sustain over five consecutive months of the northeast monsoon. The latter possibly functioned as a recovery area for the whole meadow after large-scale disturbances. Some seagrass pastures in Hervey Bay, Australia, which remained after devastating losses due to a series

of floods and cyclone in 1992, were the first meadows to recover after the event (Preen & Marsh, 1995). With very low levels of coastal development and number of inhabitants in the Sibul Archipelago, it is unlikely that anthropogenic disturbances are a major threat (Ponnampalam et al., 2015). Why seagrass cover declined over the timeframe of this study is unclear, but we speculate that low light intensity and broad-scale sediment burial caused by the northeast monsoon played the main role in shaping the meadow extent (Ooi et al., 2011a). Moreover, it is dominated by colonising species such as *Halophila ovalis* and *Halodule uninervis*, which have been shown to have weak clonal support and thus, likely to decline easily with broad-scale sediment burial (Ooi et al., 2011a).

3.6 Conclusion

Our study revealed the presence of an extensive subtidal meadow around the Sibul Archipelago that otherwise has been unmapped comprehensively, despite local knowledge of its presence and a keen interest by the government to conserve the local dugong population there since more than a decade ago. The meadows are by far the largest known seagrass beds in Malaysia with areal size of 12.88 km². Despite low human disturbance at our study site, the downward trajectory of the meadow's extent and coverage suggests that it is exposed to large effects of broad environmental processes. More research is required to further understand the long-term ecological effects of this trajectory on the capacity of the meadow to support the survivorship and area occupancy of the dugong population.

CHAPTER 4: SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF DUGONG FEEDING TRAILS

4.1 Introduction

The dugong is the only marine mammal which is strictly herbivorous, feeding almost exclusively on seagrass in its feeding habitats (Anderson & Birtles, 1978; Preen, 1995b; Chilvers et al., 2004). It is listed as vulnerable to extinction on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (Marsh & Sobotzick, 2015); many dugong populations across more than 40 range states occur in highly depleted numbers (Marsh et al., 2011). Among the many threats that cause reduction in numbers across the species' range are fragmentation and loss of seagrass habitats as a consequence of both natural events (e.g., monsoon, flood, hurricane, cyclone and disease) and human impacts (e.g., land reclamation, port expansion, increased nutrient input and pollution) (Duarte, 2002; Orth et al., 2006). As a result, food quality and quantity in seagrass meadows may be spatiotemporally patchy and dugongs must make decisions that optimize energy gain and expenditure when foraging (Sheppard, 2008).

To date, little is known about the feeding strategies of dugongs. Some studies have described the interactions between dugongs and their seagrass habitats in terms of feeding selectiveness and spatially explicit patterns of food resource selection (Preen, 1992; de Jongh et al., 1995; Masini et al., 2001; Nakanishi et al., 2006; Adulyanukosol, 2010; Sheppard et al., 2010; Tol et al., 2016), but the underlying mechanisms of how they respond to food that is distributed in heterogeneous patches are still an enigma. Confirmation of such behaviour is very difficult to obtain from direct observation or experimentation, given the animal's elusiveness and wide range of movement (Sheppard et al., 2009), as well as its common occurrence in turbid waters. Satellite tracking has been used in a few studies, particularly in Australia, but is susceptible to telemetry bias (Holley, 2006; Sheppard et al., 2010) because it detects feeding clusters in intertidal

seagrass more easily than in subtidal meadows. Feeding trails in the meadows, however, are distinct grazing signs that provide direct evidence of patch utilisation by dugongs (Marsh et al., 2011). Thus, quantifying the spatial structure of feeding trails, i.e., how trails are distributed in a meadow and their degree of clustering, is one way of gaining insight into the decision-making of dugongs when foraging.

In this chapter, I hypothesize that dugongs forage and feed in a structured manner driven by seagrass quantity, and that these strategies can be captured using the spatial pattern approach. Here, *spatial pattern* refers to the non-random distribution of dugong feeding trails within the meadow. This approach was used because a biologically induced pattern can provide information about the underlying generating process in ways that non-spatial methods are unable to (Rossi et al., 1992; Gross et al., 1995). Conventional measures such as the mean, mode and frequency distributions, for example, cannot capture the degree of clustering, dispersion, range of spatial dependence, and directional change that are an inherent part of all ecological phenomena (Koenig, 1999). Dugongs graze on seagrass by removing shoots and excavating rhizomes, creating distinct feeding trails that can be geolocated and mapped out for pattern analysis. The spatial patterns of feeding trails is regarded to be the outcome of decisions made by the dugong populations to optimize its net energy gain at a given time (Roguet et al., 1998; Harvey & Fortin, 2013) and therefore, feeding trail patterns reflect foraging strategies in terms of patch utilisation at the population level – if it is detected.

My study area in the Sibul Archipelago of Peninsular Malaysia has had confirmed sightings of dugongs in the last two decades (Mansor et al., 2000; Affendi et al., 2005; Ooi et al., 2008; Ponnampalam et al., 2015). The Sibul Archipelago is a unique location to study the dynamics of habitat use by dugongs within a completely subtidal, tropical seagrass ecosystem. It is considered one of the few pristine sites within Southeast Asia that contains a sizeable population of dugongs (Hines et al., 2012; Ponnampalam et al.,

2015). The presence of dugong herds of 20 – 43 or more animals, including mother-calf pairs (Ponnampalam et al., 2015; Ponnampalam, 2017), further underscored the value of this area; yet, baseline information on the extent of the meadow and how these herds utilise their seagrass habitat is lacking. Most studies on dugong feeding have been carried out in subtropical regions, such as Hervey Bay and Shark Bay in Australia, with fewer investigations from the tropics, particularly in an exclusively subtidal system. Our site provides the opportunity to study dugong feeding in a meadow unrestricted by low tidal height, in contrast to those studied by Anderson & Birtles (1978) and Sheppard et al. (2009, 2010). In our case, grazing patterns are not likely to be confounded by the inability of dugongs to access parts of the meadow due to shallow water depth at low tide.

This chapter describes the spatial feeding patterns of dugongs in the subtidal seagrass meadow of Sibuluan Archipelago, Malaysia. I investigated whether there was a spatial pattern in the way dugongs fed in the seagrass meadow and if so, whether feeding trails have a concentrated or dispersed pattern, what might be the average feeding patch size, and what might be the relationship between feeding pattern and seagrass quantity (i.e., seagrass cover). I then identified feeding hotspots and coldspots within the Sibuluan Archipelago meadow, and suggested reasons for their distribution.

4.2 Literature Review

Grazing herbivores are known to preserve a spatial memory of productive feeding areas which they periodically visit to monitor food resources, not only for plant quality but also for the quantity (McNaughton, 1984; Frank et al., 1998). This ‘managing’ behaviour, known as cultivation grazing *sensu* Preen (1992), has been suggested for dugongs as they depend almost exclusively on seagrass habitats and are selective towards certain species of seagrass in their diets (Sheppard et al., 2006; Marsh et al., 2011). As such, dugongs must feed strategically given that their behaviour at one point of time will affect foraging efficiency at a later time (Pyke et al., 1977). For example, dugongs and green turtles, like terrestrial herbivores (Frank et al., 1998; Vavra & Ganskopp, 1998; Bakker et al., 2016), are able to improve their forage quality in terms of nutrient (increased nitrogen, reduced fibre concentrations) and density (increased aboveground biomass) by repeatedly feeding at restricted patches. This promotes a meadow made out of fast-growing colonising species such as *Halophila ovalis* and *Halodule uninervis* (Aragones & Marsh, 2000; McMahan, 2005; Aragones et al., 2006; Fourqurean et al., 2010; Molina Hernández & van Tussenbroek, 2014; López et al., 2019). Within such meadows, however, there is no knowledge of whether dugongs strategically concentrate their feeding effort in profitable patches or whether they feed randomly within it.

The foraging strategies of dugongs are still unclear and vary between foraging grounds of different regions. In the tropics, the dynamism and patchiness of seagrass meadows is an established fact and dugongs, being obligate seagrass consumers, face high spatiotemporal variation of their food resources (Short et al., 2001; Tol et al., 2016). To cope with heterogeneity, dugongs maintain a spatial memory of productive hotspots, as they periodically visit patches to monitor the food resources, not only for plant quality but also for the availability and abundance of food resources at different times (Sheppard et al., 2006).

The goal of maximising nutrient intake is generally accepted as a pivotal motive underlying the foraging strategy of large herbivores, as opposed to merely maximising bulk energy (biomass) intake. Many studies have shown that dugongs, like other terrestrial grazers, preferentially feed on nutrient-rich food plants by selecting seagrass species with high digestible nutrients such as nitrogen in leaves and shoots (De Iongh et al., 1995; Yamamuro & Chirapart, 2005; Sheppard et al., 2007; D'Souza et al., 2015). However, there is also evidence that not all dugongs choose to feed at the most nutrient-rich patches, suggesting that nutrition may not always be the currency for foraging strategies in every pasture (Tol et al., 2016). In meadows dominated by small seagrass species such as *Halodule uninervis*, for example, dugongs have been found to forage effectively on the digestible starch in rhizomes, rather than nitrogen in leaves, resulting in maximal energy return for foraging effort (de Iongh et al., 1995; Anderson, 1998; Masini et al., 2001). In contrast to the quality-versus-quantity viewpoints, dugongs in north Queensland, Australia, have been observed feeding across all species present - except *Enhalus acoroides*. The animals also targeted high biomass areas with lower nitrogen content, thus reflecting potentially different driving mechanisms for dugong foraging behaviour in meadows with different species composition (Tol et al., 2016).

4.3 Methodology

The information used to analyse the feeding patterns of dugongs was derived from the underwater towed video footages described in Chapter 3. The video frames were subsampled at 5 m intervals to record presence/absence of dugong feeding trails, and trail counts per frame. Dugong feeding trails were indicated by bare linear or serpentine furrows on the seagrass bed formed by the animals' continuous directionally forward grazing action (**Figure 4.1**; Preen, 1992; Marsh et al. 2011; D'Souza et al., 2015). Here, we made the assumption that excavation was the main grazing mode as opposed to leaf

cropping, because the meadow is made out of small, colonising species (e.g., *Halophila ovalis*, *Halodule uninervis*) (Domning & Beatty, 2007; Wirsing et al., 2007a). To avoid double counting, each feeding trail in a video frame was checked by backtracking to the preceding frame to confirm its separation from the previous one. Feeding trail density was calculated only for frames with seagrass present and expressed as number of trails/frame.

GeoDa software (Anselin, 2005) was used to compute spatial autocorrelation of dugong foraging intensity. Several grid resolutions were tested using 50 m, 100 m, 200 m, 300 m, 400 m and 500 m cells but the 100 m grid was chosen for the final analysis because of its ability to detect local scale variation ($<10 \text{ km}^2$) (Sheppard et al., 2007). The frequency of dugong feeding trails within each cell was used to generate the spatial weights matrix for the measurement of contiguity. Queen's measure of contiguity was used to determine neighbouring cells i.e., those that share a common edge or vertex (Harris et al., 2017).

Moran's I (Moran, 1948) was applied to measure the spatial autocorrelation of dugong feeding trails in 0.01 km^2 cells. It provides an index of whether each given data point is autocorrelated to its neighbours in terms of the similarity (or dissimilarity) of values (Sokal & Oden, 1978). Indices of positive values approaching +1 indicate the existence of spatial clusters (locations with similar values), negative values approaching -1 indicate a dispersed pattern, and zero values indicate random spatial variation among locations (locations are not correlated) (**Figure 4.2**). Spatial correlograms were computed using Moran's I coefficient to estimate the spatial correlation distance for each sampling season (Mathur, 2015), i.e., average feeding patch size (Legendre & Fortin, 1989). As Moran's I can only detect the general presence of clusters, a local measure—the Getis-Ord G_i^* statistic was also used to delineate those clusters into feeding hotspots (most preferred feeding grounds), coldspots (least preferred feeding grounds), and non-significant spots

(random feeding grounds) (Getis & Ord, 1992). Hotspots were pixels with high-high values, i.e., a target pixel and its neighbours have similarly high counts of feeding trails, coldspots were pixels with low-low values, i.e., the target pixel and its neighbours have similarly low counts of feeding trails, and non-significant spots were pixels with high-low values or low-high values, i.e., target pixel and its neighbours have dissimilar high and low counts of feeding trails. The differences between clusters were examined using a Kruskal-Wallis ANOVA on ranks followed by Dunn's test for pairwise multiple comparison.

The global Moran's I statistic is expressed as:

$$I = \frac{N \sum_{i=1}^n \sum_{j=1}^n W_{ij} (x_i - \bar{x})(x_j - \bar{x})}{(\sum_{i=1}^n \sum_{j=1}^n W_{ij} \sum_i (x_i - \bar{x})^2)}$$

Where N is the number of observations of the whole region,
 \bar{x} is the mean of the variable,
 x_i is the variable value at a particular location,
 x_j is the variable value at another location, and
 W_{ij} is a spatial weight between locations of i relative to j

The Getis-Ord G_i^* local statistic is expressed in simplified form as:

$$G_i^* = \frac{\sum_{j=1}^n W_{ij}(d)x_j}{\sum_{j=1}^n x_j}$$

Where G_i^* describes the spatial dependency of incident i over all n events,
 n is total number of features,
 x_j is the magnitude of variable x at incident location j over all n (j may equal i),
 d is the neighbourhood distance, and
 W_{ij} is the spatial weight between locations i and j that represents their spatial interrelationship in reference to d



Figure 4.1 A feeding trail of dugong on the seagrass meadow

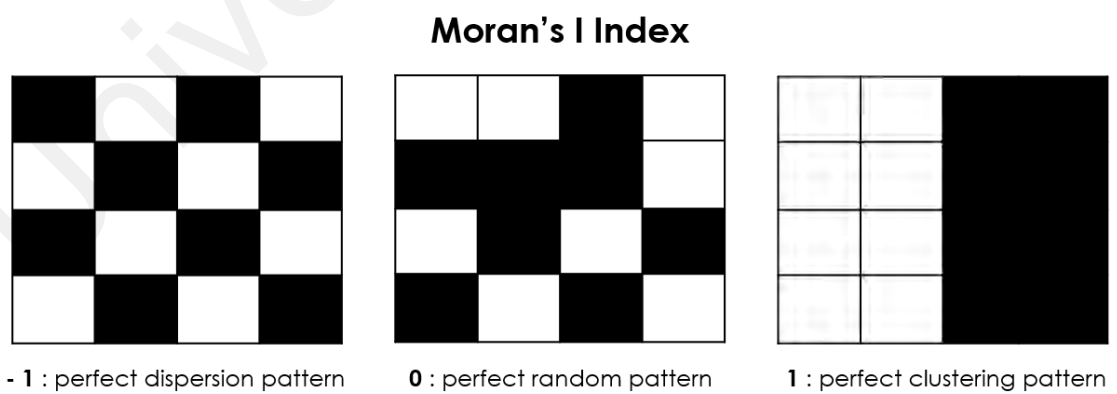


Figure 4.2 Diagrammatic interpretation of Moran's I values

4.4 Results

4.4.1 Video data

Towed video footage was acquired across approximately 22 km of transects in each season. Dugong feeding trails made up 58 – 61% of the total frames captured during the inter-monsoon and pre-monsoon and 26% during the post-monsoon (**Table 4.1**). In frames with seagrass, dugong feeding trails were present in 67 – 70% of sampling frames in the inter-monsoon and pre-monsoon, and 49% in the post-monsoon.

Table 4.1 Summary statistics for video and dugong feeding trail datasets across three sampling seasons in 2016 – 2017, Sibul Archipelago, Peninsular Malaysia. DFT is *dugong feeding trails*.

Data	Inter-monsoon		Pre-monsoon		Post-monsoon	
	<i>n</i>	% of total frames	<i>n</i>	% of total frames	<i>n</i>	% of total frames
Towed Video						
Total transect line distance (km)	22.38		22.31		22.07	
Total video frames scored	3485		3460		3292	
Dugong feeding trail present	2033	58.34	2109	60.95	870	26.43
Dugong feeding trail absent	1452	41.66	1351	39.05	2422	73.57
Dugong Feeding Trail						
Total count	8813		5380		2460	
Density (number of trails per frame)	2.92		1.77		1.38	
Mode frequency of DFT per frame	1-2		4-5		1-2	
Frames with mode frequency of DFT	1080	53.12	813	38.55	449	51.61

4.4.2 Dugong feeding trail occurrence

The density of feeding trails varied across seasons, being highest in the pre-monsoon (2.92 trails/frame) followed by the inter-monsoon (1.77 trails/frame) and lowest in the post-monsoon (1.38 trails/frame) (**Table 4.1**). Three feeding trails per frame was the average throughout all seasons, while the maximum number of feeding trails per frame was 14.

The histograms showed concurrent trends of seagrass cover and number of feeding trails (**Figure 4.3**). The most frequent occurrence was 1 – 2 feeding trails per frame during

the inter-monsoon (1080/2033 frames, 53.12%) and post-monsoon (449/870 frames, 51.61%), which coincided with high (mode 76 – 100%) and low (mode 0 – 5%) seagrass covers, respectively. During the pre-monsoon, feeding trails per frame increased to 4 – 5 feeding trails per frame (813/2109 frames, 38.55%), which coincided with moderate seagrass cover (mode 26 – 50%). In short, high feeding trails per frame occurred when seagrass cover was moderate, while low feeding trails per frame occurred when seagrass cover was both low and high.

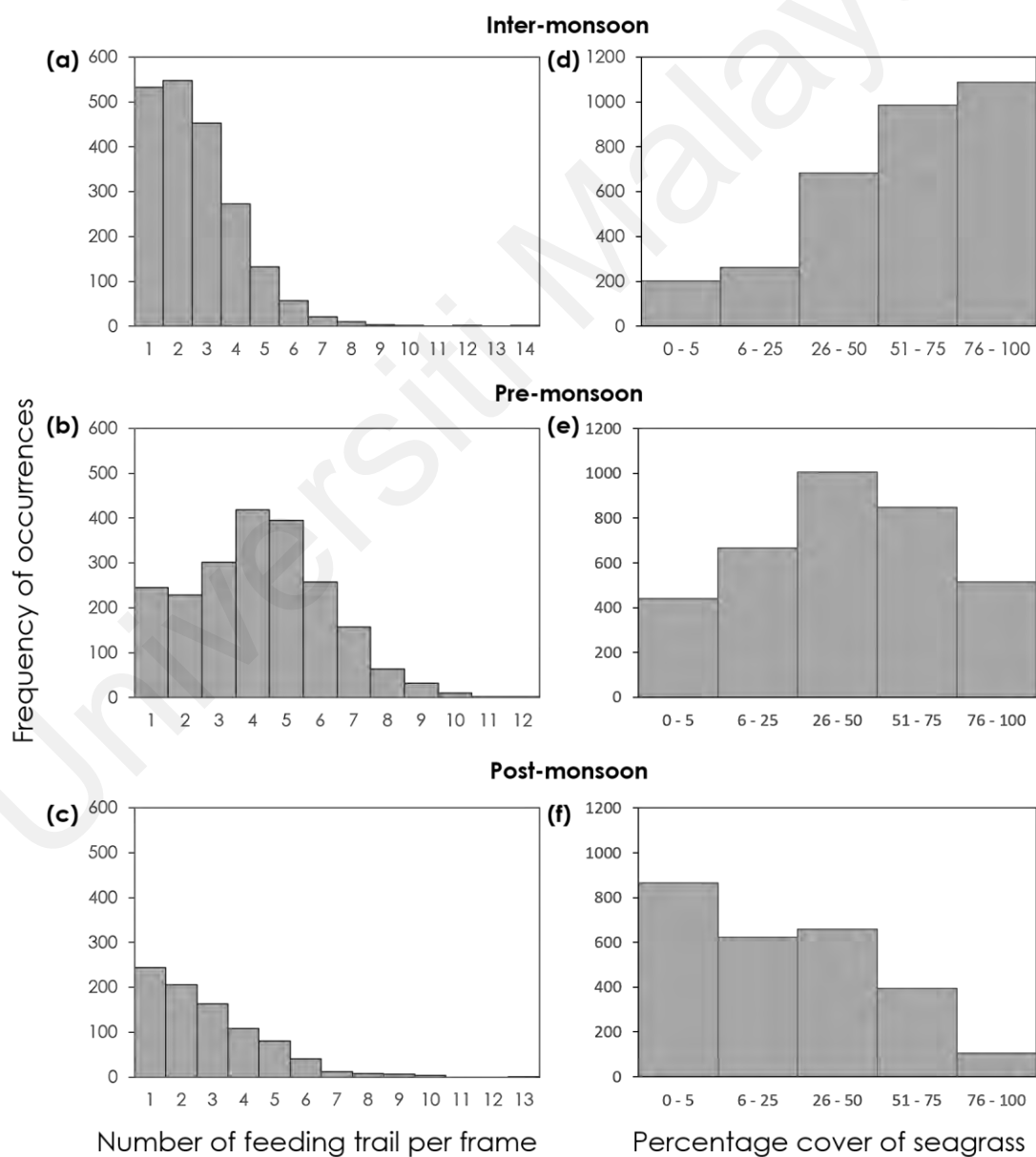


Figure 4.3 (a) – (c): Frequency plots for feeding trails; (d) – (f): Frequency plots for seagrass in the inter-monsoon, pre-monsoon and post-monsoon seasons

4.4.3 Spatial patterns of dugong feeding

Global Moran's I values revealed that dugong feeding trails across all seasons were spatially clustered (**Table 4.2**). The highest aggregation of feeding trails was found in the post-monsoon (Z score = 8.276). The null hypothesis was rejected because of high positive Z -scores ($> +2.58$) and low P -values ($P < 0.01$), indicating that the spatial distribution of high/low values in the study area were not likely due to chance (Mathur, 2015). The range of spatial autocorrelation, i.e., patch size, varied with season: dugong feeding trails were autocorrelated at <1152 m, <662 m and <1113 m for the inter-monsoon, pre-monsoon and post-monsoon seasons respectively (**Figure 4.4**).

Table 4.2 Summary of Moran's I and spatial pattern of dugong feeding trails across three sampling seasons

Sampling Season	Moran's I	Z score*	P value	Pattern	Autocorrelation range (m)
Inter-monsoon	0.323	7.287	<0.01	Clustered	<1152
Pre-monsoon	0.313	7.533	<0.01	Clustered	<662
Post-monsoon	0.438	8.276	<0.01	Clustered	<1113

* Z score value greater than 1.96 indicates that spatial autocorrelation is significant at 95% confidence level and greater than 2.58 indicates significance at 99% confidence level.

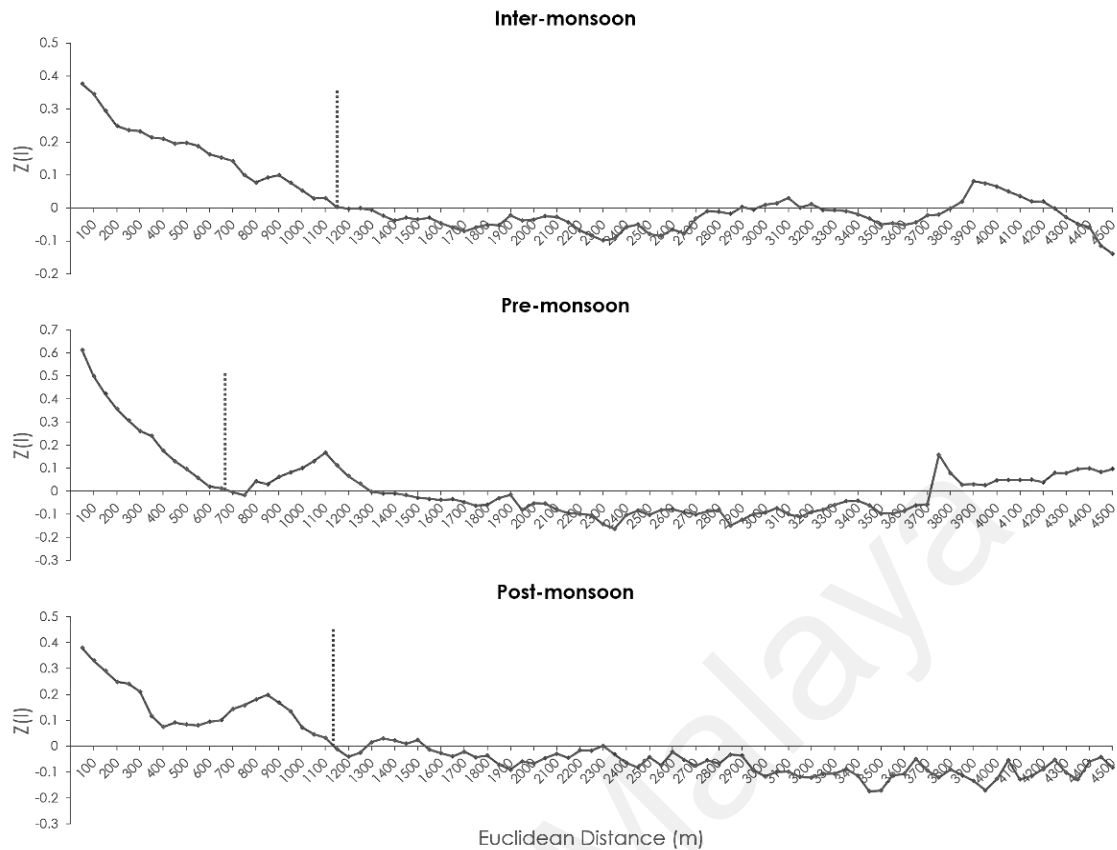


Figure 4.4 Spatial correlograms with 50 m distance class for each season. The intersection between the trendline and the x-axis represents the correlation range for feeding trail occurrences. Dugong feeding is autocorrelated within those ranges—marked by vertical lines at 1152 m, 662 m, and 1113 m—for the inter-monsoon, pre-monsoon and post-monsoon seasons, respectively.

The Getis-Ord G_i^* statistic showed that high-high spatial clusters (hotspots) and low-low spatial clusters (coldspots) co-occurred in each season (**Figure 4.5**). The total area of hotspots amounted to 0.27 km² in the inter-monsoon, 0.32 km² in the pre-monsoon, and 0.20 km² in the post-monsoon. While there was variation in the size of the meadow, several hotspot areas remained at the middle of the meadow over time. Coldspots varied with season in a similar way to hotspots: they were of intermediate size in the inter-monsoon (0.32 km²), largest in the pre-monsoon (0.37 km²), and smallest in the post-monsoon (0.28 km²). Spatially, however, coldspots occurred mostly at the edges of the meadow.

Seagrass cover was statistically distinct (Kruskal Wallis test, $\chi^2 = 469.5$, $P < 0.001$) among the hotspots (median 63.0%), coldspots (median 15.5%) and non-significant spots (areas with random spatial pattern of feeding trails, median 38.0%) (**Figure 4.6**). A post-hoc analysis using Dunn's test with Bonferroni correction showed significant differences between coldspots and hotspots ($P < 0.001$), between coldspots and non-significant spots ($P < 0.001$) and between hotspots and non-significant spots ($P < 0.001$).

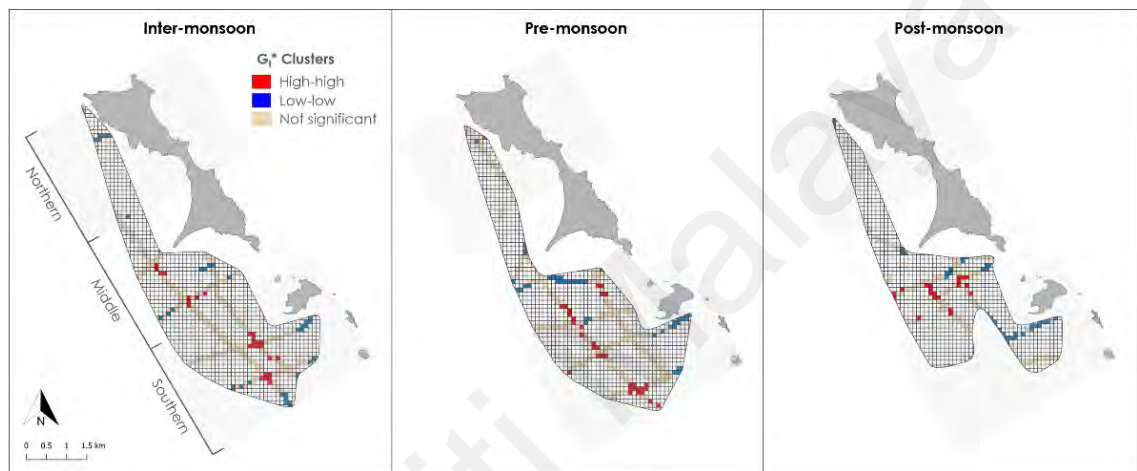


Figure 4.5 Spatial clusters of dugong feeding trails in Sibu Archipelago across three seasons in year 2016 - 2017, showing high-high clusters (hotspots), low-low clusters (coldspots) and high-low or low-high clusters (non-significant spots) analysed using the Getis-Ord G_i^* statistic.

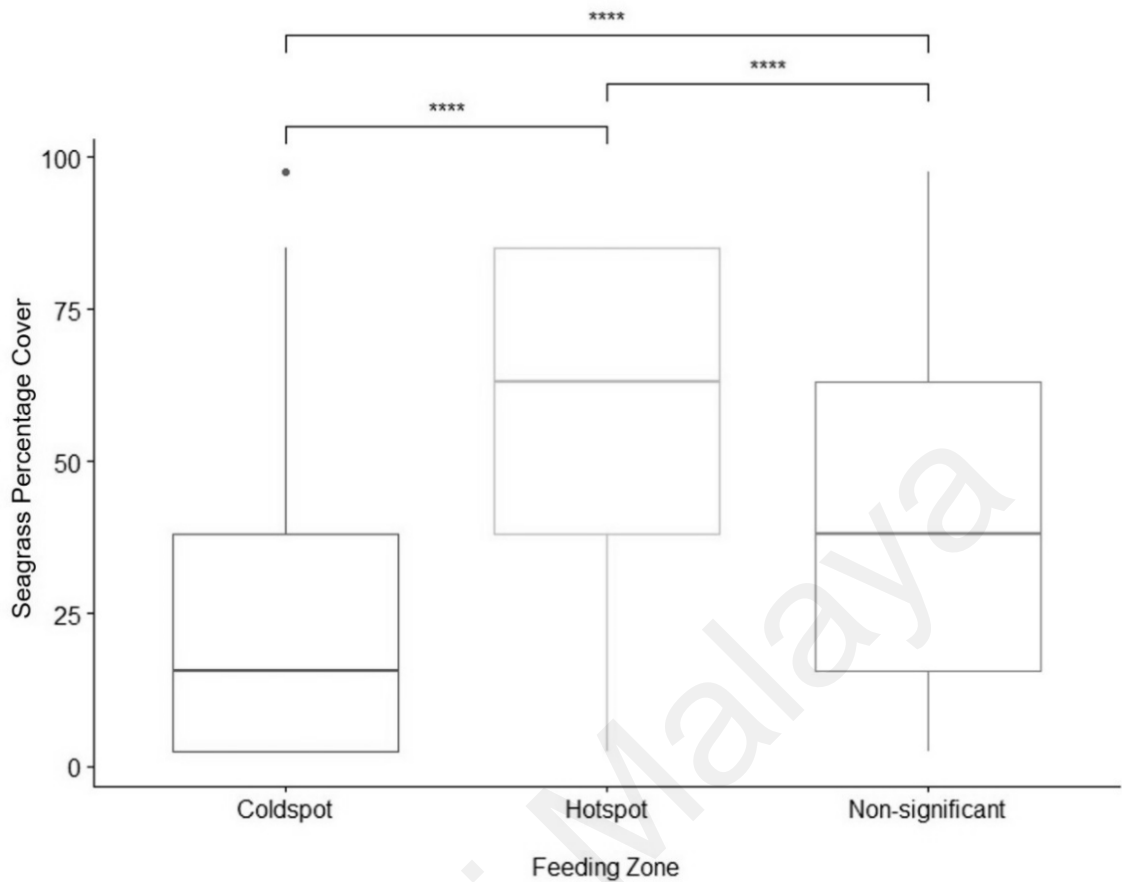


Figure 4.6 Boxplot of seagrass cover in three feeding zones – coldspot, hotspot and non-significant spot. Dunn’s test with Bonferroni correction showed significant differences between all pairings. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

4.5 Discussion

4.5.1 Dugong feeding patterns

Dugong feeding trails were present in 63% of towed video frames with seagrass, indicating substantial levels of habitat used for feeding. Feeding trails were present throughout all sampling seasons, which confirmed that the meadow was consistently utilised by dugongs. The meadow itself appeared to be an ideal feeding ground because it mainly comprised structurally simple, early-seral communities of *H. ovalis* and *H. uninervis*. These are types favoured by dugongs (Marsh et al., 1999). This type of seagrass community has been associated with the excavation feeding mode, where whole plants including roots and rhizomes are uprooted (Heinsohn et al., 1977; Anderson & Birtles,

1978; Anderson, 1998; Preen, 1992). *Halophila*-dominated meadows can recover within a short period, i.e., one to three months, although recovery rates may vary according to season and intensity of herbivory (Nakaoka & Aioi, 1999; McMahon, 2005; Rasheed et al., 2016). Hence our sampling intervals of between three to six months would have been sufficient for the meadow to recover from grazing. Feeding trails detected in each sampling season were unlikely to have been created in preceding seasons.

Dugongs fed in a spatially clustered pattern in all seasons, and the correlograms implied that the seagrass meadow—although appearing continuous—consists of a mosaic of discrete feeding patches within which dugongs feed. These patch sizes varied with season—as shown by the feeding trail autocorrelation values of <1152 m, <662 m and <1113 m for the inter-monsoon, pre-monsoon and post-monsoon periods respectively—but the pre-monsoon stood out for having feeding patches that were half the size of those of other seasons. Dugong feeding clusters in a subtidal environment have only ever been determined before in Burrum Heads, Australia, where the dugongs' locations were used to indicate feeding habitat selection (Sheppard et al., 2010). In that study, dugongs were found to form habitat clusters of $5.8 \pm 1.7 \text{ km}^2$ (mean 95% kernel home range) across 23.8 km^2 of mainly *H. uninervis* and *H. ovalis* seagrass. In this study, we estimate feeding patches to range from 1.4 - 4.2 km^2 (given that autocorrelation values are the radii of circular areas) across $9.3 - 12.3 \text{ km}^2$ of seagrass meadow. Results from both this study and that of Sheppard et al. (2010) suggest that dugongs maintain local-scale feeding clusters within meadows.

4.5.2 Dugong feeding patterns and seagrass quantity

We found that dugongs fed in discrete patches according to seagrass coverage, which suggests that dugong spatial feeding patterns were influenced by food quantity. Two main feeding patterns were detected: (1) a dispersed feeding pattern, resulting in large feeding

patches with low feeding trail density, and (2) a concentrated feeding pattern, resulting in smaller feeding patches with high feeding trail density. We propose a conceptual model of dugong feeding patterns in relation to seagrass quantity: feeding was dispersed when seagrass cover was relatively low (mode 0 – 25% cover) and high (mode 76-100% cover), but concentrated at moderate levels of seagrass cover (mode 26-75 % cover) (**Figure 4.7**).

Here, we consider some possible trade-offs that dugongs have to make when choosing their feeding ground in habitats with heterogenous food quantity. In high and low cover meadows, dugongs utilise patches less intensively, indicated by a dispersed foraging pattern in our study. This may be because: 1) when food quantity is not limiting, the animals can spend more time searching and selecting higher quality forage by moving larger distances between feeding stations (i.e., feeding trails) while maintaining intake rate (Bailey et al., 1996; Searle et al., 2005); 2) when food quantity is limiting, the animals may not select between patches for food quality because the majority of patches could have been remarkably poor; continued exploitation of any patch could have imposed higher foraging cost and limited their ability to attain minimum net energy intake (Van de Koppel et al., 1996); or 3) the animal's ability to discriminate patches may have been reduced when the difference in food quantity between alternative patches was small, meaning the dugong may not be able to tell apart a large group of individual patches with homogenous attributes, but rather perceive them as a continuous resource where the intake rate is the same (Wallis DeVries et al., 1999). This may explain the relatively large patch size of 1152 m and 1113 m during the inter-monsoon and post-monsoon seasons, when the seagrass coverage was at the highest and lowest level.

Meanwhile in moderate cover meadows, the dugongs exploit patches in a more intensive way, which resulted in a concentrated feeding pattern. Some studies have shown that dugongs graze more frequently in areas with low to moderate seagrass biomass while less frequently in dense seagrass areas (Preen, 1992; de Longh et al., 1995). Taken together,

these findings indicate that dugongs are likely to concentrate feeding within a relatively smaller patch size when the seagrass coverage is at a moderate level. Although the exact reason is unclear, it may result from profitable patches being less widely distributed in space and located further apart in moderate cover meadows than high cover meadows (Fonseca & Bell, 1998; Vásquez et al., 2006). Natural meadows with moderate food resources are spatially less predictable and thus may be less advantageous for foragers to obtain patch estimation and search for high quality food (Valone, 1991; Marshall et al., 2013). In such an environment, patches tend to be overexploited (e.g., longer residence time in a patch) especially by large herbivores to maximise their intake rate (Demment & Van Soest, 1985; Vivas & Saether, 1987; Laca et al., 1993; Distel et al., 1995; Vásquez et al., 2006). Similar phenomenon has been observed for terrestrial ungulates, such as elk and bison, that tend to maximise their net intake rate at an intermediate biomass, often coinciding with highest quality of available plants (as digestibility declined with increasing biomass due to maturation of cell wall) and less movement cost (Bergman et al., 2001; Frair et al., 2005; Hebblewhite et al., 2008; Seidel & Boyce, 2015). The matching of this functional response leads to the expectation that food quality and digestive constraint of the animal also need to be explicitly incorporated when considering the short- and long-term trade-off decision of dugongs, which could influence patterns of feeding strongly.

The proposed seagrass-dugong feeding model provides a counterpoint to classical plant-herbivore interaction in which foraging efficiency of herbivores simply increase with standing crop. If food availability were the major driver of feeding patterns in this area, as shown by dramatic reduction in meadow cover and extent following the monsoon, higher clustering of feeding trails in a moderate cover meadow indicates that the concentrated feeding strategy is generally more efficient when food resources are neither too high nor too low. Alternatively, shifting to a dispersed feeding strategy is more

optimal when the seagrass cover of the meadows is on the two extreme ends of the gradient. In salt marshes, Van de Koppel et al. (1996) found maximal grazing intensity at the intermediate level of standing crop and low grazing intensity at the high and low ends, meaning that dense vegetation areas reduced the grazing efficiency of small herbivores. The preference for intermediate biomass vegetation is also commonly observed in other mammalian grazers such as elk, bison and kudu (Owen-Smith & Novellie, 1982; Langvatn & Hanley, 1993; Wilmshurst et al., 1995; van der Wal et al., 1998). It is thus likely that feeding patterns detected in this study are strategies by dugongs to increase their ability to meet their dietary requirements when they encounter different seagrass coverage.

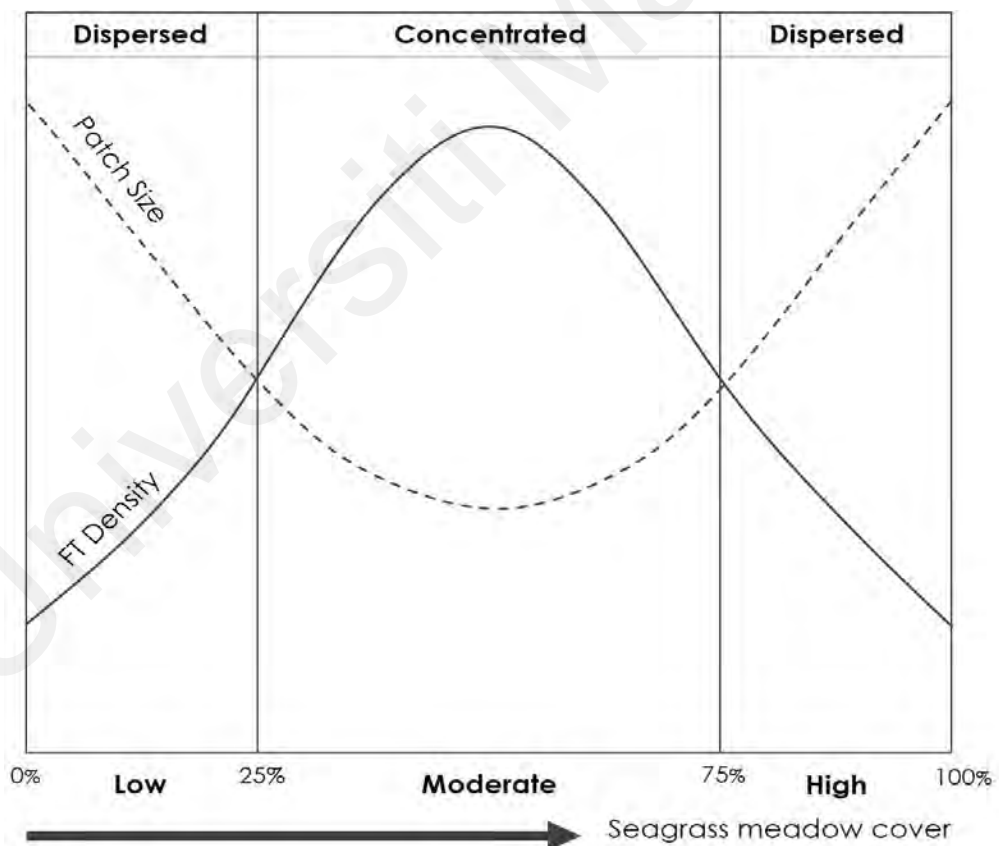


Figure 4.7 A conceptual model of dugong feeding patterns under a gradient of seagrass cover. Dugongs feed in a dispersed pattern during conditions of high and low seagrass coverage (76 – 100% and 0 – 25%) which results in larger patch size, and feed in a concentrated pattern in moderate seagrass coverage (25 – 75%) which results in smaller patch size.

4.5.3 Feeding hotspots and coldspots of dugongs in Sibul Archipelago

Using spatial statistics, dugong feeding hotspots and coldspots were detected. Hotspots occurred mainly off the southwest of the Sibul Archipelago. These locations were aligned with the highest congregation of dugongs found by Ponnampalam et al. (2015) in their aerial survey in 2010 and subsequent surveys in 2014 – 2016 where large dugong herds were sighted repeatedly in the same area (Ponnampalam, 2014; Hines et al., 2020). This provides substantial evidence of site fidelity for dugongs in tropical waters where dugongs concentrate their feeding in particular patches within a meadow, even though both the favoured species, *H. ovalis* and *H. uninervis*, are widely distributed in the rest of the meadow.

Feeding hotspots occurred between the southernmost tip of Pulau Sibul Besar and Pulau Sibul Tengah, which appeared consistent all year round, and were mostly in the interior of meadows. However, the reasons for those hotspots are unknown. If it is true that dugongs prefer feeding in sites where high quality food is available (Hines et al., 2012), it is plausible that these hotspots were either patches with naturally high quality food or are cultivated through repetitive grazing for that purpose. Dugongs form herds, from a few individuals up to a herd of a hundred or more, primarily for feeding but also presumably to create large areas with high quality feeding pastures for future use (Preen, 1992; de Iongh et al., 1998). Clustering of feeding trails in the feeding hotspots might be the result of cultivation grazing by groups of 3 – 5 individuals (the common number observed during extended periods of boat and aerial surveys (Ponnampalam, pers. obs), similar to the behaviour of dugongs in other tropical regions, i.e., Thailand (Supanwanid, 1996), Indonesia (De Iongh et al., 2007) and India (D'Souza et al., 2015). We could not confirm positive ecological feedback, i.e., that seagrass quality improved as a result of cultivation grazing due to the level of grazing in the feeding hotspots, as such observations were beyond the scope of this study. However, our results indicate that dugongs were

strategic feeders within the meadow: they fed more intensively in areas with moderate seagrass cover, resulting in feeding hotspots, and less so in areas with low seagrass cover, resulting in feeding coldspots.

The absence of feeding hotspots at the northern meadow throughout the sampling period is likely due to two factors that we observed throughout the study: 1) more anthropogenic disturbances in those sections of the meadow, and 2) less extensive seagrass in the northern meadow. Most of the resort and fishing boats travelled to and from the mainland and Pulau Sibul Besar and/or the surrounding islands such as Pulau Tinggi (~8 km northeast of Pulau Sibul Besar); hence dugongs that feed at the northern meadow are more likely exposed to higher risks such as boat strike and noise pollution (see Hodgson & Marsh, 2007). Previous aerial surveys by Ponnampalam et al. (2015) also revealed that dugongs were mostly sighted at the middle and southern meadow, likely due to areas of quiescence in those parts of the meadow where they form a safer refuge (Marsh et al., 1984; Anderson, 1998). Additionally, the narrow stretch of meadow with extremely low seagrass coverage (0 – 25% cover) at the northern part might discourage dugongs from feeding more intensively or at all. It is likely that combining high potential danger around the boat cruising routes with low food availability made the northern meadow a less favourable area for feeding.

Coldspots found in this study were often aggregated around the edges of the meadow, suggesting that the dugongs did not frequent meadow edge areas to feed as much as they did the interior. Edge avoidance for feeding, however, may be due to its coincidence with water depth - for example, meadow edges are located on the shallow and deep extremes of the depth gradient. On the shallow edge (~2 m), seagrass coverage was often lower because of physical disturbances from wave movement and boating and fishing activities (Hines et al., 2020). On the deep edge (~10 m), seagrasses are at the limits of their light requirements (McDonalds 2003; Lee et al., 2007) and as a result, are less dependable

feeding areas. There is also a potentially greater risk of predation in the meadow edges than in the interior (Wirsing et al., 2007b). Studies on risk of predation on dugongs are lacking in our site. Although bull sharks (*Carcharhinus leucas*) were occasionally sighted during aerial surveys in the area just west of the meadow's edge, towards the mainland coast (Ponnampalam, pers. comm.), no dugongs were observed around the Sibuluan Archipelago bore any wounds or scars typical of shark bite injuries. Hence, while the presence of the aforementioned bull sharks poses some predation risk and could be a reason for the dugongs to avoid feeding at patches near seagrass meadow edges, predation risk is likely to be low because common predators such as large sharks are not commonly sighted. Thus, the most likely reason for coldspots on meadow edges in this case was low seagrass cover.

4.5.4 Potential biases and limitations

This study was subjected to several biases because of its use of towed video to detect dugong feeding trails. Availability bias could have been introduced if dugongs had only grazed the belowground seagrass in a sparse-looking meadow where aboveground biomass was very low – a phenomenon observed by de Longh et al. (1995) in Ambon Island, Indonesia. Dugong feeding trails in barren substrata are easily dissipated into a flattened surface, thus remaining undetected by the video interpreter. Feeding trails might also be missed due to poor water visibility, but this bias was likely low due to overall good visibility and weather conditions during the surveys of this study. Partial appearances of feeding trails at the edges of the video frames may have possibly obscured some “true” feeding trails, but this bias was minimized in the processing stage via careful video scrutiny to confirm feeding trails on frame edges. Because of these biases, we consider our computed data to be underestimates. We were limited in our capacity to extend our survey period over one year, which restricted us from further examining if the

detected foraging patterns in this study changed or remained the same over longer periods of time, especially when the meadow itself appeared to be dynamic in terms of seagrass cover and extent.

4.6 Conclusion

Using dugong feeding trails as a proxy for direct observations of dugong feeding, we showed how a non-invasive and reproducible sampling method using an underwater towed video system can be used to collect spatially-explicit feeding data for this elusive marine mega-herbivore in a non-intertidal habitat. Dugongs did not follow a random pattern while feeding, but instead, fed in a spatially concentrated manner when the coverage of seagrasses was moderate (26 – 75%) and switched to feeding in a dispersed pattern when seagrass patches became either high (76 – 100%) or low (0 – 25%) in coverage. The trade-off between forage quantity and quality, which is crucial to understanding the way dugongs perceive the distribution of their food resources in a complex landscape, is not clear yet as it is beyond the scope of this study. Nevertheless, this results demonstrated that in one regard, food quantity had a significant effect on the habitat utilisation patterns of the dugongs, in turn highlighting its relative importance to dugongs. The middle area of the seagrass meadow in the Sibul Archipelago, off the west of Pulau Sibul Tengah, was identified as a feeding hotspot for the dugong population throughout the seasons. This study also revealed the need for further research to ascertain the drivers of observed feeding hotspots and the mid- to long-term dynamics of the meadow's growth, dieback and regrowth cycle. Data on dugong ecology in this region is generally scarce, with most research on dugong feeding ecology mainly focused on intertidal seagrass. Thus, this study provides an insight into how a mega-herbivore species with restricted local distribution changes its foraging decisions in a subtidal meadow at the patch scale. In this case, seagrass abundance (cover) was one of the driving factors

which influenced those decisions. To the best of my knowledge, this is the first in-depth spatial study of dugong spatial feeding patterns in a subtidal habitat in this region, consequently contributing to the filling of knowledge gaps and ecological understanding of this elusive and endangered species.

Universiti Malaya

CHAPTER 5: WHAT DRIVES DUGONG FEEDING PREFERENCES?

5.1 Introduction

5.1.1 Dugong -- A seagrass community specialist

Herbivores are generally thought to have an ample surplus of foods but of low and highly variable nutritional quality because a substantial portion of nutrients in plant tissues are bound to indigestible fibrous compounds (i.e., lignin) (Cebrián & Duarte, 1998; Prado & Heck, 2011). Consequently, much of the available food may not be of sufficient quality. The value of seagrasses as a quality food is, therefore, a function of its availability (i.e., distribution, abundance, morphology, and production) as well as its nutritive qualities (Thayer et al., 1984). For Sirenians, the nutritive qualities of food are mainly composed of protein (e.g., nitrogen), structural carbohydrates (e.g., fibre), and non-structural carbohydrates (e.g., starch) (Marsh et al., 2011).

Although dugongs are known to be strictly herbivorous and prefer seagrass for their diet, they are capable of exploiting a relatively wide range of different foods, especially during food plant shortage which occurs seasonally or during extreme events (Marsh et al., 1982; Preen, 1995a). The adaptation of feeding on non-seagrass foods includes consumption of macro-invertebrates (i.e., ascidians, chaetopterid worms, thin-shelled burrowing mussels) and algae (i.e., brown algae *Sargassum*). Such atypical dietary intakes are observed more frequently in the subtropical limits of their range such as Shark Bay and Moreton Bay in Australia, when dugongs encountered nutritional stress like nitrogen deficiency (Marsh et al., 1978; Preen, 1992). Therefore, dugongs have been regarded as 'seagrass community specialists' rather than just 'seagrass specialists' (Marsh et al., 2011). Yet, this deliberate omnivorous behaviour has not been confirmed for the tropical dugongs where nitrogen availability in the seagrass is less seasonally variable (Preen, 1995a).

5.1.2 Feeding selectiveness of dugongs around the world

Feeding selectiveness is an ensemble of complex feeding decisions that arise when the animals choose certain foods from an array of available items, aiming to optimise the intake of energy and essential dietary elements within the physical and chemical features of habitats (Stephens & Krebs, 1986). Dugongs are particularly selective in terms of their seagrass diet, an observation that has been consistently reported within their range (Gohar, 1957; Heinsohn & Birch, 1972; Lipkin, 1975; de Iongh et al., 1995; Nakanishi et al., 2005; Yamamuro & Chirapart, 2005).

It is a challenge to confirm the feeding preferences of dugongs in the wild, unlike terrestrial animals which can be kept in cages, ensuring food types consumed by the animals can be manipulated and measured precisely. Captivity experiments for marine mammals such as dugongs are logistically and financially costly and also produce limited insights (Marsh et al., 2011; and see de Iongh, 1996). Meanwhile, analyses of dugong stomach contents from opportunistically collected carcasses are more reflective of the generic composition of the seagrass beds at the time and location where the animals were captured, but not necessarily indicative of feeding preferences (Marsh et al., 1982). Therefore, feeding preferences of dugongs are usually determined by way of evaluating and comparing the nutritional content of the available seagrasses within dugong foraging grounds (Aragones, 1996). However, the results from this approach are influenced by many factors which should be taken into consideration, such as the relative abundance and nutritional variability of each available seagrass species that varies across time and space (Erftemeijer & Herman, 1994), as well as the capacity of food breakdown and digestion of the animal (Lanyon & Sanson, 2006a, 2006b). Therefore, a definitive hierarchy of preferred food species and determinant factors in the dugong's diet are not yet clear (Marsh et al., 2011).

Information on how dugong dietary choices are limited by their digestive physiology are well-studied (Murray et al., 1977; Best, 1981; Lanyon & Marsh, 1995; Aketa & Kawamura, 2001; Aketa et al., 2003; Goto et al., 2004, 2008; Lanyon & Sanson, 2006a, 2006b; Eigeland et al., 2012), but data on the nature of selection in a seagrass diet at a local scale is still lacking for this particular study area. Quantifying the biomass and nutritional quality of their food plants, together with abiotic factors (e.g., water depth, sediment), may therefore improve our understanding of the hierarchy of preferred seagrass species and the relative contributions of each effect towards the feeding selectiveness of dugongs (Thayer et al., 1984). In this study, the qualities of seagrass were evaluated by using two types of nutritional currencies: 1) parameters which provide important nutrients for dugong nutritional and energetic requirements (direct effect) – starch, nitrogen and fibre, and 2) parameters which are important nutrients for seagrass growth and productivity, which in turn become the source of food/ nutrient for dugongs (indirect effect) – carbon, nitrogen and phosphorus.

The aim of this chapter, therefore, is to obtain an in-depth understanding of the feeding ecology of dugongs in my study site of Sibutu Archipelago, specifically to address the question of what drives the feeding preferences of the dugongs there. Three approaches were used to collectively inform the influential factors that may affect feeding preferences of dugongs: (1) characterise grazing behaviour through the dimensions of dugong feeding trails, and investigate relationship between dimension of feeding trails with seagrass quantity and particle size of the sediment, (2) compare quantity (relative abundance), quality (nutritional content) of each food species and physical environmental properties (water depth and sediment particle size) between dugong feeding areas and non-feeding areas (these of which were identified through the work described in *Chapter 4*), and (3) assess the relative influence of each factor on feeding site selection of dugongs.

5.2 Literature Review

5.2.1 Nutritional quality of seagrass for dugongs

The nutritional qualities of seagrass species in relation to diet selection by sirenians are primarily determined by the availability of high concentrations of starch and nitrogen, and low concentration of fibre (Lanyon et al., 1989; Aragones et al., 2006; Sheppard et al., 2007, 2008), which are the energy and nutrient required under their morphological and physiological constraints (reviewed in Marsh et al., 2011). The nutritional values can vary greatly both within and among seagrass species, i.e., younger leaves of fast-growing species have higher nitrogen and lower lignin contents compared to older leaves of slower-growing species (Bjorndal, 1980; Thayer et al., 1984). Many studies have suggested that herbivores should feed preferentially on the fast-growing species which have higher nutritional quality (i.e., have relatively lower fibre and higher nitrogen and/or carbohydrate concentrations) (Preen, 1995b; Cebrián & Duarte, 1998; Mariani & Alcoverro, 1999). As the specific leaf growth rate in different seagrass species accounts for some extents of variability in herbivores' preferences, plant nutrient concentrations, i.e., carbon, nitrogen, phosphorus, and ratios of C:N:P, were also commonly assessed in seagrass herbivory studies as these are the indicators of seagrass health which influence the growth and production rate of seagrass (de longh et al., 1995; Fourqurean et al., 1997; Kirsch et al., 2002; Yamamuro & Chirapat, 2005; Valentine & Heck, 2020).

Nitrogen (protein)

Nitrogen is recognised as one of the most important nutrients for the herbivores because it helps in synthesising protein, especially for young, growing calves and females in gestation and lactation periods (Lanyon, 1991; Kwan, 2002; Sheppard et al., 2007). Hence, nitrogen is a proxy for protein. Plant tissues which are mainly made up of

carbohydrates usually contain much lower nitrogen concentrations (~1 – 2%) compared with animal tissues (~10%), making them poor sources of nutrition for herbivores (Bentley & Johnson, 1991). Moreover, most of the gut microbes which synthesise nitrogen for the herbivores are in their colons which means the nitrogen would be easily excreted out from the digestive system. Consequently, nitrogen has often been considered as a limiting nutrient in a herbivore's diet (Van Soest, 1994).

Lanyon (1991) assessed four tropical seagrass species and reported the differences in their nutrient contents. Being preferred foods for dugongs, *H. ovalis* and *H. uninervis* (narrow-leaf variety) had highest nitrogen concentration, compared to *Zostera capricorni* and *Cymodocea serrulata*. Hence, Lanyon (1991) ranked seagrasses based on their nutrient content (*in vitro*) as: *H. ovalis* > *Halodule* (narrow-leaf) > *H. uninervis* (broad-leaf) > *C. serrulata* > *Z. capricorni*. Preen (1992) later ranked the preferred food plant species of dugongs in Moreton Bay, Queensland as: *H. ovalis* ≥ *H. uninervis* (narrow-leaf) > *H. uninervis* (broad-leaf) > *H. spinulosa* ≥ *S. isoetifolium* > *Z. capricorni* (broad-leaf), suggesting dugongs forage in a way to maximise nitrogen intake. In contrast, Nurdin et al. (2019) showed that *Cymodocea* sp. was the most nutritious food for dugongs in Lingayan Island, Central Sulawesi, because it had higher protein than *Halophila* sp. and *Halodule* sp.

Generally, the nitrogen concentration in leaves is reportedly more than twice that of the rhizomes, except in *H. spinulosa* and *S. isoetifolium* (Lanyon, 1991; Aragones, 1996; Sheppard et al., 2007). The whole-plant nitrogen values for seagrasses are mostly 1 – 4% of the total nutrient content (Duarte, 1992; Aragones, 1996). Leaves of *Halodule* sp. and *Thalassia* sp. are typically higher in nitrogen content (> 1.91 and 1.6–3% dry matter, respectively) (van Tussenbroek et al., 2006; Lanyon, 1991; Aragones, 1996; Sheppard et al., 2007) while the leaves of *Amphibolis antarctica* are relatively low in nitrogen (~1–1.2% DM; Walker et al., 1988).

Repeated grazing by dugong assemblages in same plots of seagrass suggests that the animals use an optimisation strategy to maintain the grazing pastures in early seral stage which favours both preferred species, *H. ovalis* and *H. uninervis*, in addition to capitalising on the overall improved nutritional quality (particularly through increased nitrogen in new foliage and lower fibre content) (de Iongh et al., 1995, 2007; Preen, 1995b). Aragonés et al. (2006) demonstrated that whole-plant nitrogen levels in *H. ovalis* and *H. uninervis* increased by 35% and 25% respectively, even after nearly a year from simulated intensive dugong grazing, despite the concomitant decrease in starch and increase in fibre concentrations.

Starch (carbohydrate)

Starch is the most important storage carbohydrate in plants (Van Soest, 1994; Aragonés et al., 2012) which could provide energy after breakdown to sugars, and is argued to be on par with nitrogen as the most important nutritional currency for dugongs (Preen, 1992; de Iongh et al., 1995; Yamamuro & Chirapart, 2005). Starch is important for large marine mammals to meet their energy costs associated with growth and reproduction, thermoregulation, food acquisition and seasonal migration (Thewissen & Jo Schneider, 2009).

Aragonés (1996) found that, as opposed to nitrogen, starch concentration in the belowground component is always higher than the aboveground component of seagrass for seven seagrass species, except *H. spinulosa*. Relative to other species of seagrass, the roots and rhizomes of *H. uninervis* are particularly rich in water soluble carbohydrates and starch up to 25.8% DM (Lanyon, 1991). Lanyon (1991) ranked seagrasses according to soluble carbohydrate in the belowground components as: *Halodule* (narrow-leaf) > *H. uninervis* (broad-leaf) > *C. serrulata* > *Z. capricorni* > *H. ovalis*. As such, de Iongh et al.

(1995, 2007), Anderson (1998) and Masini et al. (2001) suggested that dugongs preferentially forage on *H. uninervis* to maximise energy intake from the starchy belowground parts, the biomass of which is much greater than that of the aboveground leaves.

Fibre (structural carbohydrate)

The chief components of dietary fibre are cellulose and hemicellulose, and other polymers, principally lignin, that are resistant to digestion and absorption in the small intestines but can be fermented in the big intestines (Bjorndal, 1980; Thayer et al., 1984). Lignin gives rigidity to cell walls and is the most significant factor limiting the nutrients in plant cell walls to herbivores because it is generally indigestible (Van Soest, 1994). From a physiochemical point of view, a food plant is considered to have low digestibility if its cumulative availability of net nutrients is highly limited by an undegradable entity such as lignin (Thayer et al., 1984).

The levels of fibre were compared in four species of seagrass by Lanyon (1991) whereby mean neutral detergent fibre (NDF) values ranged from 13% DM in the roots and rhizomes of *H. ovalis* to 22% DM in the leaves of *Z. capricorni*. The NDF concentrations in seagrass leaves (32% - 63%) are often higher than the corresponding values for rhizomes (Lanyon 1991; Aragonés, 1996; Sheppard et al. 2007, 2008). The differences among seagrass species are not always consistent, presumably reflecting the ages of the plants sampled. The ranking of seagrasses according to increasing fibre levels in leaves (from higher to lower digestibility), is: *H. ovalis* < *Halodule* (narrow-leaf) < *C. serrulata* < *H. uninervis* (broad-leaf) < *Z. capricorni*.

Unlike other hindgut fermenters such as horses, dugongs lack specialised dentition to mechanically break down seagrass and absorb its nutrients. Therefore, researchers

generally agree that dugongs prefer morphologically small, low biomass seagrass plants that are lower in fibre, besides selecting for the plants' high nitrogen and starch concentrations (Preen, 1992; de Iongh et al., 1995; Yamamuro & Chirapart, 2005).

Carbon

Seagrasses require inorganic carbon for growth and are known to be highly productive in producing large quantities of organic carbon (de Iongh et al., 1995). Some species, e.g., *H. ovalis*, *C. rotundata* and *S. isoetifolium*, use carbon in the form of bicarbonate as an inorganic carbon source (Hemminga & Duarte, 2000). Organic carbon is used as fuel and structural material in plants, or partially transferred to a higher trophic level after the plants are consumed by herbivores to give the animals energy. Organic carbon content is not as limited as nitrogen content to the herbivores as plant materials are primarily made up of carbon and are low in nitrogen. That being said, even abundant nitrogen is not used efficiently if available carbon is lacking (Van Soest, 1994). Hence, the C:N ratio in shoot has been used to reflect the relative availability and nutrient limitation in an ecosystem (Ferdie & Fourqurean, 2004), and also as a robust bioindicator that responds early (i.e., weeks) to light reduction and reflects sub-lethal changes in the plants (McMahon et al., 2013), all of which contribute to the health and productivity of the seagrasses. Marbà et al. (2002) observed that there is a gradient of increasing C:N ratios in the tissues of seagrass from younger to older ramets, hence the C:N ratio could also be an indicator of the age of plant tissues, where low C:N ratio represent younger, more nutritious food for herbivores.

Phosphorus

Phosphorus is one of the primary nutrients that limits seagrass growth (Duarte, 1990; Holzer & McGlathery, 2016). Phosphorus content is often associated with nitrogen, particularly through protein synthesis. Phosphorus serves as a nutrient source needed to build the animal's proteins, RNA, DNA and ATP. Therefore, diets with high nitrogen but low phosphorus would not complement well in protein synthesis for growing herbivores (Sturner & Elser, 2002). In carbonate sediment environments, seagrass growth is usually primarily limited by phosphorus as calcium carbonate strongly binds phosphorus, limiting its bioavailability to the plants (Short et al., 1990; Fourqurean et al., 1992). Meanwhile Erftemeijer & Middelburg (1993) suggested that particle size and clay content of sediment affect the bioavailability of nutrients, where predominantly fine-grained and clay-rich sediment will have greater adsorptive capacity, in which limits the plant growth.

5.2.2 Physical characteristics of feeding areas

Feeding trails in seagrass meadow

The feeding signs of a dugong in a seagrass meadow usually depend on seagrass morphology, sediment type, and compaction of the substrate (Marsh et al., 2011; Aragonés et al., 2012). For structurally small seagrasses, dugongs graze by excavating into the substratum, leaving signature feeding trails in the seagrass meadow (Nakanishi et al., 2005, 2006). The feeding trails typically appear as distinctive serpentine furrows that are 2-10 m long, 10-25 cm wide and 2–10 cm deep (Heinsohn et al., 1977; Anderson & Birtles, 1978; Preen, 1992; Nakaoka et al., 2002; Adulyanukosol, 2010). Atypically wide feeding trails with a width of 30 cm left by a large female dugong have been observed before in Marsa Alam, Egypt (Shawky, 2019).

For larger seagrass species like *Amphibolis antarctica* and *Enhalus acoroides* which are more fibrous or resistant to excavation, dugongs would only crop the leaves without grazing the rhizomes, leaving bite marks on the leaves (Anderson, 1982; Domning & Beatty, 2007; Nakanishi et al., 2008). Occasionally, the dugongs leave circular or elliptical scars when they presumably stay feeding at one spot rather than moving forward (Aragones, 1994; Anderson, 1998; Nakanishi et al., 2008; Domning, 2001). Feeding trails by means of excavation remove a substantial amount of the seagrass biomass from the foraging patches; 90 – 94% from the aboveground and 61 – 75% from the belowground (Preen, 1992; de Iongh et al., 1995; Nakaoka & Aioi, 1999). Preen (1992) found no correlation between the mean length of feeding trails and the shoot density of seagrass.

In captivity, an adult dugong consumes food about 7% (wet weight) of their body weight per day while a juvenile has a food intake of 14% (wet weight) of their body weight (Goto et al., 2004). On average, a dugong consumes between 28 to 40 kg wet mass (3.16 – 4.52 kg dry weight) per day (Preen, 1992; Aragones, 1994). Chilvers et al. (2004) calculated that a dugong's feeding time in the wild has spanned up to 16 h over a 24-h period.

Sediment effect to feeding

Grain size of sediment could affect the dugongs' capacity to sieve and masticate the grazed seagrass and affects how easily the animals can gather up seagrass rhizomes into their mouths. Sirenians are known to be efficient rhizome feeders, especially dugongs, a capability attributed to their much-deflected downward rostrum that targets rhizomes within the substrate (Marshall et al., 2003). Hence, aside from seagrass morphology, the properties of the substrate may be significant to the dugongs' feeding site selection if using the excavation method (Domning & Beatty, 2007; Marsh et al., 2011). Preen (1992) found no significant difference between the mean grain size in feeding sites and non-

feeding sites in Moreton Bay, Australia. However, feeding sites dominated by *Zostera capricorni* were deliberately sampled in his study and dugongs were observed to use the leaf cropping method instead of excavation method when feeding in dense *Z. capricorni* areas. Hence, it is possible that Preen's sampled feeding sites might be biased towards areas where dugong feeding choices was less affected by the grain size of sediment as dugongs did not need to disturb the substrate when feeding.

5.3 Methodology

5.3.1 Study site

The Sibul-Tinggi Archipelago lies within the Sultan Iskandar Marine Park, 10 - 12 km off the southeast coast of Peninsular Malaysia (**Figure 5.1**). It consists of five main islands, the Sibul group of islands which included Pulau Sibul Besar (*pulau* = island), Pulau Sibul Tengah, Pulau Sibul Kukus and Pulau Sibul Hujung, and Pulau Tinggi positioned in a northeasterly direction of Pulau Sibul Besar. Of these, only Pulau Sibul Besar and Pulau Tinggi are inhabited. These islands are strongly affected by heavy rainfall, strong waves and currents on the windward side during the northeast monsoon (November to March) but have relatively calm and dry weather during the southwest monsoon (May to October). The area is regarded as being host to possibly the most significant population of dugongs in Peninsular Malaysia (Ponnampalam et al. 2015), owing to the presence of extensive subtidal multi-specific seagrass meadows that extend in the forereef zone to about 10 m depth (Ooi et al. 2011b).

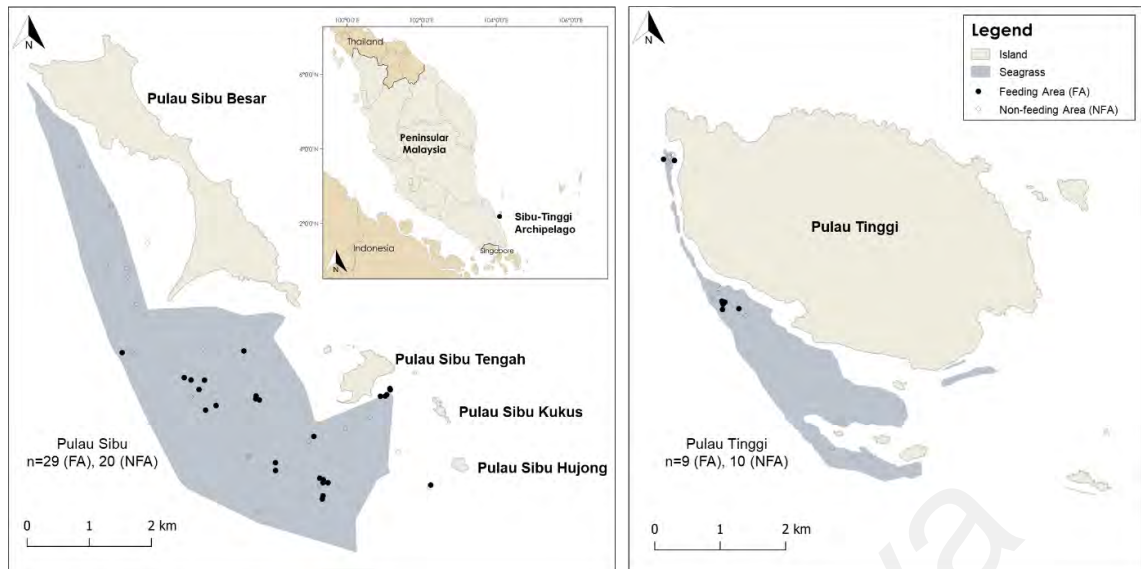


Figure 5.1 Location of sampling points (dugong feeding areas and non-feeding areas) around Sibiu-Tinggi Archipelago, eastern coast of Johor, Peninsular Malaysia, across 2016 – 2018. Locator map of Peninsular Malaysia with Sibiu-Tinggi Archipelago highlighted

5.3.2 Underwater sampling protocol

Feeding Areas (FA)

Dugong feeding trails were examined underwater by SCUBA diving; areas with feeding trails present were categorised as feeding areas (FA). A freshness criteria protocol was developed to differentiate between old and new feeding trails (**Figure 5.2**), based on the simulation of dugong feeding trails in the field and complemented by Adulyanukosol (2010) and D’Souza et al. (2015). Five random artificial trails were created by removing all seagrass biomass in trenches that were 3 cm deep. The recovery state of the artificial trails was observed at 2-day intervals for seven days, by which time the trails had almost completely filled back in. ‘Fresh/ Relatively Fresh’ trails were distinguished from ‘Old Trails’ based on (1) presence of a distinct depression, (2) presence of remnant seagrass, (3) substrate colour, (4) position of shoots, (5) water turbidity, (6) leaf/shoot colour, and (7) sign of leaf cropping. Only trails categorized as ‘Fresh/Relatively Fresh’ were sampled

to ensure consistency. Photo-quadrats of the feeding trail, seagrass and sediment samples were collected from the selected feeding trails.

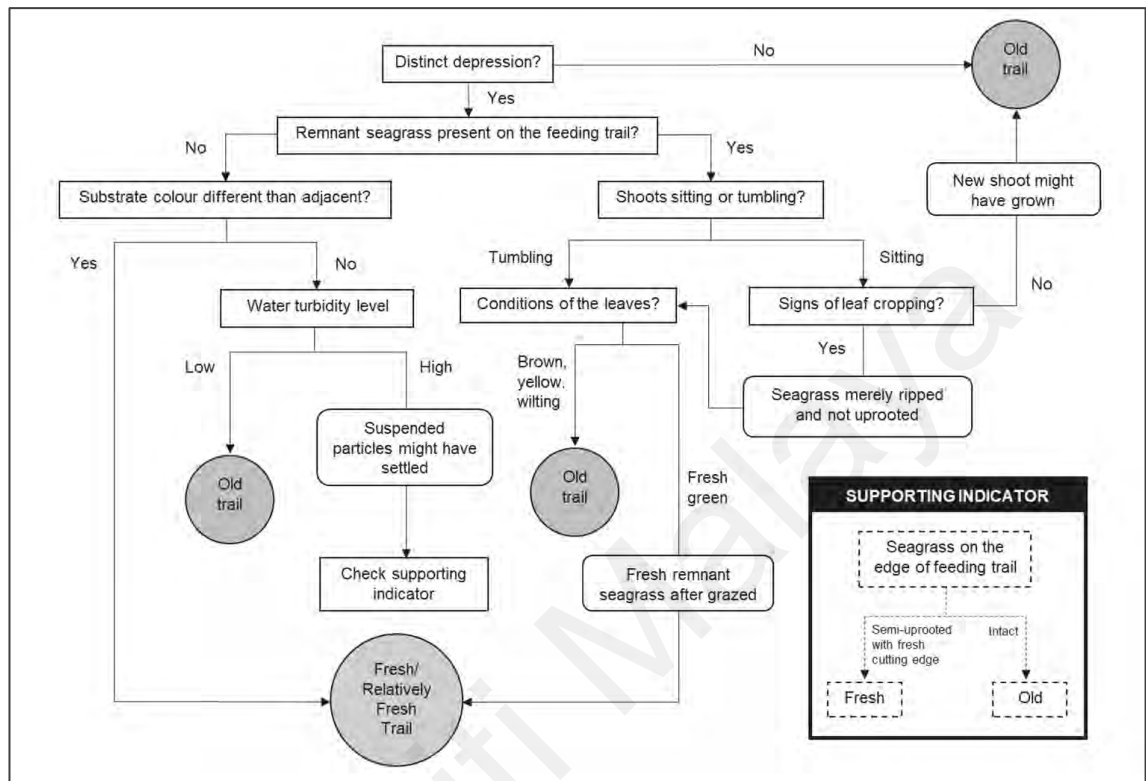


Figure 5.2 Underwater sampling protocol for classifying freshness of dugong feeding trails

Non-feeding Areas (NFA)

Seagrass and sediment samples were collected from identified non-feeding areas (NFA) within the same meadow, which acted as a control for this study. Radial survey technique was employed by two divers to confirm the absence of dugong feeding trails in the area before sampling. By making a reference point randomly on the meadow, the divers swam in a circular pattern from the reference point to visually inspect the area for feeding trails. After two consecutive revolutions with an increasing radius of 6 m, the site was chosen for sampling when there was no dugong feeding trail within the 12 m radius circular area, which corresponds to an area of 452.4 m². Seagrass and sediment samples were then collected within the circular area.

5.3.3 Feeding trail photogrammetry

The trench depth of each chosen feeding trail was measured *in-situ* by using a plastic ruler, while the length, width and area were measured and computed using photogrammetry method. Photographs were obtained by placing a series of 0.5 x 0.5 m² quadrat from one end to the other end of the feeding trails (Lanyon & Marsh, 1995; Duarte & Kirkman, 2001). Each photoquadrat print was stitched together to produce a single image and was analysed in CPCe (Coral Point Count with Excel extensions) software version 4.1 (Kohler & Gill, 2006). All measurements were taken thrice to calculate mean values. For width and depth, the triplicate readings were acquired from both ends and middle of the trail, a protocol adapted from Tol et al. (2016).

5.3.4 Seagrass abundance analysis

To estimate the quantity of the seagrass consumed by dugongs, three replicate cores (internal core diameter 11 cm, height 15 cm) of seagrass samples were collected from both ends and mid-sections of the trails to gain adequate representation of the entire feeding trails. Each core was taken from at least 0.5 m from the outer edge of the feeding trail, a distance close enough for the samples to represent the quantity of seagrass to that of the trail, but not too close to be affected by the act of grazing. Although dugongs typically leave some seagrasses ungrazed in the feeding trails (Anderson & Birtles, 1978), I assumed that whole plants were removed completely in this study and thus the quantity outside was considered as equal to the quantity inside the feeding trails. Seagrasses in each core were identified up to species level based on Kuo & den Hartog (2001) and counted for shoot density. Samples were washed and the epiphytes removed. The biomass of seagrass was determined for the aboveground (leaves and shoots) and belowground (rhizomes and roots) components (Sheppard et al. 2006) by oven drying to a constant weight at 60 °C for 24 to 72 h (Duarte & Kirkman, 2001). The biomass obtained from

each core was expressed in grams of dry weight per metre square (g DW m⁻²). The ratios of aboveground to belowground biomass (AG:BG) were computed to determine if relative biomass between the aboveground and belowground component of the plants influenced the feeding selection of dugongs. The same procedures were used for seagrass samples collected from non-feeding areas.

5.3.5 Seagrass nutrient analysis

Six different nutrient parameters were analysed for each seagrass species that were present around the feeding trails and non-feeding areas, which were carbon, nitrogen and phosphorus, the indicators of seagrass health, C:N ratio, the indicator of light stress and age of the plant tissues, and nitrogen (protein), starch (energy) and fibre (digestibility), the key nutrients for herbivores. All procedures for nutrient analyses were conducted in external chemical laboratories. A CN analyser was used to analyse the carbon, C and nitrogen, N contents (total %) of the seagrass following the AOAC Official Method 972.43. The aboveground and belowground samples of seagrass were homogenized and dried in $100 \pm 10^\circ\text{C}$ for 1 h prior to combustion at high temperature (900 - 1000°C) in the CN analyser. Phosphorus, P concentrations (mg/ kg) were determined by HNO₃ – H₂O₂/ HClO₄/ HCl digestion, followed by analysis using an Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES) (Temminghoff & Houba, 2004; Christianen et al., 2018). Minority seagrass species which constituted less than 25% of the seagrass cover were omitted due to being insufficient for their nutrient content evaluation.

Starch content (g/ 100g) of the seagrass was determined by acid hydrolysis. Plant samples were refluxed for two hours with 0.5 NHCl in a 95°C water bath. Hydrolysed samples were filtered through Whatman no. 541 filter paper and continued with the Lane-Eynon general volumetric method (AOAC Official Method 923.09) to determine the

sugar content. Starch was computed by multiplying the glucose content by the glucose equivalent of 0.9 (Chow & Landhäusser, 2004; Sørensen et al., 2018).

An enzymatic procedure for total dietary fibre (g/ 100g) was performed using a commercial assay kit (Megazyme Total Dietary Fibre Kit; Megazyme International, Bray, Ireland). The homogenized samples were gelatinized with heat-stable α -amylase and then enzymatically digested sequentially with protease and amyloglucosidase to remove the protein and starch. The samples were then treated with heated EtOH to precipitate dietary fibre before being filtered and washed with 78% EtOH, 95% EtOH and acetone. The residue weight was calculated by correcting with indigestible protein, ash and blank (based on the AACC Method 32-05.01 and AOAC Method 985.29). The step-by-step test procedures for the chemical analyses above are provided in **Appendix A**.

5.3.6 Water depth analysis

The recorded water depths taken during samplings by using dive computer (Suunto Zoop Novo) with a depth resolution of 0.1 m. The recorded water depths were corrected for tidal height at the time of sampling according to the Tide Table of Malaysia (Mersing as standard port, and Pulau Babi Besar as secondary port) published by the National Hydrographic Centre, Malaysia.

5.3.7 Sediment – particle size analysis

Sediment samples were cored within the feeding trails in three replicates (both ends and mid-section) by using a corer that was 29 cm in length and 4.8 cm in diameter. For grain size analysis, each core was subsampled further to mix with 30% H₂O₂ in order to remove organic matter. After the organic matter was removed, the sediments were oven dried in 60°C for 24 h (Erftemeijer & Koch, 2001), and dry sieved for 15 min through a series of graded sieves into Wentworth scale fractions of gravel and shell (> 2mm), coarse

sand (0.25 – 2 mm), fine sand (63 μm – 0.25 mm) and silt-clay (<63 μm). Each fraction was expressed as percentage of total weight.

5.3.8 Statistical analysis and modelling framework

(1) Characterisation of grazing behaviour through feeding trail dimension

The central tendencies and error estimates were reported as means \pm 1 standard deviation. The relationships between the feeding trail dimension (response) with shoot density, biomass of seagrass, and particle size of sediment (explanatory) were first tested using Spearman's correlation analysis. Linear regression (log-linear model) was then used to determine the effect of: (1) seagrass quantity at the plant community level and species level, and (2) particle size of sediment, in influencing the length and depth of feeding trails.

(2) Comparisons of quantity, quality of food and physical properties between sites

A total of 10 main variables: two quantity parameters (shoot density, biomass), six quality parameters (carbon, nitrogen, phosphorus, starch, dietary fibre, C:N ratio), and two physical parameters (water depth, sediment particle size), were analysed to examine the significance of differences among four seagrass species (*H. ovalis*, *H. uninervis*, *C. serrulata*, *S. isoetifolium*) between locations (feeding areas, non-feeding areas). For biomass, data were divided into "whole-plant", "aboveground", "belowground", and "ratio of aboveground to belowground". Subsequently for all quality parameters, data were divided into "aboveground", "belowground", and "whole-plant" (= averaged reading of aboveground and belowground). All analyses were undertaken at two levels – species-level (by species) and community-level (all species).

All variables were compared between feeding areas (FA) and non-feeding areas (NFA) by using parametric 2-sample unpaired student T-test or non-parametric Mann-Whitney U Test (also known as Wilcoxon Rank-Sum Test) when the variable(s) was not normally distributed, or when the sample size was small ($n \leq 15$). Variables were log-transformed whenever necessary to satisfy the normal distribution assumption of parametric test. The hypothesis was meant to compare two means or medians of the two independent groups, as stated below:

H₀: The two populations are equal;

H₁: The two populations are not equal, with level of significance ($\alpha=0.05$).

Kruskal-Wallis one-way nonparametric tests were conducted to test differences among species as the observations of less abundant species, i.e., *C. serrulata* and *S. isoetifolium* were not normally distributed due to low number of counts. Whenever differences were significant ($p < 0.05$), post-hoc Wilcoxon Rank-Sum tests were used for pairwise comparisons. The hypothesis of Kruskal-Wallis test was meant to compare the mean ranks/ medians of more than two independent groups, as stated below:

H₀: The population medians are equal;

H₁: The population medians are not equal, with level of significance ($\alpha=0.05$).

(3) Assessment of weight of potential factors in driving feeding site selection

To determine which predictor variables were significant to feeding site selection, all plant and physical variables which were significantly different between dugong feeding areas and non-feeding areas were grouped into a binary locality dataset (0 = non-feeding areas; 1 = feeding areas) and examined by using multivariate regression. A generalized linear model (GLM) with a binomial distribution (logit link) was used, with locality as the binary response variable while explanatory variables comprised of four seagrass

quantity factors (i.e., shoot density, aboveground biomass, belowground biomass, ratios of AG:BG biomass), four seagrass quality factors (i.e., carbon, nitrogen, fibre, C:N ratio), and one physical factor (i.e., particle size of sediment). Following the low detection of starch in the *H. ovalis* and *H. uninervis* samples resulting in underrepresentation, the parameter was not considered in the modelling process. The observations for nutrient parameters of *C. serrulata* and *S. isoetifolium* were omitted in the analyses due to low sample size as a consequence of relatively low occurrences in the seagrass meadows.

Missing-at-random data was present in most of the nutrient parameters due to insufficient amount of samples present at the sampling site for the chemical analysis or technical errors that probably arose during laboratory analysis such as human errors. To avoid relatively higher or lower mean obtained for those parameters, missing values were estimated using multiple imputation, which uses distribution of the observed data points to estimate multiple possible values for the missing data points with no subsequent loss of statistical power (Polit, 2010). Multiple imputation was performed using *mice* package (imputation method: predictive mean matching) in R software with all other predictor variables considered for use in the regression modelling later. Variables with no missing values in the raw dataset were configured to not be imputed. Five imputed datasets were generated, and each dataset was run with regression separately to obtain their parameter estimates.

All candidate variables were checked with correlation coefficient in prior, to explore their relationships. The variables with variance inflation factor (VIF) > 3 (package *car* v. 3.0-7) were eliminated to reduce multicollinearity effect in the regression model (Zuur et al., 2007). Due to numerous candidate factors deriving from the quantity, quality and physical attributes of each seagrass species compared to the number of observations, in addition to the fact that the seagrass community exhibited high variability in terms of those attributes among species, a three-stage analysis was carried out. Firstly, potential

factor variables were filtered and selected by running separate models for quantity and quality attributes for each species of seagrass. Secondly, a full model was fitted by using the significant variables that were detected in the first stage, followed by AIC-based stepwise regression (package MASS v. 7.3-51.5) to find the best subset of significant variables. Finally, the significant quantity and quality variables were then integrated with the significant physical variables to form the final predictive model. Due to the exploratory characteristic of this study, no interaction term was added so as to maintain a parsimonious model (simple model with great explanatory predictive power).

All models were compared and evaluated with amount of deviance explained, as expressed in adjusted D^2 (package modEVA v. 2.0) and adjusted pseudo R^2 – McFadden's and Nagelkerke's values (package DescTools v. 0.99.37). Small-sample corrected Akaike Information Criterion (AICc) (package AICcmodavg v. 2.3-0) was reported for each model due to the ratio between the sample size and number of parameters being small (< 40) (Burham & Anderson, 2002). The parameter estimates of five imputed datasets were pooled together into one final regression coefficient to give the averaged effect sizes of each predictor in the predictive model. Predictions with 95% confidence intervals were plotted for each covariate using the best supported model set among the five, based on AICc value. All analyses were performed in R version 4.0.0 (R Core Team, 2020).

5.4 Results

5.4.1 Characterisation of dugong grazing behaviour through feeding trail dimension

Shapes and dimensions of feeding trails

All feeding trails were left in a long and serpentine form on the seagrass meadows (**Figure 5.3**). No straight and linear, or circular scars were observed. A total of 31 dugong feeding trails were measured, but old feeding trails ($n = 3$) were not included in the analysis to maintain a standardised sampling protocol. The average length, width and depth (\pm SD) of feeding trails were 7.16 ± 5.64 m (range = 2.00 – 21.63 m), 14.12 ± 3.10 cm (range = 8.96 – 20.16 cm), 2.8 ± 0.6 cm (range = 1.7 – 4.8 cm), respectively. Feeding trails with the mean length category of 0 – 10 m, mean width of 13 – 14 cm and mean depth of 2.6 – 3.0 cm, were most frequently encountered (**Figure 5.4-5.6**). The average area per feeding trail was 1.29 ± 1.25 m² (range = 0.21 – 5.74 m²) while average biomass per feeding trail was 54.10 ± 54.34 g DW (range = 5.54 – 275.50 g DW).

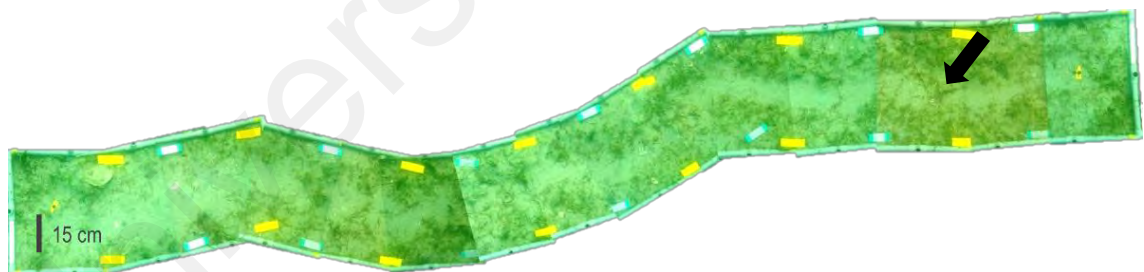


Figure 5.3 A scaled feeding trail (light patches of bare sediment on the seagrass meadow, marked with an arrow) projected by stitching the photo-quadrats

Among all dimension parameters, only the mean length and mean width of feeding trails were positively correlated (Spearman's correlation: $\rho = 0.556$, $p = 0.003$) (**Figure 5.7**). The mean depth was not significantly correlated with the mean length ($\rho = -0.211$, $p = 0.280$) and mean width ($\rho = -0.290$, $p = 0.134$).

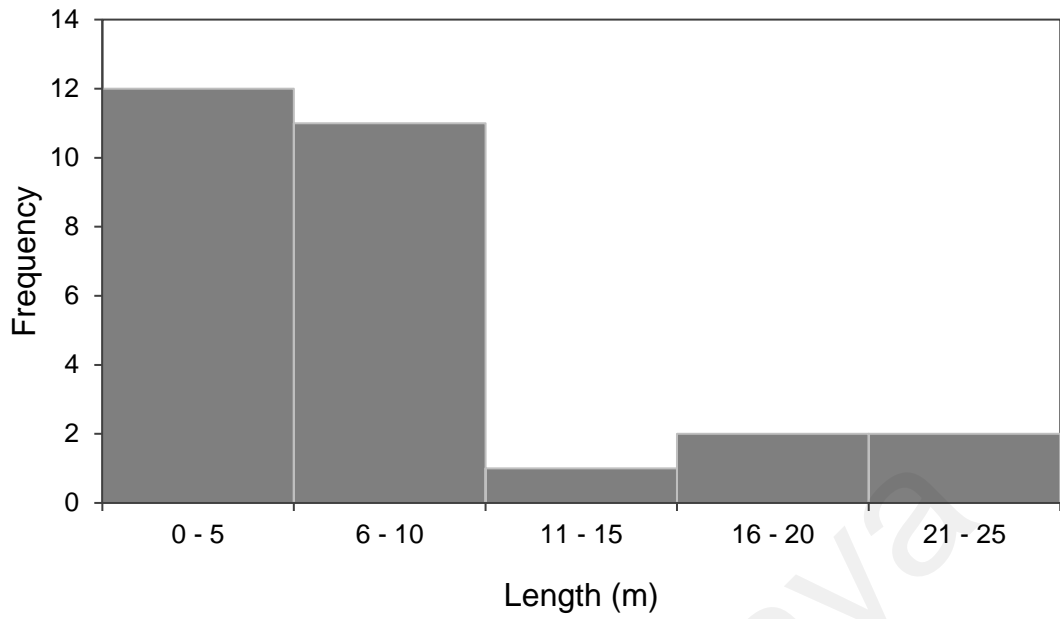


Figure 5.4 Frequency distribution of the length of dugong feeding trails

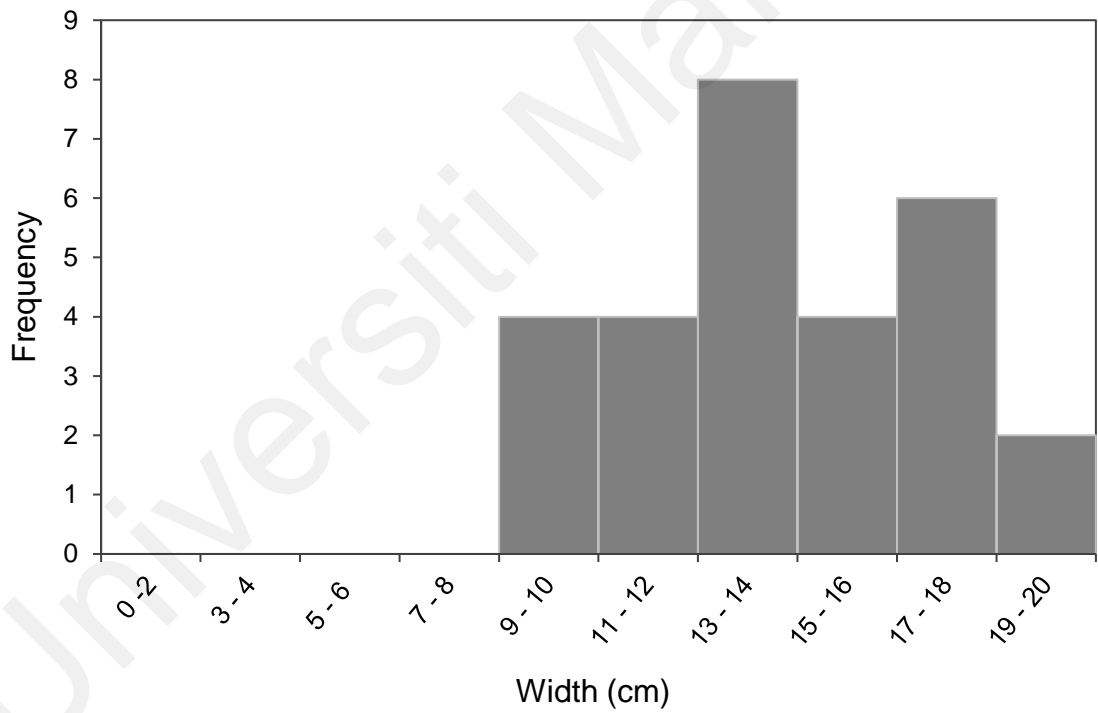


Figure 5.5 Frequency distribution of the width of dugong feeding trails

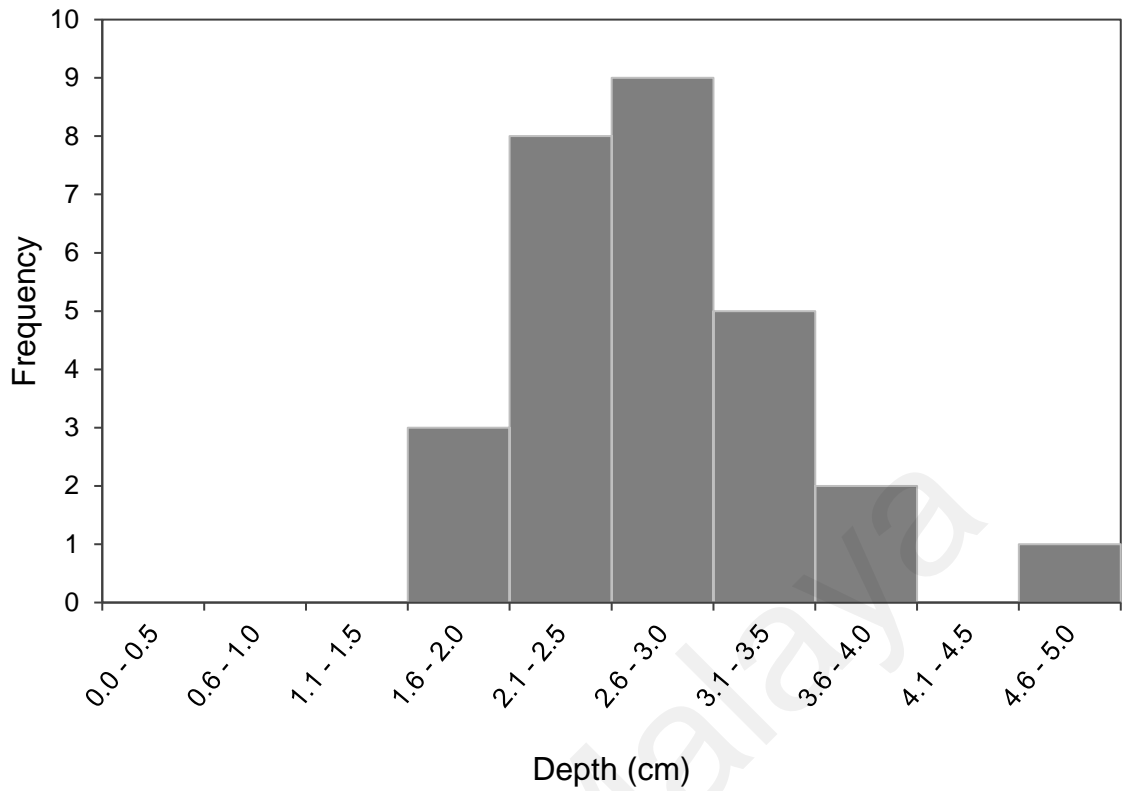


Figure 5.6 Frequency distribution of the depth of dugong feeding trails

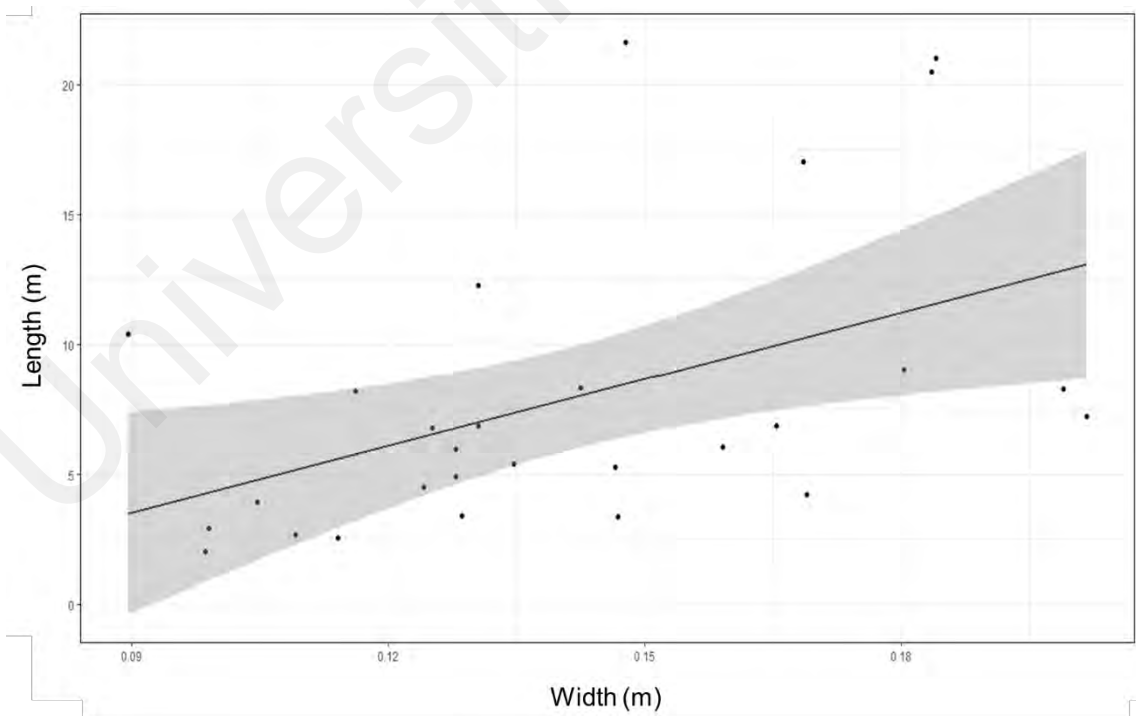


Figure 5.7 Correlation between the length and width of feeding trails. Spearman's rank correlation coefficient, $\rho = 0.556$ ($p = 0.003$)

Seagrass species association

Dugong feeding trails were distributed and associated with all seagrass species present in the meadows that were adjacent to the feeding trails. These were *H. ovalis* complex (hereinafter referred to as *H. ovalis*), *H. uninervis* (wide and thin variants), *C. serrulata* and *S. isoetifolium*. In feeding areas, *H. ovalis* and *H. uninervis* dominated or co-dominated 37 (97%) and 34 (89%) out of 38 samples respectively, while *C. serrulata* and *S. isoetifolium* were only present in 11 (29%) and 6 (16%) out of 38 samples respectively (**Appendix B**). In non-feeding areas, *H. ovalis* and *H. uninervis* were still the dominant or co-dominant species, and were present in 28 (93%) and 29 (97%) out of 30 samples respectively, while *C. serrulata* and *S. isoetifolium* occurred more frequently compared to feeding areas, with 18 (60%) and 8 (27%) out of 30 samples respectively.

Relationship with seagrass quantity

The length of feeding trails was negatively correlated with the belowground biomass of seagrass (Spearman's correlation: $\rho = -0.579$, $p = 0.004$), while there were no significant correlations between the length of feeding trails with the shoot density, total biomass, aboveground biomass and ratios of AG:BG biomass of seagrass ($\rho = -0.203$, $p = 0.300$; $\rho = 0.037$, $p = 0.866$; $\rho = -0.321$, $p = 0.865$; $\rho = 0.325$, $p = 0.130$, respectively) (**Table 5.1**). Among all species, only the shoot density and aboveground biomass of *H. ovalis* showed significant positive correlations with the length of feeding trails ($\rho = 0.382$, $p = 0.045$; $\rho = 0.429$, $p = 0.030$, respectively). However, linear (log-link) models indicated that all species-level quantity variables were not statistically significant in influencing the length of feeding trails. The AG:BG biomass ratio of seagrass appeared to be a significant factor in explaining the variability in the length of feeding trails ($r^2 = 0.20$, $\beta = 0.41$, $p = 0.0498$).

The depth of feeding trails was negatively correlated with the AG:BG biomass ratio of seagrass ($\rho = -0.510, p = 0.013$), while there were no significant correlations between the depth of feeding trails with the shoot density, total biomass, aboveground biomass and belowground biomass of seagrass ($\rho = -0.345, p = 0.073; \rho = -0.403, p = 0.051; \rho = -0.246, p = 0.216; \rho = 0.237, p = 0.277$, respectively). Among all species, the shoot density, total biomass, aboveground biomass and belowground biomass of *H. ovalis*, as well as AG:BG biomass ratio of *H. uninervis*, were negatively correlated with the depth of feeding trails ($\rho = -0.456, p = 0.015; \rho = -0.405, p = 0.036; \rho = -0.468, p = 0.016; \rho = -0.453, p = 0.018; \rho = -0.450, p = 0.028$, respectively), while there was no significant relationship detected between the depth of feeding trails with the quantity of *C. serrulata* and *S. isoetifolium*. Linear regression (log-linear model) revealed that the depth of feeding trails was significantly influenced by the belowground biomass of *H. uninervis* ($r^2 = 0.20, \beta = -0.16, p = 0.0402$).

Relationship with sediment particle size

Based on Spearman's correlation, all particle sizes of sediment were not significantly correlated with the length (Gravel: $\rho = 0.008, p = 0.975$; Coarse sand: $\rho = 0.240, p = 0.293$; Fine sand: $\rho = -0.184, p = 0.422$; Silt-clay: $\rho = -0.181, p = 0.432$) and depth of feeding trails (Gravel: $\rho = 0.409, p = 0.067$; Coarse sand: $\rho = 0.010, p = 0.966$; Fine sand: $\rho = -0.110, p = 0.633$; Silt-clay: $\rho = -0.038, p = 0.872$). Linear model also showed that none of the particle sizes was statistically significant to explain the variability in the length and depth of feeding trails.

Table 5.1 Correlation matrix for the length and depth of feeding trails with seagrass quantity and sediment particle size variables. HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*; AG: aboveground; BG: belowground. Table continued on next page

	Feeding trail		Shoot density					Biomass							
	Length	Depth	Total	HO	HU	CS	SI	Total	AG	BG	AG:BG	HO Total	HO AG	HO BG	HO AG:BG
Length of feeding trail	1.000														
Depth of feeding trail	-0.211	1.000													
Total shoot density	-0.203	-0.345*	1.000												
Shoot density of HO	0.382*	-0.456*	0.533**	1.000											
Shoot density of HU	-0.135	0.096	0.439*	-0.063	1.000										
Shoot density of CS	-0.273	0.276	-0.170	0.054	-0.359	1.000									
Shoot density of SI	-0.066	0.081	0.087	0.217	-0.057	0.379*	1.000								
Total biomass	0.037	-0.403*	0.420*	0.490*	0.297	-0.076	0.260	1.000							
AG biomass	-0.321	-0.246	0.455*	-0.002	0.224	-0.133	-0.339	0.169	1.000						
BG biomass	-0.579**	0.237	0.090	-0.157	0.454*	0.238	0.235	0.461*	0.434*	1.000					
AG:BG biomass	0.325	-0.510*	0.571*	0.731**	-0.033	-0.139	-0.269	-0.078	0.468*	-0.395	1.000				
Total biomass of HO	0.351*	-0.405*	0.142	0.618**	0.046	-0.089	-0.199	0.452*	0.411*	0.229	0.567**	1.000			
AG biomass of HO	0.429*	-0.468*	0.207	0.772**	-0.134	-0.035	-0.143	0.383	0.349	-0.034	0.756**	0.958**	1.000		
BG biomass of HO	0.312	-0.453*	0.206	0.696**	-0.028	0.008	-0.096	0.500*	0.231	0.141	0.481*	0.825**	0.876**	1.000	
AG:BG biomass of HO	0.084	-0.109	0.246	0.242	-0.293	0.118	-0.044	-0.126	0.372	-0.099	0.605**	0.126	0.303	-0.091	1.000

Table 5.1 (Cont.)... Correlation matrix for the length and depth of feeding trails with seagrass quantity and sediment particle size variables. HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*; AG: aboveground; BG: belowground. Table continued on next page

	Feeding trail		Biomass											
	Length	Depth	HU Total	HU AG	HU BG	HU AG:BG	CS Total	CS AG	CS BG	CS AG:BG	SI Total	SI AG	SI BG	SI AG:BG
Length of feeding trail	1.000													
Depth of feeding trail	-0.211	1.000												
Total biomass of HU	-0.169	0.262	1.000											
AG biomass of HU	-0.110	-0.004	0.881**	1.000										
BG biomass of HU	-0.326	0.288	0.895**	0.705**	1.000									
AG:BG biomass of HU	0.333	-0.450*	-0.447*	-0.044	-0.707**	1.000								
Total biomass of CS	-0.251	0.274	-0.128	-0.303	-0.201	-0.160	1.000							
AG biomass of CS	-0.247	0.251	-0.120	-0.289	-0.200	-0.130	0.998**	1.000						
BG biomass of CS	-0.216	0.177	-0.236	-0.369	-0.242	-0.185	0.930**	0.928*	1.000					
AG:BG biomass of CS	0.238	-0.429	0.357	0.405	0.286	0.429	-0.357	-0.095	-0.357	1.000				
Total biomass of SI	-0.063	0.077	-0.109	-0.379	0.052	-0.318	0.321	0.335	0.370	0.419	1.000			
AG biomass of SI	-0.063	0.085	-0.098	-0.374	0.067	-0.327	0.329	0.344	0.379*	0.495	0.997**	1.000		
BG biomass of SI	-0.126	0.067	-0.159	-0.402*	-0.010	-0.253	0.265	0.280	0.311	0.191	0.930**	0.902**	1.000	
AG:BG biomass of SI	0.500	-0.200	0.700	0.700	0.200	0.300	-0.154	-0.154	-0.154	0.500	-0.600	-0.600	-0.600	1.000

Table 5.1 (Cont.)... Correlation matrix for the length and depth of feeding trails with seagrass quantity and sediment particle size variables. HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*; AG: aboveground; BG: belowground

	Feeding trail		Sediment size			
	Length	Depth	Gravel	Coarse sand	Fine sand	Silt-clay
Length of feeding trail	1.000					
Depth of feeding trail	-0.211	1.000				
Gravel	0.008	0.409*	1.000			
Coarse sand	0.240	0.010	0.469*	1.000		
Fine sand	-0.184	-0.110	-0.595**	-0.970**	1.000	
Silt-clay	-0.181	-0.038	-0.512*	-0.669**	0.638**	1.000

All correlations measured through Spearman tests. Significant correlations are in bold and marked with * ($P < 0.05$) and ** ($P < 0.01$).

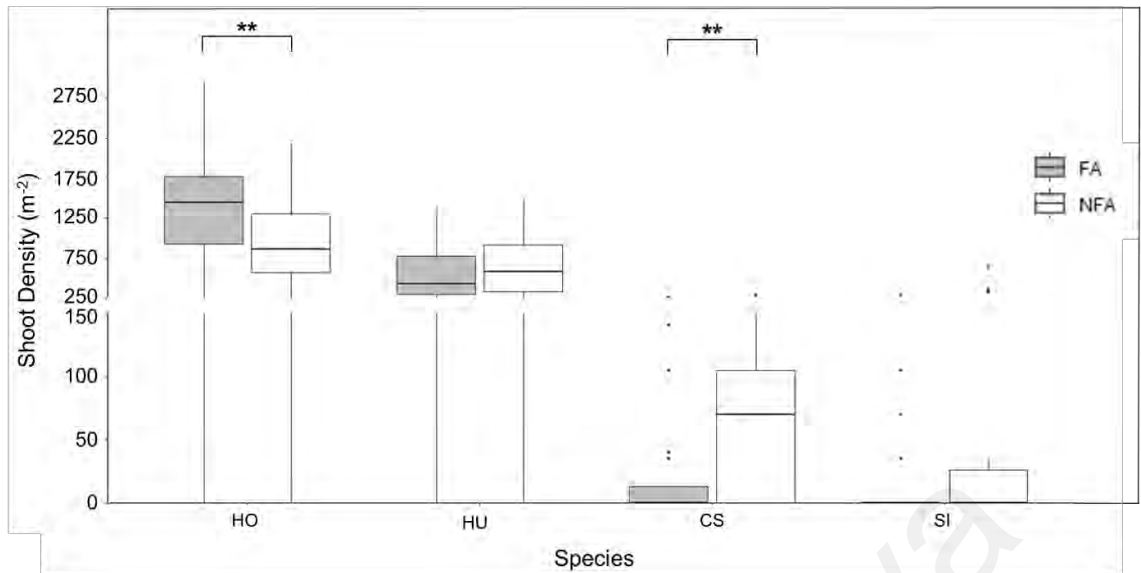
5.4.2 Comparisons of food quantity and quality and physical properties between feeding areas and non-feeding areas

5.5.2.1 Food quantity

Shoot density

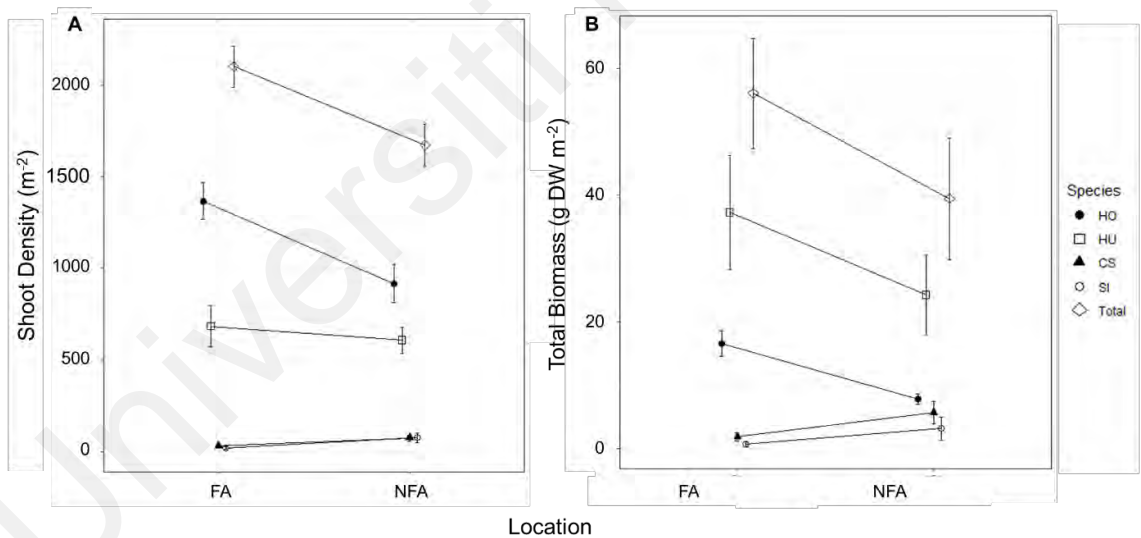
Four same species of seagrass were present in both feeding areas and non-feeding areas. *Halophila ovalis* and *H. uninervis* were the most abundant species. In terms of shoot density, each constituted 68.8% and 33.1% respectively in the feeding areas, and 56.3% and 40.9% respectively in the non-feeding areas. *Cymodocea serrulata* and *S. isoetifolium* occurred in relatively much lesser densities, only 5.8% and 5.4% in the feeding areas, and 7.0% and 14.0% in the non-feeding areas. The mean densities were 2101.93 shoots m⁻² (SD = 687.90, range = 806.74 – 3893.38) across 38 samples in feeding areas, and 1673.10 shoots m⁻² (SD = 631.50, range = 736.59 – 2841.12) across 30 samples in non-feeding areas (**Table 5.2**).

The total shoot density in the feeding areas was significantly higher than that in the non-feeding areas (Welch's t-test, $T_{64.5} = 2.67$, $p = 0.01$) (**Table 5.3**). Within species, *H. ovalis* (Welch's t-test: $T_{64.4} = 3.10$, $p = 0.003$) and *C. serrulata* (Wilcoxon rank sum test: $n = 38-30$, $W = 378$, $p = 0.009$) showed significant differences but *H. uninervis* (Welch's t-test: $T_{58.1} = -1.00$, $p = 0.32$) and *S. isoetifolium* (Wilcoxon rank sum test: $n = 38-30$, $W = 492.5$, $p = 0.18$) did not differ significantly between the feeding areas and non-feeding areas (**Figure 5.8**).



Each box represents first and third quartile, horizontal lines within box represent median, whiskers represent minimum and maximum values, dots represent extreme values. Asterisks denote significant difference between group ($*0.01 \leq P < 0.05$, $**0.001 \leq P \leq 0.01$, $*** P < 0.001$). HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*

Figure 5.8 Boxplots showing the distributions of shoot density for each species in the dugong feeding areas (FA) and non-feeding areas (NFA)



Error bars indicate standard error. HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*; Total: sum of four species

Figure 5.9 Relationship plots of shoot density (A) and total biomass (B) of seagrass in the dugong feeding areas (FA) and non-feeding areas (NFA)

Seagrass biomass

The seagrass biomass measured from the feeding areas ranged from 9.40 – 126.01 g DW m⁻² with an average of 39.67 g DW m⁻² ± 28.56 (SD), while seagrass biomass in the non-feeding areas ranged from 6.62 – 304.47 g DW m⁻² with an average of 39.39 g DW m⁻² ± 52.46 (SD) (**Table 5.2**). The mean of belowground biomass was approximately double the mean of aboveground biomass in both feeding areas and non-feeding areas (**Figure 5.10**). The AG:BG biomass ratios were 0.85 ± 0.55 and 0.61 ± 0.25 in the feeding areas and non-feeding areas respectively. Welch's t-test indicated a significant difference between the feeding areas and non-feeding areas for aboveground biomass ($T_{60.2} = 4.46$, $p < 0.0001$) and AG:BG biomass ratio ($T_{59.6} = 2.15$, $p = 0.04$). Total biomass ($T_{57.1} = 1.95$, $p = 0.06$) and belowground biomass ($T_{53.4} = 1.65$, $p = 0.11$) did not differ significantly across the two sites (**Table 5.3**).

Among species, *H. uninervis* had the highest biomass (40.39 ± 56.84 g DW m⁻²) followed by *H. ovalis* (16.92 ± 12.18 g DW m⁻²), *C. serrulata* (5.83 ± 5.07 g DW m⁻²) and *S. isoetifolium* (4.20 ± 4.31 g DW m⁻²) in the feeding areas. In the non-feeding areas, seagrass biomass was highest for *H. uninervis* (25.07 ± 34.67g DW m⁻²), followed by *S. isoetifolium* (11.69 ± 17.78 g DW m⁻²), *C. serrulata* (9.41 ± 11.09 g DW m⁻²) and *H. ovalis* (8.32 ± 3.95 g DW m⁻²) (**Figure 5.9**). For all species, the belowground component possessed greater biomass than the aboveground component based on the mean AG:BG ratio, except *H. ovalis* in the feeding areas, and *S. isoetifolium* in the non-feeding areas.

All biomass parameters of *H. ovalis* varied significantly between feeding and non-feeding areas as shown by Welch's t-test, including total biomass ($T_{54.3} = 4.37$, $p < 0.0001$), aboveground biomass ($T_{49.0} = 4.86$, $p < 0.0001$), belowground biomass ($T_{60.6} = 2.84$, $p = 0.006$) and AG:BG biomass ratio ($T_{61.0} = 4.21$, $p < 0.0001$) (**Table 5.3, Figure 5.11**). For *H. uninervis*, only the aboveground biomass was significantly different between locations (Welch's t-test: $T_{57.5} = 2.05$, $p = 0.04$). For *C. serrulata*, the significant

parameters included its total biomass (Wilcoxon rank sum test: $n = 38-29$, $W = 380$, $p = 0.01$), aboveground biomass (Wilcoxon rank sum test: $n = 38-29$, $W = 373$, $p = 0.007$), and belowground biomass (Wilcoxon rank sum test: $n = 38-29$, $W = 380.5$, $p = 0.008$). *Syringodium isoetifolium* showed no significant differences for all its biomass parameters.

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Table 5.2 Summary of descriptive statistics of seagrass quantity variables in the feeding areas ($n=38$) and non-feeding areas ($n=30$) in the Sibutu Archipelago. Table continued on next page.

Quantity variable	Mean \pm Standard deviation	Minimum – Maximum
Community-level		
– Feeding Areas		
Shoot density (m^{-2})	2101.93 \pm 687.90	806.74 – 3893.38
Total biomass (g DW m^{-2})	55.98 \pm 53.26	9.40 – 277.42
Aboveground biomass (g DW m^{-2})	18.50 \pm 10.98	5.26 – 55.42
Belowground biomass (g DW m^{-2})	37.49 \pm 47.40	2.75 – 251.43
Aboveground: Belowground Ratio	0.85 \pm 0.55	0.10 – 2.91
– Non-feeding Areas		
Shoot density (m^{-2})	1673.10 \pm 631.50	736.59 – 2841.12
Total biomass (g DW m^{-2})	39.39 \pm 52.46	6.62 – 304.47
Aboveground biomass (g DW m^{-2})	13.80 \pm 20.94	3.41 – 122.87
Belowground biomass (g DW m^{-2})	25.59 \pm 32.18	3.21 – 181.60
Aboveground: Belowground Ratio	0.61 \pm 0.25	0.24 – 1.15
Species-level		
<i>Halophila ovalis</i>		
– Feeding Areas		
Shoot density (m^{-2})	1367.89 \pm 623.96	0.00 – 2946.34
Total biomass (g DW m^{-2})	16.48 \pm 12.32	0.00 – 67.90
Aboveground biomass (g DW m^{-2})	9.73 \pm 8.47	0.00 – 45.54
Belowground biomass (g DW m^{-2})	6.75 \pm 4.70	0.00 – 22.37
Aboveground: Belowground Ratio	1.60 \pm 1.22 (n=37)	0.44 – 8.23
– Non-feeding Areas		
Shoot density (m^{-2})	916.64 \pm 574.19	0.00 – 2174.68
Total biomass (g DW m^{-2})	7.77 \pm 4.36	0.00 – 15.24
Aboveground biomass (g DW m^{-2})	3.67 \pm 2.14	0.00 – 7.81
Belowground biomass (g DW m^{-2})	4.09 \pm 2.41	0.00 – 7.86
Aboveground: Belowground Ratio	0.98 \pm 0.32 (n=28)	0.45 – 1.83
<i>Halodule uninervis</i>		
– Feeding Areas		
Shoot density (m^{-2})	648.17 \pm 684.93	0.00 – 3051.57
Total biomass (g DW m^{-2})	37.21 \pm 55.58	0.00 – 277.42
Aboveground biomass (g DW m^{-2})	7.94 \pm 7.85	0.00 – 33.86
Belowground biomass (g DW m^{-2})	29.27 \pm 48.96	0.00 – 251.43
Aboveground: Belowground Ratio	0.47 \pm 0.25 (n=35)	0.10 – 1.19
– Non-feeding Areas		
Shoot density (m^{-2})	607.98 \pm 389.10	0.00 – 1473.17
Total biomass (g DW m^{-2})	24.24 \pm 34.38	0.00 – 189.45
Aboveground biomass (g DW m^{-2})	6.42 \pm 9.37	0.00 – 52.36
Belowground biomass (g DW m^{-2})	17.82 \pm 25.44	0.00 – 137.09
Aboveground: Belowground Ratio	0.47 \pm 0.04 (n=29)	0.14 – 1.61

Table 5.2 (Cont.)... Summary of descriptive statistics of seagrass quantity variables in the feeding areas ($n=38$) and non-feeding areas ($n=30$) in the Sibutinggi Archipelago.

Quantity variable	Mean \pm Standard deviation	Minimum – Maximum
<i>Cymodocea serrulata</i>		
– Feeding Areas		
Shoot density (m^{-2})	31.40 ± 68.57	0.00 – 245.53
Total biomass (g DW m^{-2})	1.83 ± 3.90	0.00 – 15.39
Aboveground biomass (g DW m^{-2})	0.71 ± 1.54	0.00 – 6.52
Belowground biomass (g DW m^{-2})	1.15 ± 2.56	0.00 – 12.06
Aboveground: Belowground Ratio	0.16 ± 0.33 ($n=9$)	0.28 – 1.15
– Non-feeding Areas		
Shoot density (m^{-2})	73.66 ± 87.07	0.00 – 280.60
Total biomass (g DW m^{-2})	5.65 ± 9.70	0.00 – 49.79
Aboveground biomass (g DW m^{-2})	2.49 ± 5.38	0.00 – 29.38
Belowground biomass (g DW m^{-2})	3.16 ± 4.67	0.00 – 20.41
Aboveground: Belowground Ratio	0.46 ± 0.55 ($n=17$)	0.28 – 2.12
<i>Syringodium isoetifolium</i>		
– Feeding Areas		
Shoot density (m^{-2})	18.46 ± 55.75	0.00 – 280.60
Total biomass (g DW m^{-2})	0.66 ± 2.22	0.00 – 10.67
Aboveground biomass (g DW m^{-2})	0.22 ± 0.62	0.00 – 3.00
Belowground biomass (g DW m^{-2})	0.45 ± 1.62	0.00 – 7.66
Aboveground: Belowground Ratio	0.65 ± 0.27 ($n=5$)	0.32 – 0.85
– Non-feeding Areas		
Shoot density (m^{-2})	74.83 ± 152.40	0.00 – 631.36
Total biomass (g DW m^{-2})	3.12 ± 10.19	0.00 – 55.30
Aboveground biomass (g DW m^{-2})	1.79 ± 6.87	0.00 – 37.76
Belowground biomass (g DW m^{-2})	1.32 ± 3.45	0.00 – 17.54
Aboveground: Belowground Ratio	0.30 ± 0.61 ($n=8$)	0.53 – 2.33

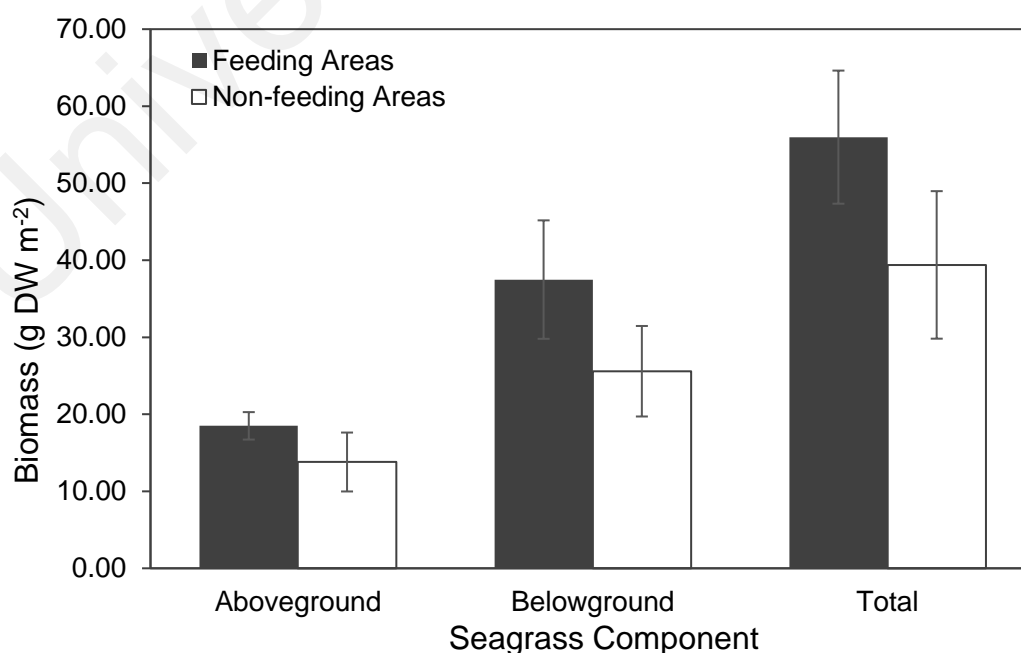
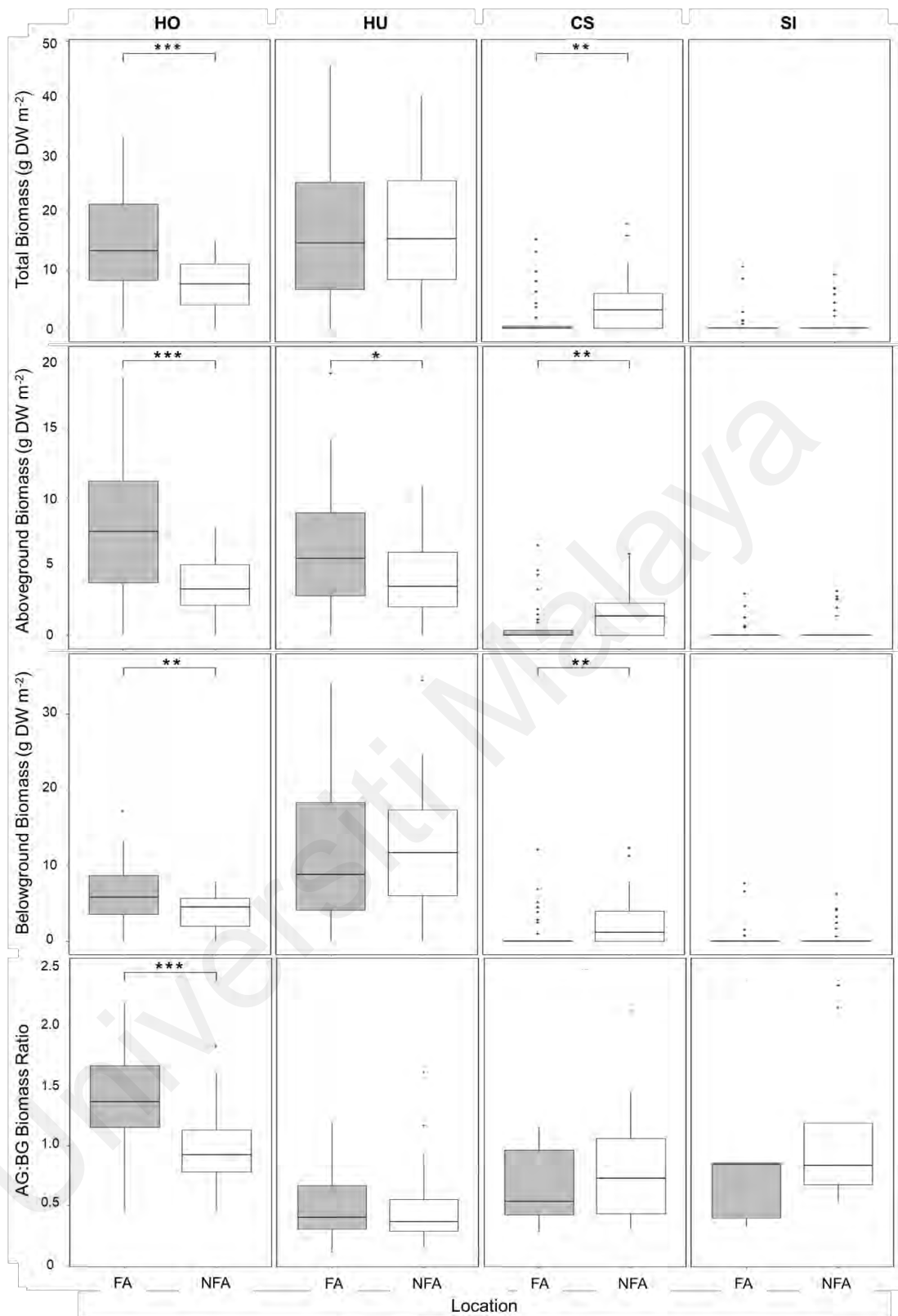


Figure 5.10 Total, aboveground and belowground biomass of seagrass present in feeding areas and non-feeding areas. Error bars indicate standard error.

Table 5.3 Results of Welch t-test (TT) and Mann-Whitney-Wilcoxon rank sum test (MW) of differences in terms of quantity between the feeding areas and non-feeding areas.

Seagrass species	Quantity variable	T/ W	df	P
Community level	Shoot density	2.67 ^{TT}	64.45	0.0095
	Total biomass (log-t)	1.95 ^{TT}	57.08	0.0559
	Aboveground biomass (log-t)	4.46 ^{TT}	60.15	<0.0001
	Belowground biomass	1.65 ^{TT}	53.44	0.1050
	AG:BG biomass ratio	2.15 ^{TT}	59.57	0.0359
Species level				
<i>Halophila ovalis</i>	Shoot density	3.10 ^{TT}	64.40	0.0029
	Total biomass	4.37 ^{TT}	54.282	<0.0001
	Aboveground biomass	4.86 ^{TT}	49.04	<0.0001
	Belowground biomass	2.84 ^{TT}	60.58	0.0061
	AG:BG biomass ratio	4.21 ^{TT}	60.96	<0.0001
<i>Halodule uninervis</i>	Shoot density	-1.00 ^{TT}	58.12	0.3193
	Total biomass	0.12 ^{TT}	57.86	0.9060
	Aboveground biomass	2.05 ^{TT}	57.53	0.0445
	Belowground biomass	430.5 ^{MW}	-	0.8011
	AG:BG biomass ratio (log-t)	0.30 ^{TT}	59.95	0.7646
<i>Cymodocea serrulata</i>	Shoot density	378 ^{MW}	-	0.0086
	Total biomass	380 ^{MW}	-	0.0096
	Aboveground biomass	373 ^{MW}	-	0.0071
	Belowground biomass	380.5 ^{MW}	-	0.0076
	AG:BG biomass ratio	69 ^{MW}	-	0.7113
<i>Syringodium isoetifolium</i>	Shoot density	492.5 ^{MW}	-	0.1783
	Total biomass	498 ^{MW}	-	0.2114
	Aboveground biomass	493 ^{MW}	-	0.1811
	Belowground biomass	490 ^{MW}	-	0.1525
	AG:BG biomass ratio	15 ^{MW}	-	0.5237

Type of test was indicated by superscript letters and statistical significance values ($P < 0.05$) were shown in bold. Log-transformed variables were labelled in parentheses.



Each box represents first and third quartile, horizontal lines within box represent median, whiskers represent minimum and maximum values, dots represent extreme values. Asterisks denote significant difference between group ($*0.01 \leq P < 0.05$, $**0.001 \leq P \leq 0.01$, $*** P < 0.001$). HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*

Figure 5.11 The total biomass, aboveground biomass, belowground biomass and AG:BG biomass ratio of each seagrass species in the dugong feeding areas (FA) and non-feeding areas (NFA).

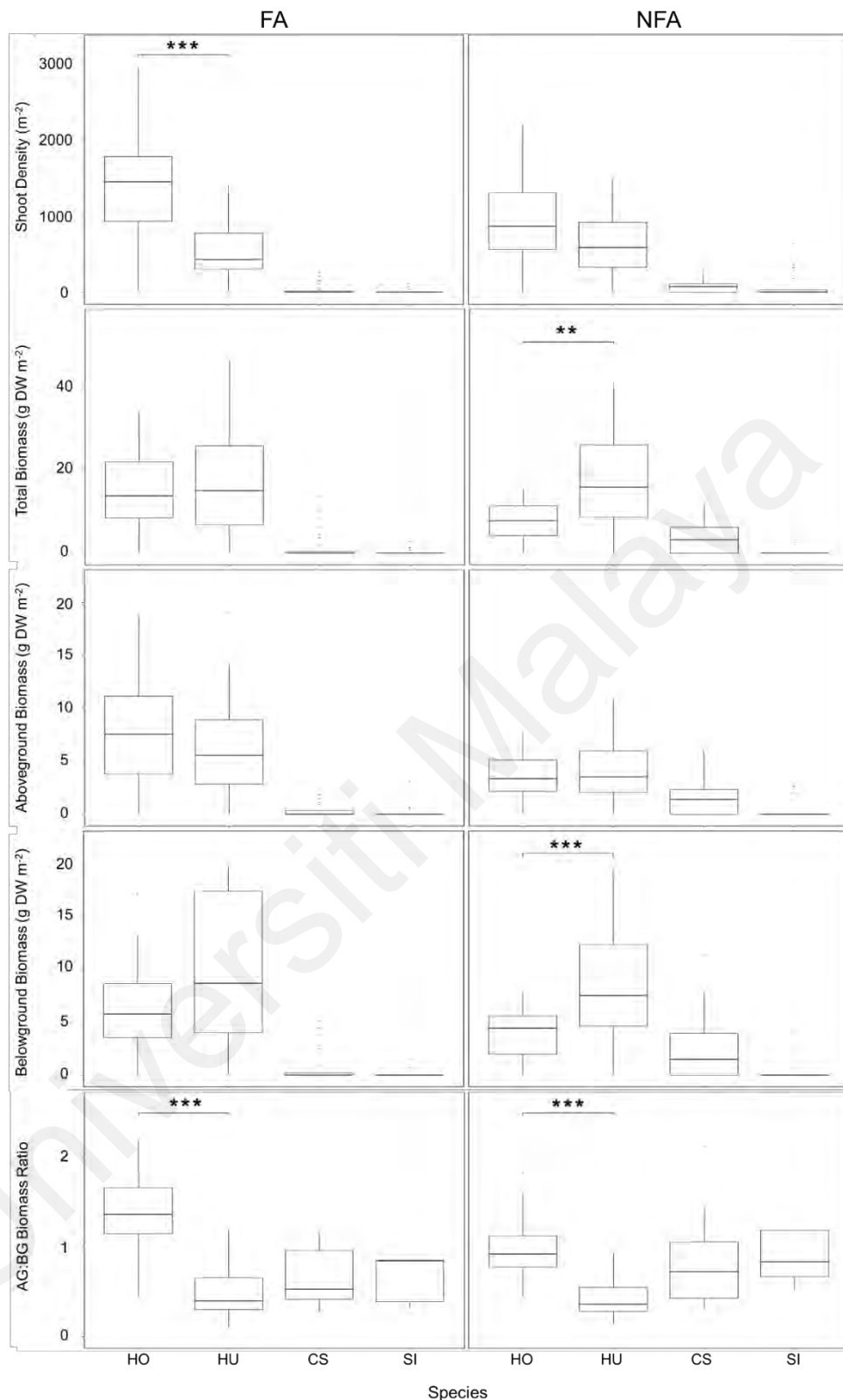
Variations of seagrass quantity between species

Kruskal-Wallis rank sum test showed that all quantity variables of seagrass differed significantly between species in both feeding areas and non-feeding areas (shoot density: $\chi^2 = 113.92$, $df = 3$, $p < 0.0001$; total biomass: $\chi^2 = 89.00$, $df = 3$, $p < 0.0001$; aboveground biomass: $\chi^2 = 95.45$, $df = 3$, $p < 0.0001$; belowground biomass: $\chi^2 = 83.81$, $df = 3$, $p < 0.0001$; AG:BG biomass ratio: $\chi^2 = 53.14$, $df = 3$, $p < 0.0001$), except that pairwise comparisons using Wilcoxon rank sum test showed no significant difference at all between *C. serrulata* and *S. isoetifolium* (Bonferroni adjusted p-values: shoot density = 1.00; total biomass = 0.89; aboveground biomass = 0.84; belowground biomass = 1.00; AG:BG biomass ratio = 1.00) (**Table 5.4**).

Halophila ovalis had significantly higher shoot density than *H. uninervis* in the feeding areas but not in the non-feeding areas (Bonferroni adjusted p-values: FA < 0.0001; NFA = 0.17). Conversely, the total and belowground biomass of *H. uninervis* were significantly higher than *H. ovalis* in the non-feeding areas but not in the feeding areas (total biomass: FA = 1.00, NFA = 0.009; belowground biomass: FA = 0.082, NFA < 0.001) (**Figure 5.11**). No significant difference was found between the two species in terms of their aboveground biomass (FA = 0.40; NFA = 1.00), yet their ratio of AG:BG biomass were significantly different at both areas (FA < 0.0001; NFA < 0.0001).

Table 5.4 Results of Kruskal-Wallis tests comparing quantity variables among seagrass species – *H. ovalis*, *H. uninervis*, *C. serrulata* and *S. isoetifolium*. Statistical significance values ($P < 0.05$) were shown in bold.

Location	Quantity variable	χ^2	df	<i>P</i>
Feeding areas	Shoot density	113.92	3	<0.0001
	Total biomass	89.00	3	<0.0001
	Aboveground biomass	95.45	3	<0.0001
	Belowground biomass	83.81	3	<0.0001
	AG:BG biomass ratio	53.14	3	<0.0001
Non-feeding areas	Shoot density	69.88	3	<0.0001
	Total biomass	54.51	3	<0.0001
	Aboveground biomass	47.51	3	<0.0001
	Belowground biomass	56.11	3	<0.0001
	AG:BG biomass ratio	29.59	3	<0.0001



Each box represents first and third quartile, horizontal lines within box represent median, whiskers represent minimum and maximum values, dots represent extreme values. Asterisks denote significant difference between group ($*0.01 \leq P < 0.05$, $**0.001 \leq P \leq 0.01$, $*** P < 0.001$). Only differences between HO and HU were denoted. HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*

Figure 5.12 Differences between seagrass species in terms of total biomass, aboveground biomass, belowground biomass and AG:BG biomass ratio, in the dugong feeding areas (FA) and non-feeding areas (NFA).

5.5.2.2 Food quality

By averaging the nutrient values of the particular species which were present within feeding and non-feeding areas, they represent the quality pool of the respective sites as a whole. The leaves-shoots contained higher concentrations of carbon, nitrogen, phosphorus, starch and dietary fibre than the roots-rhizomes (**Table 5.5**). The roots-rhizomes however, had higher C:N ratio than the leaves-shoots.

All quality variables were significantly different between feeding areas and non-feeding areas except for phosphorus (**Table 5.6**). The variables that were significantly higher in the feeding areas were: (1) nitrogen (Wilcoxon rank sum test: $n = 36-30$, $W = 313.5$, $p = 0.004$), (2) starch (Wilcoxon rank sum test: $n = 11-12$, $W = 11$, $p = 0.0003$), and (3) dietary fibre (Welch t-test: $T_{39.1} = 2.22$, $p = 0.03$). The variables that were significantly lower in the feeding areas were: (1) carbon (Welch t-test: $T_{28.9} = -3.09$, $p = 0.004$), and (2) C:N ratio (Wilcoxon rank sum test: $n = 22-27$, $W = 130$, $p = 0.0006$).

For all species, the aboveground component possessed greater nitrogen content than the belowground component, while the values varied across areas for other quality variables (**Table 5.5**). Both *H. ovalis* and *H. uninervis* had greater carbon and phosphorus contents in their aboveground component. *Halodule uninervis* had greater starch content in its belowground component in contrast to *H. ovalis* which had higher starch in its aboveground component (**Figure 5.14**).

The two dominant species, *H. ovalis* and *H. uninervis* showed significant differences in their nutrient contents between the feeding areas and non-feeding areas, while only the aboveground carbon content was significantly different in *C. serrulata*, and none of the quality variables of *S. isoetifolium* was statistically significant (**Table 5.6**). For *H. ovalis*, the significant variation occurred with: (1) total, aboveground and belowground carbon (total: $T_{27.7} = -2.99$, $p = 0.006$; AG: $T_{29.5} = -2.29$, $p = 0.03$; BG: $T_{26.3} = -3.31$, $p = 0.03$); (2) total, aboveground and belowground nitrogen (total: $n = 34-27$, $W = 285.5$, $p = 0.01$;

AG: $n = 34-27$, $W = 282$, $p = 0.01$; BG: $n = 34-27$, $W = 321$, $p = 0.045$); (3) total, aboveground and belowground dietary fibre (total: $T_{25.0} = 3.65$, $p = 0.001$; AG: $T_{27.6} = 3.18$, $p = 0.004$; BG: $T_{20.5} = 2.89$, $p = 0.009$); and (4) C:N ratio ($n = 20-25$, $W = 101.5$, $p = 0.0007$).

For *H. uninervis*, the significant differences were indicated for: (1) total, aboveground and belowground carbon (total: $n = 23-25$, $W = 431$, $p = 0.003$; AG: $n = 21-25$, $W = 374.5$, $p = 0.01$; BG: $n = 22-25$, $W = 403$, $p = 0.007$); (2) total and aboveground nitrogen (total: $n = 34-28$, $W = 330.5$, $p = 0.04$; AG: $n = 34-28$, $W = 334.5$, $p = 0.046$); (3) total, aboveground and belowground phosphorus (total: $T_{52.9} = -4.36$, $p < 0.0001$; AG: $T_{58.7} = -3.18$, $p = 0.002$; BG: $T_{42.1} = -3.91$, $p = 0.0003$); (4) total, aboveground and belowground starch (total: $n = 11-9$, $W = 1$, $p < 0.0001$; AG: $n = 11-6$, $W = 0$, $p = 0.0002$; BG: $n = 9-9$, $W = 7$, $p = 0.004$); and (5) C:N ratio ($n = 21-25$, $W = 136$, $p = 0.005$).

Variations of seagrass quality between species

The four seagrass species differed significantly from each other in different ways in the feeding areas and non-feeding areas. In feeding areas, the four species only differed significantly from each other for total phosphorus (Kruskal-Wallis rank sum: $\chi^2 = 52.50$, $df = 3$, $p < 0.0001$), C:N ratio ($\chi^2 = 8.96$, $df = 3$, $p = 0.03$), and total starch between *H. ovalis* and *H. uninervis* (Wilcoxon rank sum: $n = 10-11$, $W = 20$, $p = 0.01$) (**Table 5.7**). However, there were no significance differences for total carbon ($\chi^2 = 7.47$, $df = 3$, $p = 0.06$), total nitrogen ($\chi^2 = 2.50$, $df = 3$, $p = 0.48$), and total dietary fibre ($\chi^2 = 5.40$, $df = 3$, $p = 0.15$).

In non-feeding areas, the four species differed significantly for total carbon ($\chi^2 = 38.47$, $df = 3$, $p < 0.0001$), total phosphorus ($\chi^2 = 35.76$, $df = 3$, $p < 0.0001$), total dietary fibre ($\chi^2 = 15.00$, $df = 3$, $p = 0.002$), while not significantly different for total nitrogen ($\chi^2 =$

2.62, $df = 3$, $p = 0.46$) and CN ratio ($\chi^2 = 1.53$, $df = 3$, $p = 0.68$). There was also no significant difference found for total starch in between *H. ovalis* and *H. uninervis* (Wilcoxon rank sum: $n = 4-9$, $W = 28$, $p = 0.15$). The starch values for *C. serrulata* and *S. isoetifolium* were not determined due to very small quantity of samples collected.

As we narrowed down our focus to the two dominant species, *H. ovalis* and *H. uninervis*, the greatest variations between them occurred with total carbon (non-feeding areas), total dietary fibre (non-feeding areas), and total phosphorus (both areas) (**Figure 5.15**). The Wilcoxon rank sum post-hoc test showed that their differences in carbon and dietary fibre concentrations were much larger in the non-feeding areas (carbon: mean difference = $4.68 \pm 0.57\%$, $p < 0.0001$; fibre: mean difference = $6.24 \pm 1.55\%$, $p = 0.002$) compared to the feeding areas (carbon: mean difference = $3.94 \pm 0.45\%$, $p = 0.06$; fibre: mean difference = $2.67 \pm 1.03\%$, $p = 0.15$). *Halophila ovalis* and *H. uninervis* were significantly different for phosphorus in both areas (FA: mean difference = $0.012 \pm 0.001\%$, $p < 0.0001$; NFA: mean difference = $0.007 \pm 0.001\%$, $p < 0.0001$).

Conversely, the difference for total starch and C:N ratio between *H. ovalis* and *H. uninervis* were significant in the feeding areas (starch: mean difference = $0.95 \pm 0.31\%$, $p = 0.013$; C:N ratio: mean difference = 5.06 ± 4.10 , $p = 0.030$), and not significant in the non-feeding areas (starch: mean difference = $0.26 \pm 0.13\%$, $p = 0.15$; C:N ratio: mean difference = 25.58 ± 14.77 , $p = 0.68$). At the species level, there was no significant difference between *H. ovalis* and *H. uninervis* for their total nitrogen concentration in both areas (FA: $p = 0.48$; NFA: $p = 0.46$).

Table 5.5 Mean % nutrient values of seagrass quantity variables in the feeding areas and non-feeding areas in the Sibiu-Tinggi Archipelago. C, total carbon; N, total nitrogen; P, total phosphorus; S, total starch; DF, total dietary fibre; C:N, ratio of carbon to nitrogen

Seagrass species	Plant component	C		N		P		S		DF		C:N	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Community level													
Feeding areas	Whole plant	31.28	1.01	1.01	0.11	0.017	0.001	2.37	0.16	8.86	0.68	41.09	12.54
	Aboveground	31.80	1.19	1.48	0.16	0.021	0.001	2.49	0.21	8.98	0.87	30.14	10.55
	Belowground	30.67	0.86	0.54	0.19	0.013	0.001	2.14	0.18	8.29	0.61	77.84	15.20
Non-feeding areas	Whole plant	34.76	0.32	0.65	0.13	0.017	0.001	0.53	0.28	7.94	0.99	160.95	20.95
	Aboveground	36.22	0.36	0.91	0.19	0.022	0.001	0.72	0.37	8.43	1.33	134.09	18.78
	Belowground	33.30	0.38	0.38	0.07	0.013	0.001	0.60	0.31	7.09	0.88	271.30	49.50
Species level													
<i>Halophila ovalis</i>													
Feeding areas	Whole plant	29.50	1.02	1.00	0.12	0.023	0.001	1.83	0.21	7.43	0.78	43.25	14.59
	Aboveground	30.67	1.08	1.39	0.16	0.030	0.002	2.03	0.29	8.41	0.93	31.81	11.30
	Belowground	28.33	1.02	0.61	0.08	0.017	0.002	1.50	0.24	6.36	1.10	93.13	29.03
Non-feeding areas	Whole plant	32.17	0.49	0.69	0.15	0.022	0.001	0.79	0.45	5.17	0.66	174.05	25.41
	Aboveground	33.79	0.37	0.93	0.20	0.030	0.002	1.00	0.61	4.94	0.58	142.95	21.84
	Belowground	30.54	0.77	0.45	0.10	0.014	0.001	0.45	0.45	5.30	1.10	280.59	48.45
<i>Halodule uninervis</i>													
Feeding areas	Whole plant	33.03	1.15	1.02	0.11	0.011	0.001	2.87	0.24	9.35	0.98	39.47	11.05
	Aboveground	33.65	1.51	1.56	0.18	0.015	0.001	2.82	0.31	9.08	1.24	30.22	11.22
	Belowground	32.04	0.80	0.47	0.05	0.008	0.001	2.92	0.32	9.47	0.97	76.65	9.85
Non-feeding areas	Whole plant	36.87	0.26	0.74	0.14	0.015	0.001	0.61	0.31	11.60	1.82	150.42	23.56
	Aboveground	38.61	0.33	1.08	0.22	0.019	0.001	0.64	0.41	15.48	3.50	135.05	24.80
	Belowground	35.13	0.35	0.40	0.07	0.010	0.001	0.72	0.37	8.57	1.06	266.41	54.50
<i>Cymodocea serrulata</i>													
Feeding areas	Whole plant	32.36	2.03	0.90	0.20	0.013	0.002	-	-	9.86	2.50	84.40	40.98
	Aboveground	30.81	2.60	1.35	0.26	0.013	0.001	-	-	9.76	1.45	38.09	22.38
	Belowground	32.85	1.95	0.39	0.09	0.012	0.002	-	-	8.95	2.59	136.41	41.83
Non-feeding areas	Whole plant	35.41	0.52	0.67	0.17	0.014	0.001	-	-	7.74	1.28	152.92	30.02
	Aboveground	36.17	0.89	0.98	0.25	0.014	0.001	-	-	7.42	0.84	115.99	23.31
	Belowground	34.66	0.53	0.36	0.08	0.014	0.001	-	-	8.36	1.76	255.18	54.12
<i>Syringodium isoetifolium</i>													
Feeding areas	Whole plant	34.40	2.50	0.56	0.28	0.010	0.001	-	-	4.85	0.65	131.98	109.20
	Aboveground	33.40	3.60	0.67	0.38	0.010	0.001	-	-	4.27	0.17	103.64	87.08
	Belowground	35.40	1.40	0.46	0.20	0.010	0.002	-	-	5.43	1.13	181.29	147.29
Non-feeding areas	Whole plant	35.32	0.73	0.55	0.25	0.010	0.001	-	-	4.38	0.77	196.12	56.64
	Aboveground	36.23	0.77	0.69	0.33	0.010	0.001	-	-	5.91	1.72	187.38	57.69
	Belowground	34.40	0.81	0.42	0.18	0.010	0.001	-	-	2.34	1.68	230.52	71.86

Table 5.6 Results of Welch t-test (TT) and Mann-Whitney-Wilcoxon rank sum test (MW) of differences in terms of quality variables between the feeding areas and non-feeding areas. Type of test was indicated by superscript letters and statistical significance values ($P < 0.05$) were shown in bold. Table continued on next page.

Seagrass species	Quality variable	T/ W	df	P
Community level	Total carbon			
	Whole plant	-3.09 ^{TT}	28.87	0.0044
	Aboveground	160 ^{MW}		0.0012
	Belowground	197.5 ^{MW}		0.0106
	Total nitrogen			
	Whole plant	313.5 ^{MW}		0.0036
	Aboveground	326.5 ^{MW}		0.0061
	Belowground	327.5 ^{MW}		0.0063
	Total phosphorus			
	Whole plant	640 ^{MW}		0.2001
	Aboveground (log-t)	-0.75 ^{TT}	63.22	0.4534
	Belowground (log-t)	-0.32 ^{TT}	63.60	0.7484
	Total starch			
	Whole plant	11 ^{MW}		0.0003
	Aboveground	11 ^{MW}		0.0023
	Belowground	12 ^{MW}		0.0045
	Total dietary fibre			
Whole plant	2.22 ^{TT}	39.10	0.0325	
Aboveground	98 ^{MW}		0.0129	
Belowground	1.60 ^{TT}	35.51	0.1187	
C:N ratio	130 ^{MW}		0.0006	
Species level <i>Halophila ovalis</i>	Total carbon			
	Whole plant	-2.99 ^{TT}	24.78	0.0063
	Aboveground	-2.29 ^{TT}	29.49	0.0293
	Belowground	-3.31 ^{TT}	26.32	0.0027
	Total nitrogen			
	Whole plant	285.5 ^{MW}		0.0120
	Aboveground	282 ^{MW}		0.0103
	Belowground	321 ^{MW}		0.0456
	Total phosphorus			
	Whole plant	0.81 ^{TT}	58.97	0.4197
	Aboveground	1.27 ^{TT}	55.44	0.2091
	Belowground (log-t)	1.24 ^{TT}	58.94	0.2201
	Total starch			
	Whole plant	6 ^{MW}		0.0540
	Aboveground	8 ^{MW}		0.2141
	Belowground	-		-
	Total dietary fibre			
Whole plant	3.65 ^{TT}	25.01	0.0012	
Aboveground	3.18 ^{TT}	27.63	0.0036	
Belowground	2.89 ^{TT}	20.49	0.0088	
C:N ratio	101.5 ^{MW}		0.0007	

Table 5.6 (Cont.)... Results of Welch t-test (TT) and Mann-Whitney-Wilcoxon rank sum test (MW) of differences in terms of quality variables between the feeding areas and non-feeding areas. Type of test was indicated by superscript letters and statistical significance values ($P < 0.05$) were shown in bold. Table continued on next page.

Seagrass species	Quality variable	T/ W	df	P
<i>Halodule uninervis</i>	Total carbon			
	Whole plant	431 ^{MW}		0.0032
	Aboveground	374.5 ^{MW}		0.0139
	Belowground	403 ^{MW}		0.0065
	Total nitrogen			
	Whole plant	330.5 ^{MW}		0.0402
	Aboveground	334.5 ^{MW}		0.0459
	Belowground	353 ^{MW}		0.0828
	Total phosphorus			
	Whole plant	-4.36 ^{TT}	52.92	<0.0001
	Aboveground	-3.18 ^{TT}	58.75	0.0024
	Belowground	-3.91 ^{TT}	42.14	0.0003
	Total starch			
	Whole plant	1 ^{MW}		<0.0001
	Aboveground	0 ^{MW}		0.0002
	Belowground	7 ^{MW}		0.0035
	Total dietary fibre			
	Whole plant	144 ^{MW}		0.8692
	Aboveground	146 ^{MW}		0.8077
	Belowground	169 ^{MW}		0.9879
	C:N ratio	136 ^{MW}		0.0047
<i>Cymodocea serrulata</i>	Total carbon			
	Whole plant	84 ^{MW}		0.3396
	Aboveground	92 ^{MW}		0.0418
	Belowground	62 ^{MW}		0.9227
	Total nitrogen			
	Whole plant	75.5 ^{MW}		0.3528
	Aboveground	64 ^{MW}		0.2458
	Belowground	72 ^{MW}		0.4439
	Total phosphorus			
	Whole plant	129 ^{MW}		0.1311
	Aboveground	98.5 ^{MW}		0.6210
	Belowground	112 ^{MW}		0.0960
	Total starch			
	Whole plant	-		-
	Aboveground	-		-
	Belowground	-		-
	Total dietary fibre			
	Whole plant	33 ^{MW}		0.6388
	Aboveground	8 ^{MW}		0.1490
	Belowground	32 ^{MW}		0.5789
	C:N ratio	31 ^{MW}		0.3023

Table 5.6 (Cont.)... Results of Welch t-test (TT) and Mann-Whitney-Wilcoxon rank sum test (MW) of differences in terms of quality variables between the feeding areas and non-feeding areas. Type of test was indicated by superscript letters and statistical significance values ($P < 0.05$) were shown in bold.

Seagrass species	Quality variable	T/ W	df	P
<i>Syringodium isoetifolium</i>	Total carbon			
	Whole plant	7 ^{MW}		0.8571
	Aboveground	8 ^{MW}		0.6429
	Belowground	4 ^{MW}		0.6429
	Total nitrogen			
	Whole plant	10 ^{MW}		0.5273
	Aboveground	9.5 ^{MW}		0.4487
	Belowground	10.5 ^{MW}		0.5699
	Total phosphorus			
	Whole plant	20.5 ^{MW}		0.4946
	Aboveground	15 ^{MW}		0.9321
	Belowground	20 ^{MW}		0.5508
	Total starch			
	Whole plant	-		-
	Aboveground	-		-
	Belowground	-		-
	Total dietary fibre			
	Whole plant	-		-
	Aboveground	-		-
	Belowground	-		-
	C:N ratio	-		-

Table 5.7 Results of Kruskal-Wallis tests comparing quality variables among seagrass species – *H. ovalis*, *H. uninervis*, *C. serrulata* and *S. isoetifolium*.

Location	Quality variable	χ^2 / W	df	P
Feeding areas	Carbon	7.47	3	0.0584
	Nitrogen	2.50	3	0.4752
	Phosphorus	52.50	3	<0.0001
	Starch	20 ^{MW}		0.0127
	Dietary fibre	5.40	3	0.1447
	C:N ratio	8.96	3	0.0298
Non-feeding areas	Carbon	38.47	3	<0.0001
	Nitrogen	2.62	3	0.4549
	Phosphorus	35.76	3	<0.0001
	Starch	28 ^{MW}		0.1483
	Dietary fibre	15.00	3	0.0018
	C:N ratio	1.531	3	0.6751

Starch variable was compared with Mann-Whitney-Wilcoxon rank sum test (MW) due to unavailable data for *C. serrulata* and *S. isoetifolium*. Statistical significance values ($P < 0.05$) were shown in bold.

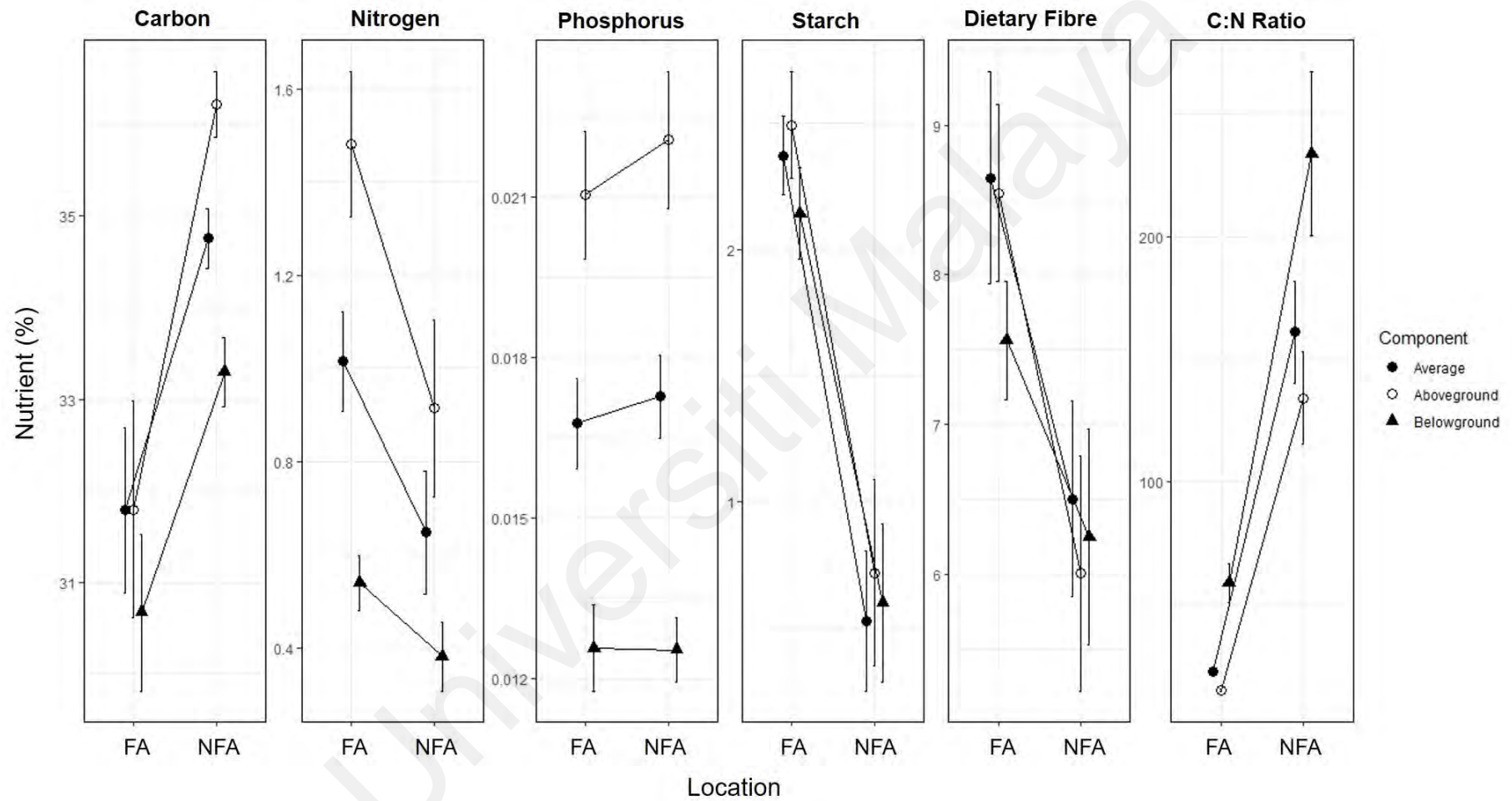


Figure 5.13 Plots of mean carbon, nitrogen, phosphorus, starch, dietary fibre concentrations and C:N ratio of seagrass in the dugong feeding areas (FA) and non-feeding areas (NFA). Error bars indicate standard error.

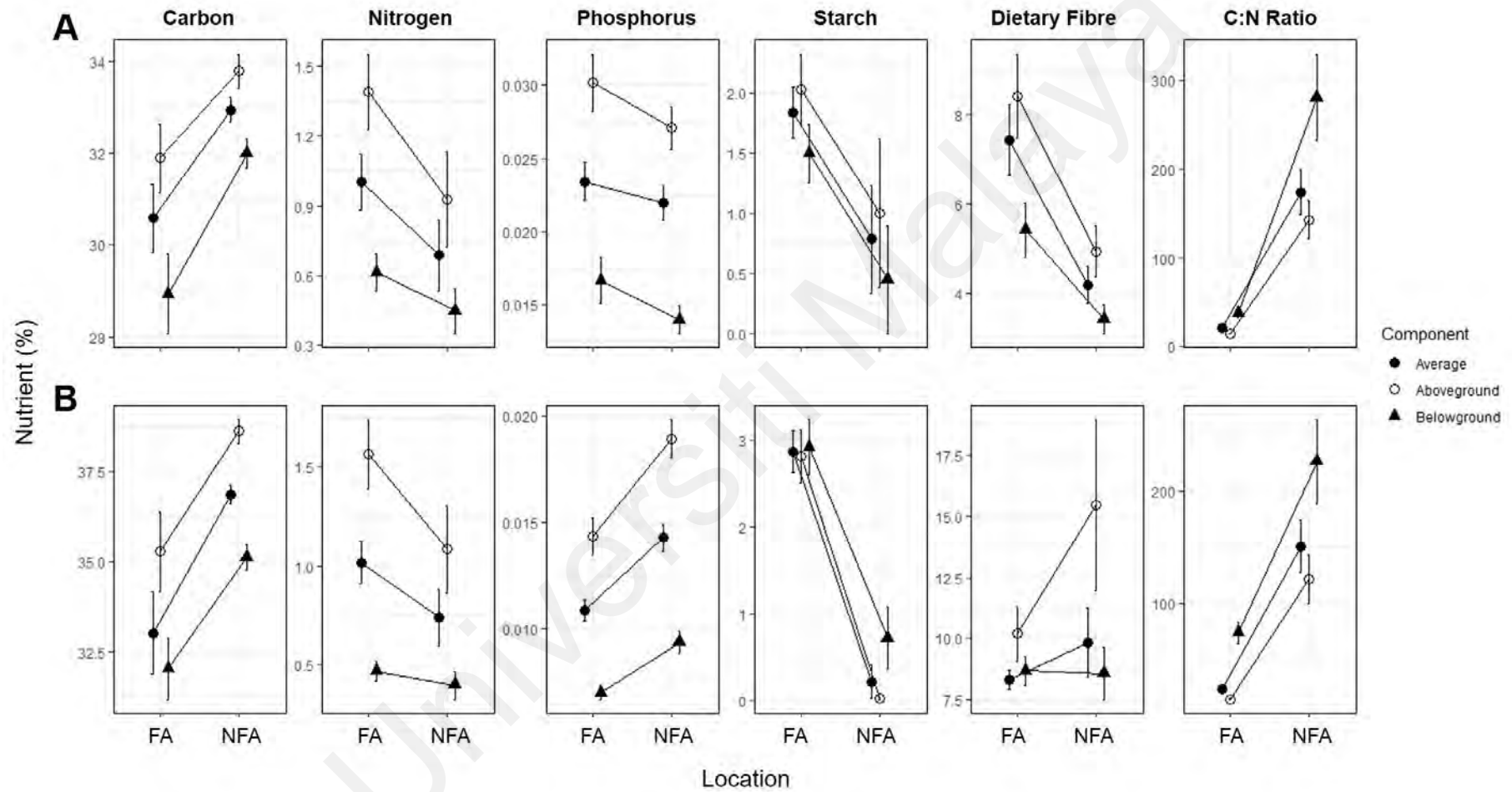
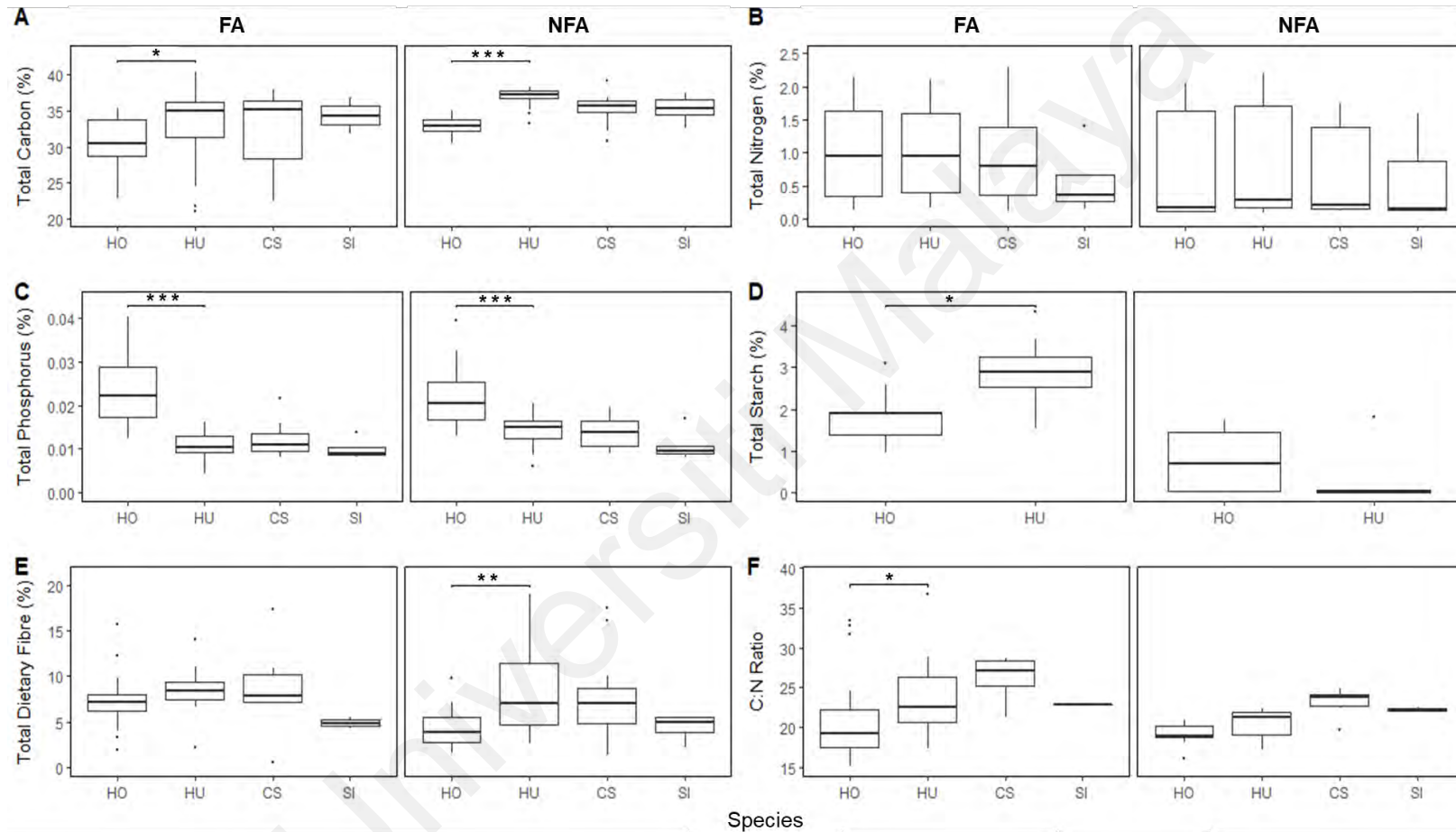


Figure 5.14 Plots of mean carbon, nitrogen, phosphorus, starch, dietary fibre concentrations and C:N ratio of (A) *Halophila ovalis* and (B) *Halodule uninervis* in the dugong feeding areas (FA) and non-feeding areas (NFA). Error bars indicate standard error.



Each box represents first and third quartile, horizontal lines within box represent median, whiskers represent minimum and maximum values, dots represent extreme values. Asterisks denote significant difference between group (* $0.01 \leq P < 0.05$, ** $0.001 \leq P \leq 0.01$, *** $P < 0.001$). HO: *Halophila ovalis*; HU: *Halodule uninervis*; CS: *Cymodocea serrulata*; SI: *Syringodium isoetifolium*

Figure 5.15 Differences between seagrass species in terms of total carbon, nitrogen, phosphorus, starch, dietary fibre and C:N ratio, in the dugong feeding areas (FA) and non-feeding areas (NFA).

5.5.2.3 Physical properties

The feeding areas in the Sibutu Archipelago had mean water depth of 4.5 ± 0.3 m, and was not significantly different from the mean water depth of 4.2 ± 0.3 m in the non-feeding areas (Welch t-test: $T_{37.9} = -0.56, p = 0.58$) (Table 5.8 & Table 5.9). The deepest sampled feeding trail was at 9.7 m relative to datum, while the shallowest was at 2.6 m (Figure 5.16).

The sediments in the seagrass meadows (regardless of feeding or non-feeding areas) were mainly composed of fine sands (54.6%) and coarse sands (40.9%) with very low proportions of gravel and shells (2.0%) and silt-clays (2.5%) (Table 5.8, Figure 5.17). There was no significant difference between all particle sizes in the feeding areas and non-feeding areas, except for silt-clay (Welch t-test: $T_{42.6} = -4.34, p < 0.0001$) (Table 5.9).

Table 5.8 Mean and ranges of values of physical variables in the feeding areas and non-feeding areas.

Physical variable	Mean \pm Standard error	Minimum – Maximum
Feeding Areas		
Water depth, m ($n=22$)	4.5 ± 0.3	2.6 – 9.3
Sediment, % DW ($n=27$)		
Gravel + shell	2.71 ± 0.45	0.28 – 7.43
Coarse sand	41.70 ± 3.19	12.44 – 80.79
Fine sand	53.96 ± 3.35	11.73 – 81.75
Silt-clay	1.63 ± 0.18	0.13 – 3.83
Non-feeding Areas		
Water depth, m ($n=27$)	4.2 ± 0.3	1.0 – 7.2
Sediment, % DW ($n=30$)		
Gravel + shell	1.40 ± 0.21	0.05 – 5.32
Coarse sand	40.15 ± 3.18	10.27 – 72.91
Fine sand	55.11 ± 3.16	20.46 – 84.49
Silt-clay	3.35 ± 0.35	0.41 – 8.14

Table 5.9 Results of Welch t-test (TT) and Mann-Whitney-Wilcoxon rank sum test (MW) of differences in terms of physical variables between the feeding areas and non-feeding areas.

Physical variable	<i>T/W</i>	df	<i>P</i>
Water depth	-0.56 ^{TT}	37.86	0.5761
Sediment size			
Gravel	495 ^{MW}		0.1537
Coarse sand	0.34 ^{TT}	54.83	0.7317
Fine sand	-0.25 ^{TT}	54.32	0.8040
Silt-clay	-4.34 ^{TT}	42.58	<0.0001

Type of test was indicated by superscript letters and statistical significance values ($P < 0.05$) were shown in bold.

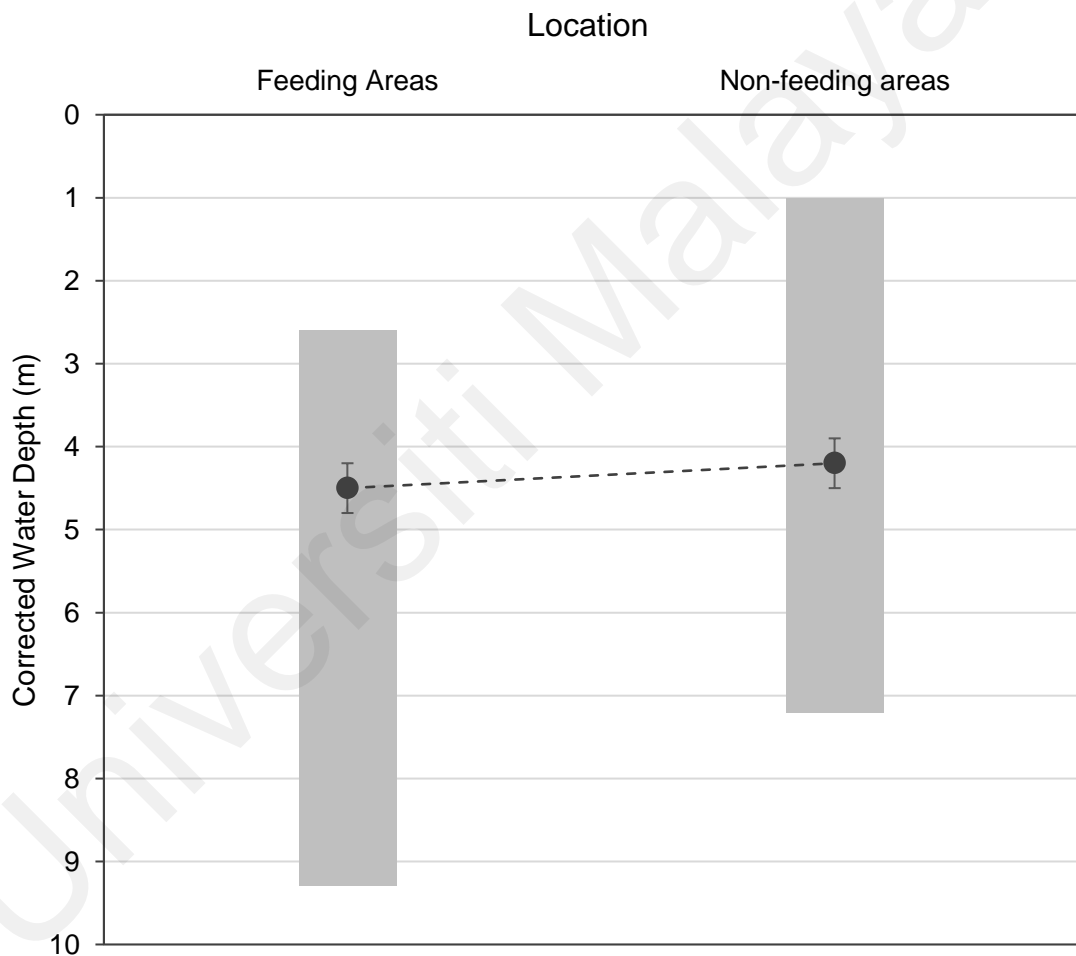


Figure 5.16 Mean water depth (corrected to chart datum) with standard error bars for seagrass samples collected in dugong feeding areas and non-feeding areas. Grey bars represent the range of water depth.

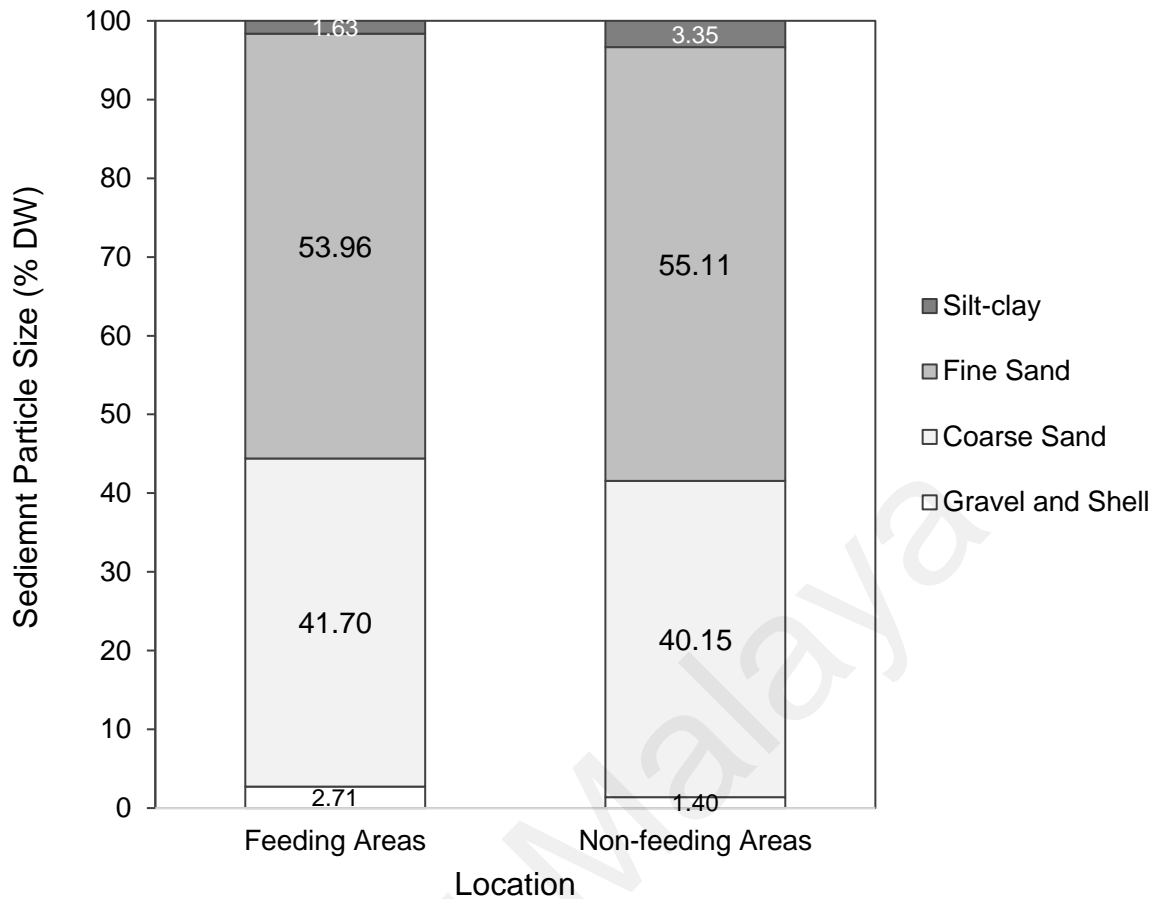


Figure 5.17 Percentage of each sediment particle size category in dugong feeding areas and non-feeding areas, classified from silt-clay <math><63 \mu\text{m}</math>, fine sand 0.063 – 0.25 mm, coarse sand 0.25 – 2.00 mm, to gravel and shell >2 mm.

5.4.3 Effects of quantity-quality-physical factors on dugong food selection

The best explained predictive model was fitted with five variables that encompassed quantity and physical factors, which included aboveground biomass of *H. ovalis*, AG:BG biomass ratio of *H. ovalis*, and proportion of gravel, fine sand and silt-clay in the sediment ($\text{adj } D^2 = 55.57\%$, $\text{adj } R^2 = 0.46$, $\text{AICc} = 51.75$) (Table 5.10). Each variable in the fitted model had $\Delta\text{AIC} > 2$, indicating support of each variable to the full model (Table 5.11).

The dugongs' feeding occurrence was predicted by the model to be more likely at meadows with high aboveground biomass, high AG:BG biomass ratio of *H. ovalis*, high proportion of gravel and fine sand, and low proportion of silt-clay. Among the predictors, the GLM confirmed that the effects of aboveground biomass of *H. ovalis* and AG:BG

biomass ratio of *H. ovalis* were significant ($P = 0.004, 0.016$, respectively). Both aboveground biomass and AG:BG biomass ratio of *H. ovalis* were consistently selected as the final predictors in each of the imputed dataset, highlighting their strong influence as a factor in driving dugong feeding preference (with combined explained deviances of 38.0% out of 56.0%). Next in line was the proportion of silt-clay that contributed 12.0% of the total explained deviances. Despite silt-clay appearing to be a significant factor in all imputed datasets, its averaged effect was not significant in the final model ($P > 0.05$). Nonetheless, all three sediment size variables were consistently being selected as the final predictors in each of the imputed dataset, similar to the food quantity variables of *H. ovalis*.

Table 5.10 Model performance metrics for best fitted GLM model.

Performance metric	Coefficient	Value
Predictive power	D ² (adj)	0.56
	McFadden's R ² (adj)	0.46
	Nagelkerke's R ²	0.74
Goodness-of-fit	Unweighted Sum of Squares Test*	0.51
Accuracy	Area under ROC curve (AUC)	0.95

* le Cessie-van Houwelingen-Copas-Hosmer unweighted sum of squares test

Table 5.11 The best fitted generalized linear model for dugong feeding preferences. Statistical significance values ($P < 0.05$) were shown in bold.

Factor	df	Estimate	SE	% Explained Deviance	ΔAIC	Odds Ratio	95% CI	<i>P</i>
AG biomass of HO		0.516	0.171	24.72	15.84	1.68	1.19 - 2.36	0.0038
AG:BG biomass ratio of HO		3.426	1.371	13.25	8.82	30.75	1.94 - 486.22	0.0161
Gravel		0.834	0.423	6.37	5.69	2.30	0.98 - 5.40	0.0548
Fine sand		0.069	0.035	2.55	3.82	1.07	1.00 - 1.15	0.0547
Silt-clay		-0.956	0.456	11.99	9.39	0.38	0.15 - 1.01	0.0527

5.5 Discussion

5.5.1 Feeding trail dimensions as indicators of dugong grazing behaviour

The results showed that the average length of dugong feeding trails in the subtidal seagrass meadows was up to approximately six times longer than the dugong feeding trails measured in intertidal seagrass meadows such as those in Tanjung Adang, Malaysia and Talibong Island, Thailand and in parts of Australia and other localities (**Table 5.12**). This variation could be a result of dugongs being more likely to submerge for longer periods while feeding in deeper subtidal meadows in order to maximise their feeding time before surfacing for breath (Chilvers et al., 2004, Hodgson, 2004).

The width of feeding trails which ranged from 9 to 20 cm matched the normal width of the dugong's facial disc (Marshall et al., 2003; Marsh et al., 2011). By comparing the width of feeding trails with the mean width of a calf's facial disc (9.0 ± 1.4 cm) in Thailand (Adulyanukosol, 2010), 11% of the feeding trails were possibly left by calves while 89% of were left by either juveniles or adults. The significant positive correlation between lengths and widths of feeding trails might indicate that time/ effort spent on feeding might be a factor of age, where adults spent a longer time feeding in one feeding bout (resulting in longer trails) compared to calves. Hodgson (2004) also observed that calves do not spend as much time feeding on seagrass as the mothers because calves also rely on suckling for their dietary needs.

The maximum length of dugong feeding trails in this study (21.6 m) was approximately doubled than that of the maximum lengths recorded in other regions (<10 m), and the closest one to this study was a 14 m long feeding trail which was observed in the Philippines (Kataoka et al., 1995). Because the time at which the measurements took place after the dugongs' grazing is likely different from one feeding trail to another, and as feeding trails would lose their shapes with increasing time, we could not confirm whether the trails that were longer than 10 m in this study ($n = 5$) were over-measured

(i.e., whereby more than one feeding trail were continuously photographed during *in situ* sampling) or truly distinctly longer than observed in the other studies. Nonetheless, regional variations in terms of the dimension of feeding trails are common as dugong feeding behaviour appears to be varied based on the types and distributions of food species, substrates, and predation danger in the feeding ground (Preen, 1992; Wirsing et al., 2007a; Adulyanukosol, 2010). More feeding trail samples from the subtidal habitat from different areas are needed to verify the results.

Based on the average biomass per feeding trail (38.16 ± 24.40 g DW m⁻² – only include ≤ 10 m trails) and the dugong feeding rate (1100 g DW day⁻¹) observed by Mukai et al. (1999), it is estimated that dugongs leave an average of 29 feeding trails per day per individual. However this estimation is highly varied among individuals and locations (Mukai et al., 1999). Nonetheless, the average area of feeding trail in this study (0.82 ± 0.77 m² – only include ≤ 10 m trails) was close to the average size of feeding trails in Talibong Island, Thailand (0.87 m²) (Wongsuryrat et al., 2011)

Halophila ovalis and *H. uninervis* were the two seagrass species that were most associated with the dugong feeding trails (>85% occurrence in the sampled feeding trails) while the other two seagrass species, *C. serrulata* and *S. isoetifolium* were less associated to the trails (<30% occurrence in the feeding trails). This indicated that dugongs potentially feed on all available seagrass species in the meadows but seemed to selectively feed on *H. ovalis* and *H. uninervis*. This is consistent with previous studies where dugongs were observed feeding on most of the seagrass species present in their feeding grounds. Additionally, all four seagrass species in this study have been found in the mouths and stomachs of dugongs, but with *H. ovalis* and *H. uninervis* occurring in higher percentages (Johnstone & Hudson, 1981; Marsh et al., 1982; Erfteimeijer et al., 1993; Adulyanukosol et al., 2004; Adulyanukosol, 2010). However, the inference of the results here, which is based on the presence-absence of species is insufficient to strongly support a definitive

conclusion that the dugongs selectively fed on *H. ovalis* and/or *H. uninervis*, as both species were naturally more abundant in the meadows and hence more likely to be present around the feeding trails. Investigating the comparison between food quantity and quality in the feeding areas versus non-feeding areas provided a more robust foundation in supporting the selective feeding behaviour of dugongs and is discussed in the proceeding section.

Relationship with seagrass quantity

Overall, it was shown that seagrass quantity (biomass) affected the grazing process of dugongs, in which higher ratios of aboveground to belowground biomass of seagrass facilitated for longer trails, while higher belowground biomass of *H. uninervis* facilitated for shallower trails. There was no significant correlation between the mean length of feeding trails and shoot density of seagrass, which is similar to the findings of Preen (1992). The ratios of AG:BG biomass had a positive relationship with the length of the produced trails, indicating that dugongs might spend relatively more time/effort on each feeding trail in patches with high ratios of AG:BG biomass (greater amount of leaves and shoots in relation to roots and rhizomes). In contrast, the negative relationship between belowground biomass of *H. uninervis* with the depth of feeding trails indicates that dugongs tended to not dig deeper into the substratum with dense belowground component of *H. uninervis*, presumably because *H. uninervis* has very fine and fibrous roots which can form a dense intertwining rhizome mat below the substrate (Larkum et al., 2006)). This might impede feeding dugongs from burrowing at a deeper depth of substrate as it consumes more energy.

Table 5.12 Summary of mean and range of dugong feeding trail dimensions across distributional regions. (-): no data; (*): standard error. Abbreviation: HCMNP = Haad Chao Mai National Park

Study area	Length (m)			Width (cm)			Depth (cm)			Reference
	Mean \pm SD	Min - Max	N	Mean \pm SD	Min - Max	N	Mean \pm SD	Min - Max	N	
Malaysia										
Sibu-Tinggi Archipelago	7.16 \pm 5.64	2.00 – 21.63	28	14.12 \pm 3.10	8.96 – 20.16	28	2.8 \pm 0.6	1.7 – 4.8	28	This study
Tanjung Adang, Johor	3.52 \pm 1.50	2 – 9	29	17 \pm 4	10 – 28	29	-	-	-	Zulkifli Poh (2009)
Australia										
Shoalwater Bay	-	1 - 5	-	-	19 – 25	-	-	3 – 5	-	Heinsohn et al. (1977)
Shoalwater Bay (Cliff Point)	8.05 \pm 0.35	-	40	23.3 \pm 1.6	20 – 26	40	4.5	-	40	Anderson & Birtles (1978)
Shoalwater Bay (North Cove)	2.94 \pm 0.19	-	47	-	-	47	4.5	-	47	
Moreton Bay	2.27 \pm 0.14*	10	32	11.8 \pm 0.2*	12 – 23	32	-	5 – 10	32	Preen (1992)
	4.79 \pm 0.28*	-	10	22.7 \pm 0.6*	-	10	-	-	-	
Thailand										
Koh Bae Na, HCMNP	2.3	-	-	15	-	-	-	3 - 5	-	Mukai et al. (1999)
Talibong Island	1.49 \pm 0.80	-	77	15.0 \pm 2.7	-	77	-	-	-	Tsutsumi et al. (2005)
Talibong Island	-	-	-	-	-	-	3.1 \pm 0.5	-	30	Nakanishi et al. (2009)
Talibong Island	1.10 \pm 1.15	0.64 – 9.91	213	18.85 \pm 5.65	8 – 48	213	-	1 – 4	213	Adulyanukosol (2010)
Talibong Island	4.47	2.32 – 6.15	25	19	15 – 25	25	15	8 – 20	25	Wongsuryrat et al. (2011)
Indonesia										
Alor Island, East Nusa Tenggara	-	0.8 – 1.0	-	-	15 – 20	-	-	-	-	WWF-Indonesia (2016)
Egypt										
Marsa Alam	3.2 \pm 1.4	0.6 – 3.1	-	17.2 \pm 4	9 - 26	-	-	-	-	Shawky (2018)
Wadi El Gemal National Park	3.3 \pm 1.3	1.2 – 8.6	-	17.6 \pm 1.3	7 - 26	-	-	-	-	Shawky (2018)
Wadi El Gemal National Park	-	0.9 – 8.0	20	20.3 \pm 5.8	6 - 30	20	-	-	-	Shawky (2019)
Philippines										
	-	? - 14	-	-	-	-	-	-	-	Kataoka et al. (1995)
India										
Gulf of Kachchh, India	-	1.0 – 5.2	-	-	20 - 28	-	-	-	-	Apte et al. (2019)

Relationship with sediment particle size

None of the particle sizes of sediment influenced the length and depth of feeding trails, indicating that the soft substrates in the study site which were predominated by medium-grained sands did not cause serious interference for dugongs when ingesting seagrass from the substrata, nor inhibited the extraction of rhizomes (Domning & Beatty, 2007). This matched the result of Adulyanukosol (2010) where no correlation was found between the substrate type and the feeding trail dimensions, even though the substrates in her study sites in Thailand were slightly different (muddy sand bottom) compared to this study (sandy bottom). Higher shell content in the sediments could make it more difficult for dugongs to chew on their food (Preen, 1992), however the proportion of shells found in the samples was negligible and thus is not an influencing factor to this study.

5.5.2 Food quantity and quality and physical properties between feeding areas and non-feeding areas

5.5.2.1 Food quantity

Seagrass meadow structure

The total shoot density recorded in this study (1912.74 ± 692.78 shoots m^{-2}) was consistent with the result obtained in Pulau Tinggi in 2010 (1869.70 ± 936.77 shoots m^{-2} , cf. Ooi et al., 2011b) (**Table 5.13**). The total biomass of seagrass recorded in this study (48.66 ± 53.17 g DW m^{-2}) was similar to the result obtained in the same study site in 2005 (57.56 ± 47.23 g DW m^{-2} , cf. Affendi et al., 2005), but much higher than the results in 2007 (7.39 ± 9.65 g DW m^{-2} , cf. Ooi et al., 2008). Meanwhile, the total biomass of seagrass was approximately half of the values determined for the meadow in Pulau Tinggi in 2010 (92.38 ± 209.58 g DW m^{-2} , cf. Ooi et al., 2011b). While these limited information were unable to provide further deduction on the trends or changes in the meadow structure over time and space, it seems that seagrass biomass was highly variable. This indicates

that seagrasses in the Sibutu-Tinggi Archipelago were distributed with high spatial heterogeneity of vegetation across the landscape with a distance of approximately 8 km between Pulau Tinggi and Pulau Sibutu Besar.

The results of this study support previous reports on the species diversity of seagrass in the meadows of the Sibutu-Tinggi Archipelago, however the seagrass community structure appeared to have shifted. Four species of seagrass were well represented in the meadows and occurred in mixed stands. The biomass of *H. uninervis* (31.49 ± 47.54 g DW m⁻²) was the greatest among all species, similar to the findings of Affendi et al. (2005) and Ooi et al. (2008), followed by *H. ovalis* (12.63 ± 10.54 g DW m⁻²), *C. serrulata* (3.51 ± 7.27 g DW m⁻²) and *S. isoetifolium* (1.75 ± 7.01 g DW m⁻²). Subsequently Affendi et al. (2005) reported that the biomass of *C. serrulata* (27.56 ± 28.43 g DW m⁻²) was higher than that of *H. ovalis* (7.46 ± 7.50 g DW m⁻²), and Ooi et al. (2008) reported that the biomass of *C. serrulata* (5.39 ± 5.30 g DW m⁻²) and *S. isoetifolium* (7.16 ± 9.49 g DW m⁻²) were higher than *H. ovalis* (3.21 ± 3.47 g DW m⁻²). This indicates that the present meadow composition might have shifted to having greater abundance of colonising species (*H. ovalis* and *H. uninervis*) rather than the opportunistic species (*C. serrulata* and *S. isoetifolium*) that dominated the meadows a decade ago.

Compared to the meadows utilised by dugongs across their range, the mean total shoot density of seagrass recorded in this study (1912.74 ± 692.78 shoots m⁻²) was similar to other meadows in the tropics, i.e., Andaman and Nicobar Islands (mean 2442.45 shoots m⁻², range 1333.33 – 3781.25 m⁻², cf. D'Souza et al., 2015) and Marsa Alam, Egypt (median 2585 shoots m⁻², cf. (Nasr et al., 2019), but lower than the meadow in subtropical Moreton Bay, Australia (mean 3926.62 shoots m⁻², range 319 – 8953 shoots m⁻², cf. Preen, 1992) (**Table 5.13**). In terms of total biomass, the mean value recorded in this study (48.66 ± 53.17 g DW m⁻²) was similar with Talibong Island, Thailand ($40.9 \pm 17.4 - 49.0 \pm 15.5$ g DW m⁻², cf. Nakaoka et al., 2002), but more than 17 times higher than Alor

Island, Indonesia (2.77 g DW m⁻², cf. WWF-Indonesia, 2006). When compared to subtropical meadows, however, mean biomass was lower than in Moreton Bay, Australia (163.64 g DW m⁻², range 14.27 - 349.45 g DW m⁻², cf. Preen, 1992) and Shark Bay, Australia (59.2 ± 3.81 [SE] g DW m⁻²). Most of the other meadows utilised by dugongs were similar to this study, in that they were dominated by *H. ovalis* and/or *H. uninervis*.

Quantity variations within community level and implications to dugong feeding

The total shoot density and aboveground biomass of seagrass in the dugong feeding areas were significantly higher (25% - 34%) than in the non-feeding areas, and the ratios of AG:BG biomass were also significantly higher in the feeding areas. These variations indicated that dugong feeding more likely occurred in areas with high abundance of seagrass, particularly in meadows with plenty of leaves and shoots. Shoot density, aboveground biomass and ratios of AG:BG biomass are all parameters that show the quantity of standing crop, which allow foragers to easily locate patches with plenty of food rewards from a distance (Roguet et al., 1998; Gross et al., 1995). Sheppard et al. (2006) suggested that dugongs possess spatial memory that remember locations with their relative availability and quality of food, and dugongs may periodically visit specific locations with quality food resources repeatedly to monitor the quantity and quality of the food as a way to cope with the heterogeneity of seagrass meadows. My findings suggest that food quantity, i.e., aboveground biomass and density, which can be detected by visual senses, may play an important role as the reference point for dugongs to distinguish the amounts of food found at various locations during each visit to a foraging patch.

The belowground biomass which commonly makes up most of the total plant biomass, was not significantly higher in the feeding areas when compared to the non-feeding areas. This emphasised that dugong feeding was less influenced by the quantity of roots and

rhizomes that lie below the substrate. This finding is in contrary with the study of de Iongh et al. (1995) in East Ambon, Indonesia, which suggested that dugongs prefer grazing in sparse seagrass meadows with low aboveground biomass and high belowground biomass of *H. uninervis*. However, it is worth mentioning that the ratios of AG:BG biomass that are based on *H. uninervis* alone in that study (0.05 – 0.45) are lower than the mean ratios of AG:BG biomass of all species in this study (0.85 in feeding areas and 0.61 in non-feeding areas), which means that the meadows sampled in de Iongh et al. (1995) were generally sparse in terms of aboveground component thus the dugongs in that site might not have had the opportunity to preferentially select dense meadows for feeding. Therefore, the hypothesis proposed by de Iongh et al. (1995) might be applied to low ratio of AG:BG biomass meadows, but not meadows with high ratio of AG:BG biomass where dugongs can forage for high quantity of shoots and leaves.

Quantity variations within species level and implications to dugong feeding

The most notable difference between two sites was that *H. ovalis* was more abundant in the feeding areas (1.5 times more density) than the non-feeding areas, while *C. serrulata* was more abundant in the non-feeding areas (>2 times more density) than in the feeding areas. Nakanishi et al. (2006) observed that dugongs concentrate feeding on the *H. ovalis* community but not on the *C. serrulata* community in Talibong Island, Thailand, even though both species formed their own monospecific patches and were equally dominant on the whole meadow. Therefore, the results here suggest that feeding area selection by dugongs is likely driven by high availability of *H. ovalis* in the meadows, and are less drawn towards areas with high availability of *C. serrulata*.

Nonetheless, *H. ovalis* and *H. uninervis* were the most abundant species in the dugong feeding areas of the Sibutu Archipelago, with approximately 20 times more biomass

than *C. serrulata* and *S. isoetifolium*. These results agree with previous studies that dugongs prefer feeding on *H. ovalis* and *H. uninervis* (Preen, 1992; Mukai et al., 1999; Sheppard et al., 2008; Adulyanukosol, 2010). The nutritional benefits of *H. ovalis* and *H. uninervis*, i.e., high nitrogen and digestibility, coupled with their widespread distribution in the meadows likely make them the most preferred species, while the limited availability and lower quality benefits of *C. serrulata* (more fibrous) and *S. isoetifolium* (less starch) likely make them less favoured by the dugongs. The nutritional quality of each species will be discussed in sub-section 5.5.2.2.

Despite the relatively high abundance of *H. uninervis* in the Sibutu-Tinggi meadows, dugongs seemed to primarily feed in areas with higher abundance of *H. ovalis*. This was shown by *H. ovalis* having significantly higher shoot density than *H. uninervis* in feeding areas, whereas the difference was not distinct in the non-feeding areas. Moreover, the aboveground biomass of *H. ovalis*, which was significantly higher than *H. uninervis* in the feeding areas, was lower than *H. uninervis* in the non-feeding areas. *Halodule uninervis* is generally a larger plant than *H. ovalis* as it has higher total plant biomass, which provides greater food biomass per bite to a herbivore. Despite this, my results showed that the dugongs have a strong feeding preference towards the smallest, highly digestible species of seagrass in the meadows, which is *H. ovalis* (Aragones, 1996).

The meadow composition in the Sibutu-Tinggi Archipelago, which were maintained by pioneer/colonising species of seagrasses, namely *H. ovalis* and *H. uninervis*, might be an outcome of “cultivation grazing” by dugongs (Preen, 1995b). These species grow and recover from grazing faster than the other opportunistic species such as *C. serrulata* and *S. isoetifolium*, with a biomass turnover rate of <10 days to two months (Supanwanid, 1996; Nakaoka & Aioi, 1999). Several grazing experiments have shown that the shoot density and biomass of *H. ovalis* and *H. uninervis* in natural and simulated grazed areas are significantly higher than in ungrazed areas after a 4 – 10 months duration (Preen,

1995b; Aragoes & Marsh, 2000). Although the brief timeline and limitations of this study rendered me unable to confirm whether the Sibutinggi meadow compositions were driven by cultivation grazing by the dugongs, the results of this study showed that it was likely that the animals facilitate a positive feedback in terms of quantity at the very least, which in turn provides them the benefit of continuous food supply.

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Table 5.13 Summary of mean shoot density and biomass (\pm SD/SE) of seagrass community across dugong habitats. Table continued on next page.

Species/ Location	Meadow characteristic	Shoot density (m ⁻²)	Aboveground biomass (g DW m ⁻²)	Belowground biomass (g DW m ⁻²)	Total Biomass (g DW m ⁻²)	Reference
Community level						
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	1912.74 \pm 692.78	16.43 \pm 16.19	32.24 \pm 41.53	48.66 \pm 53.17	This study
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI, HP, CR)	-	-	-	57.56 \pm 47.23	Affendi et al. (2005)
Pulau Tinggi, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	1869.70 \pm 936.77	45.72 \pm 145.07	46.65 \pm 68.11	7.39 \pm 9.65	Ooi et al. (2008)
Andaman and Nicobar Islands, India	Subtidal, mono (HO) and mixed (HO, HU)	2442.25	-	-	92.38 \pm 209.58	Ooi et al. (2011)
Moreton Bay, Australia	Subtidal, mixed (HO, HU, HS, ZC, SI)	3926.62	46.58	117.06	-	D'Souza et al. (2012)
Shark Bay, Australia	Subtidal, mono (HU)	-	10.4 \pm 0.8 [§]	48.8 \pm 3.26 [§]	163.64	Preen (1992)
Marsa Alam, Egypt	Subtidal, mixed (HO, HU, CR, HST)	2585	-	-	59.2 \pm 3.81 [§]	Masini et al. (2001)
					-	Nasr et al. (2019)
Species level						
<i>Halophila ovalis</i>						
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	1168.81 \pm 639.26	T: 7.06 \pm 7.13 FA: 6.75 \pm 4.70 NFA: 4.09 \pm 2.41	T: 5.58 \pm 4.06 FA: 6.75 \pm 4.70 NFA: 4.09 \pm 2.41	T: 12.63 \pm 10.54 FA: 16.48 \pm 12.32 NFA: 7.77 \pm 4.36	This study
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI, HP, CR)	-	-	-	7.46 \pm 7.50	Affendi et al. (2005)
Pulau Tinggi, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	1454.57 \pm 795.47	11.41 \pm 8.90	14.11 \pm 10.73	3.21 \pm 3.47	Ooi et al. (2008)
Koh Bae Na, HCMNP, Thailand	Intertidal, mixed (HO, CR, CS, EA)	-	FA: ~9 NFA: ~40	FA: ~10 NFA: ~32	25.53 \pm 15.53	Ooi et al. (2011)
Koh Bae Na, HCMNP, Thailand	Intertidal, mono (HO)	-	-	-	FA: ~19 NFA: ~72	Nakaoka & Aioi (1999)
Laem Yong Lam, HCMNP, Thailand	Intertidal, mono (HO)	-	-	-	FA: 14.8 \pm 8.4 NFA: 432.7 \pm 19.9	Nakaoka et al. (2002)
Laem Yong Lam, HCMNP, Thailand	Intertidal, mixed (HO, TH)	-	-	-	FA: 161.7 \pm 105.3 NFA: 981.9 \pm 195.3	Nakaoka et al. (2002)
Laem Yong Lam, HCMNP, Thailand	Intertidal, mixed (HO, TH)	-	-	-	FA: 304.7 \pm 127.0 NFA: 843.4 \pm 159.2	Nakaoka et al. (2002)

(-): no data. (*): standard error. ([§]) *Cymodocea* spp.. Abbreviations: HCMNP = Haad Chao Mai National Park; mixed = mixed species meadow; mono = monospecific meadow; FA = feeding areas; NFA = non-feeding areas; T = combination of feeding areas and non-feeding areas; HO = *Halophila ovalis*; HU = *Halodule uninervis*; CS = *Cymodocea serrulata*; SI = *Syringodium isoetifolium*; HP = *Halodule pinifolia*; TH = *Thalassia hemprichii*; CR = *Cymodocea rotundata*; EA = *Enhalus acoroides*; ZC = *Zostera capricorni*, HST = *Halophila stipulacea*.

Table 5.13 (Cont.)... Summary of mean shoot density and biomass (\pm SD/SE) of seagrass community across dugong habitats. Table continued on next page.

Species/ Location	Meadow characteristic	Shoot density (m ⁻²)	Aboveground biomass (g DW m ⁻²)	Belowground biomass (g DW m ⁻²)	Total Biomass (g DW m ⁻²)	Reference
Talibong Island, Thailand	Intertidal, mixed (HO, CS, HP)	-	-	-	61.0 – 79.5	Amamoto et al. (2009a)
Talibong Island, Thailand	Intertidal, mixed (HO, CR, CS, HP, HU)	-	-	-	18.3 (\pm 4.6) – 23.0 (\pm 10.3)	Amamoto et al. (2009b)
Alor Island, Indonesia	Subtidal, mixed (EA, TH, HO, CS, CR, HU, SI)	565 - 1082	-	-	-	WWF-Indonesia (2016)
Double Island, Australia	Intertidal, mixed (HU, HO, SI, TH, Cymodocea spp.)	-	-	-	0.12 \pm 0.02	Tol et al. (2016)
Magnetic Island, Australia	Intertidal, mixed (HU, HO, TH, Cymodocea spp.)	-	-	-	0.80 \pm 0.01	Tol et al. (2016)
Cape Pallarenda, Australia	Intertidal, mixed (HU, HO)	-	-	-	0.64 \pm 0.02	Tol et al. (2016)
Moreton Bay, Australia	Subtidal, mixed (HO, HU, HS, ZC, SI)	491	6.08	8.94	15.02	Preen (1992)
<i>Halodule uninervis</i>						
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	650.56 \pm 571.01	T: 7.27 \pm 8.52 FA: 7.94 \pm 7.85 NFA: 6.42 \pm 9.37	T: 24.22 \pm 40.46 FA: 29.27 \pm 48.96 NFA: 17.82 \pm 25.44	T: 31.49 \pm 47.54 FA: 37.21 \pm 55.58 NFA: 24.24 \pm 34.38	This study
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI, HP, CR)	-	-	-	29.79 \pm 26.22	Affendi et al. (2005)
Pulau Tinggi, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	861.67 \pm 371.91	11.25 \pm 5.78	31.67 \pm 19.16	11.67 \pm 12.97	Ooi et al. (2008)
Talibong Island, Thailand	Intertidal, mixed (HO, CR, CS, HP, HU)	-	-	-	42.91 \pm 28.56	Ooi et al. (2011)
East Ambon Island, Indonesia	Intertidal, mono (HU)	-	8.9 (\pm 1.5) – 20.9 (\pm 3.9)	58.8 (\pm 14.2) – 147.9 (\pm 29.2)	1.6 \pm 2.5	Amamoto et al. (2009b)
Double Island, Australia	Intertidal, mixed (HU, HO, SI, TH, Cymodocea spp.)	-	-	-	67.7 – 168.8	de Iongh et al. (1995)
Cape Pallarenda, Australia	Intertidal, mixed (HU, HO)	-	-	-	0.59 \pm 0.04	Tol et al. (2016)
Magnetic Island, Australia	Intertidal, mixed (HU, HO, TH, Cymodocea spp.)	-	-	-	1.30 \pm 0.09	Tol et al. (2016)
					0.36 \pm 0.09	Tol et al. (2016)

(-): no data. (*): standard error. (*) *Cymodocea* spp.. Abbreviations: HCMNP = Haad Chao Mai National Park; mixed = mixed species meadow; mono = monospecific meadow; FA = feeding areas; NFA = non-feeding areas; T = combination of feeding areas and non-feeding areas; HO = *Halophila ovalis*; HU = *Halodule uninervis*; CS = *Cymodocea serrulata*; SI = *Syringodium isoetifolium*; HP = *Halodule pinifolia*; TH = *Thalassia hemprichii*; CR = *Cymodocea rotundata*; EA = *Enhalus acoroides*; ZC = *Zostera capricorni*, HST = *Halophila stipulacea*.

Table 5.13 (Cont.)... Summary of mean shoot density and biomass (\pm SD/SE) of seagrass community across dugong habitats.

Species/ Location	Meadow characteristic	Shoot density (m ⁻²)	Aboveground biomass (g DW m ⁻²)	Belowground biomass (g DW m ⁻²)	Total Biomass (g DW m ⁻²)	Reference
Shark Bay, Australia	Subtidal, mono (HU)	-	FA: 9.2 \pm 1.8* NFA: 22.4 \pm 2.4*	FA: 80.8 \pm 7.5* NFA: 143.7 \pm 19.5*	FA: 90* NFA: 166.1*	Masini et al. (2001)
Moreton Bay, Australia	Subtidal, mixed (HO, HU, HS, ZC, SI)	903.88	4.44	42.6	47.03	Preen (1992)
<i>Cymodocea serrulata</i>						
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	50.05 \pm 79.53	T: 1.49 \pm 3.82 FA: 0.71 \pm 1.54 NFA: 2.49 \pm 5.38	T: 2.05 \pm 3.76 FA: 1.15 \pm 2.56 NFA: 3.16 \pm 4.67	T: 3.51 \pm 7.27 FA: 1.83 \pm 3.90 NFA: 5.65 \pm 9.70	This study
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI, HP, CR)	-	-	-	27.56 \pm 28.43	Affendi et al. (2005)
Pulau Tinggi, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	95.50 \pm 100.70	2.98 \pm 5.00	10.50 \pm 16.89	5.39 \pm 5.30	Ooi et al. (2008)
Talibong Island, Thailand	Intertidal, mixed (HO, CS, HP)	-	-	-	13.47 \pm 9.52	Ooi et al. (2011)
Talibong Island, Thailand	Intertidal, mixed (HO, CR, CS, HP, HU)	-	-	-	13.0 – 13.1	Amamoto et al. (2009a)
Double Island, Australia	Intertidal, mixed (HU, HO, SI, TH, <i>Cymodocea</i> spp.)	-	-	-	21.0 \pm 18.8	Amamoto et al. (2009b)
Magnetic Island, Australia	Intertidal, mixed (HU, HO, TH, <i>Cymodocea</i> spp.)	-	-	-	0.24 \pm 0.05 [‡]	Tol et al. (2016)
<i>Syringodium isoetifolium</i>						
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	43.33 \pm 112.09	T: 0.91 \pm 4.61 FA: 0.22 \pm 0.62 NFA: 1.79 \pm 6.87	T: 0.83 \pm 2.61 FA: 0.45 \pm 1.62 NFA: 1.32 \pm 3.45	T: 1.75 \pm 7.01 FA: 0.66 \pm 2.22 NFA: 3.12 \pm 10.19	This study
Sibu-Tinggi Archipelago, Malaysia	Subtidal, mixed (HO, HU, CS, SI, HP, CR)	-	-	-	5.48 \pm 0.01	Affendi et al. (2005)
Pulau Tinggi, Malaysia	Subtidal, mixed (HO, HU, CS, SI)	439.30 \pm 291.10	4.46 \pm 3.77	12.83 \pm 9.45	7.16 \pm 9.49	Ooi et al. (2008)
Double Island, Australia	Intertidal, mixed (HU, HO, SI, TH, <i>Cymodocea</i> spp.)	-	-	-	17.28 \pm 5.19	Ooi et al. (2011)
Moreton Bay, Australia	Subtidal, mixed (HO, HU, HS, ZC, SI)	5344.67	101.74	195.8	0.06 \pm 0.02	Tol et al. (2016)
					297.54	Preen (1992)

(-): no data. (*): standard error. (‡) *Cymodocea* spp.. Abbreviations: HCMNP = Haad Chao Mai National Park; mixed = mixed species meadow; mono = monospecific meadow; FA = feeding areas; NFA = non-feeding areas; T = combination of feeding areas and non-feeding areas; HO = *Halophila ovalis*; HU = *Halodule uninervis*; CS = *Cymodocea serrulata*; SI = *Syringodium isoetifolium*; HP = *Halodule pinifolia*; TH = *Thalassia hemprichii*; CR = *Cymodocea rotundata*; EA = *Enhalus acoroides*; ZC = *Zostera capricorni*, HST = *Halophila stipulacea*.

5.5.2.2 Food quality

Seagrass nutritional profile

The nutritional profiles of the four tropical seagrass species studied here are generally within the range of information reported in other seagrass nutrient studies, except for phosphorus. However, the nutritional profile is not clear for total dietary fibre as there are not many seagrass nutrient studies that examined the parameter. For indicators of seagrass health, the average C value in the leaves ($33.09 \pm 0.56\%$) was consistent with the average values reported for tropical seagrasses ($33.6 \pm 0.31\%$; cf. Duarte, 1990; 30.5%, cf. Yamamuro & Chirapat, 2005). The average N value in the leaves ($1.22 \pm 0.13\%$) of the four seagrass species was consistent with those reported by Lawler et al. (2006), i.e., ~1.3%, but lower than those reported for tropical seagrasses elsewhere (1.5 – 1.6%, cf. Birch, 1975; 1.82%, cf. Duarte, 1990; 1.7 – 2.3%, cf. Amamoto et al., 2009b). It was lower than 1.8%, the indicative value of N-limitation in seagrass (Duarte, 1990). The relatively lower C:N ratios observed in the aboveground component (79.5 ± 12.6) compared to the belowground component (168.6 ± 28.6) in this study supported the overall notion that seagrass leaves contain higher nitrogen concentration than roots and rhizomes, as the leaves of actively growing seagrasses are adapted to take up both ammonium and nitrate from the water column, rather than just ammonium from the sediment porewater by roots (Stapel et al., 1996; Vonk et al., 2008).

The average whole-plant P value ($0.022 \pm 0.001\%$) in this study was considerably lower compared to studies elsewhere ($0.23 \pm 0.011\%$, cf. Duarte, 1990; $0.19 \pm 0.04\%$ SD, cf. Serusi, 2010), and also lower than 0.2%, which is the nutrient-limiting threshold (Duarte, 1990). This could be an indication that P might be limited in the study area. However, it is not confirmed whether P was indeed limited in the study site or whether the concentrations of P were lost during the interval between field harvesting and sample processing because the water sample was not collected in this study to determine the

concentration of P. The large range and standard errors for the seagrass health parameters (i.e., carbon, nitrogen and phosphorus) suggest seasonal variations of nutrient availability in the subtidal environment; hence, a nutrient-limiting scenario could have been present during some part of the sampling period. Nonetheless, previous studies have suggested that faster-growing seagrass species like *H. ovalis* and *H. uninervis* still thrive in N- and/or P-limited environments (Kilminster et al., 2006; Burkholder et al., 2013).

The average 1.53% (± 0.23 SE) whole-plant starch concentration of *H. ovalis* in this study was higher than the majority of reported values in the tropical and subtropical regions of Australia ($\sim 0.5 - 1.0\%$, cf. Aragonés et al., 2006; $0.9 - 1.0\%$, cf. Lawler et al., 2006; $0.75 \pm 0.24\%$, cf. Sheppard et al., 2007), but lower than the $2.76 \pm 0.12\%$ value reported by Sheppard et al. (2008) in Torres Strait. The average 1.74% (± 0.31 SE) whole-plant starch concentration of *H. uninervis* was also many times lower than the reported values in the subtropical Australian region ($\sim 5.5 - 6.5\%$, cf. Aragonés et al., 2006; averaged 7.5%, cf. Lawler et al., 2006; $6.42 \pm 0.50\%$, cf. Sheppard et al., 2007; $6.0 - 7.7\%$, cf. Sheppard et al., 2010). Previous findings have showed that seagrass rhizomes serve as a principal non-soluble carbohydrate storage (Birch, 1975; Lanyon, 1991; Mellors, 2003; Aragonés et al., 2006; Sheppard et al., 2007); this was similarly demonstrated for *H. uninervis* in this study.

The 8.29% (± 0.66 SE) whole-plant total dietary fibre (TDF) concentration for all four species in this study was higher than the TDF concentration of *C. serrulata* + *S. isoetifolium* + *H. ovalis* in the Gulf of Mannar, India ($3.7 \pm 0.1\%$, cf. Jeevitha et al., 2013). In the Australian region, seagrasses have been found to have increasing fibre (lignin/neutral detergent fibre) concentrations with increasing latitude, which may reflect environmental factors specific to the regions (Sheppard et al., 2008, also see values recorded by Aragonés et al., 2006 and Sheppard et al., 2007). My results were not able to confirm this pattern as different fibre parameters were used from those other studies. Yet,

it has been suggested that samples collected from different tidal zones may have different fibre concentrations; seagrasses that grow in the subtidal zone may utilise their energy in other physiological performances to compensate for their lower photosynthesis rate in light-limited depths instead of investing more on fibre tissues, while the reduced wave action in subtidal areas may release the plants from accumulating structural component as compared to seagrasses that grow in the intertidal zone (Sheppard et al., 2008). Hence, the TDF values recorded in this study could be lower than that of other studies in intertidal seagrass samples.

Nutritional variations within community and species levels and implications to dugong feeding

Statistical comparisons showed higher nitrogen, starch and fibre concentrations, and lower carbon and C:N ratio in the feeding areas as compared to the non-feeding areas, indicating that dugongs might have selected patches based on the above parameters relative to availability. The phosphorus concentration, on the other hand, was not a potential parameter in driving food selection of dugongs due to lack of significant difference. Dugongs are believed to select food resources in response to the quality of their food resources to optimise intakes across heterogenous pastures, by consuming food with high nitrogen, starch and digestibility (Heinsohn & Birch, 1972; Marsh et al., 1982; Lanyon et al., 1989; Aragonés et al., 2006; Sheppard et al., 2007, 2008). My results support the hypothesis that nitrogen, starch and fibre constitute the major quality criteria for food selection by dugongs.

The seagrasses in feeding areas had 1.6 times higher mean nitrogen content than in non-feeding areas. Nitrogen has been suggested as a main limiting nutrient in the dugong's diet as a result of low nitrogen content that are present in the seagrass plants

(generally 1 – 4% of the total nutrients) as well as the physiological constraints of hindgut fermenters (Lanyon, 1991; Duarte, 1992). Hence it is necessary for dugongs to maximise their nitrogen intake by feeding on seagrass with relatively higher nitrogen content, an observation which is consistent with my results. The significant difference in nitrogen levels between the feeding and non-feeding areas indicated that (1) dugongs had a preference towards higher nitrogen foods, and/or (2) nitrogen content of seagrass was increased after intensive grazing. Sheppard et al. (2007) has assumed, based on the nutritional requirement of other mammalian grazers, that food plant with nitrogen concentration below 1% threshold is considered inadequate nutrition and subsequently optimal feeders should selectively graze on high nitrogen food. In Hervey Bay, Australia, the mean nitrogen levels of both prevalent species, *H. ovalis* and *H. uninervis*, were 1.21% and 1.28% respectively, and dugongs were found consistently associated with seagrass patches considered as having high nitrogen content when those patches were available during high tide (Sheppard et al., 2010). The current study demonstrated similar results in which dugong feeding areas were associated with relatively high nitrogen in the seagrass, and the mean nitrogen values recorded in the leaves of *H. ovalis* and *H. uninervis* (1.18% and 1.35%, respectively) were close to those of Sheppard et al. (2010). Thus the first speculation is supported. On the other hand, previous research has demonstrated that nitrogen concentration was significantly elevated following grazing even after a year (Aragones et al., 2006; Vonk et al., 2008). In this study, dugongs feeding was associated with seagrass with lower C:N ratios, indicating that feeding areas had younger, more nutritious seagrass plants. The improvement in nutritional quality of food plants could be due to the effect of promotion of regrowth in particular areas by intensive grazing, as proposed by Preen (1992). In **Chapter 4**, dugongs were shown to consistently feed in an intensive manner (indicated by feeding hotspots) in some parts of the meadows

with high abundance of seagrass. Taken together, I suggest that cultivation grazing might be at play in this study area.

The starch content was four times higher in the seagrasses that were collected from the feeding areas as compared to the non-feeding areas. Several studies have claimed that dugongs prefer foods rich in starch as dugongs actively graze on the rhizome component of *H. uninervis* for its starch reserves which serve as a main source of energy (Birch, 1975; Masini, 1983; Lanyon, 1991; Mellors, 2003; Sheppard et al., 2007). My results support the view that dugong feeding might be influenced by starch content of the seagrass, however, there wasn't strong evidence that dugongs preferentially selected *H. uninervis* for their rhizomes in this area. This is because the belowground component of *H. uninervis* only possessed a slightly higher starch concentration (1.1 times) than the aboveground component in this study. In contrast, the starch in the belowground component was much higher, by more than eight times, than the aboveground component of *H. uninervis* in Hervey Bay, Australia (Sheppard et al., 2007). Meanwhile, the relatively higher starch concentration of *H. ovalis* in this study compared to the values reported from the Australian regions (Sheppard et al., 2007, 2008) might contribute to the reasons for why *H. ovalis* was mainly selected by dugongs in the study site. However, it is difficult to draw a firm conclusion because this study used a different methodology to quantify starch content.

Seagrasses in the feeding areas possessed significantly higher fibre content than in the non-feeding areas, mostly owing to the fibre contributions from *H. ovalis*. The reason that fibre concentration of *H. ovalis* was higher in the feeding areas is not clear, however it is suspected to be a physiological adaptation of the species in the non-feeding areas whereby the plants are less invested on building structural tissues. The premise of this speculation comes from the result of the sediment size analysis, whereby the percentage of silt-clay particles was shown to be significantly higher in the non-feeding areas (see sub-section

5.4.2.3), the circumstance of which might have created a light-limited environmental condition. If this was the case, *H. ovalis* that grows in the non-feeding areas might have utilised more of their energy for compensating the low photosynthesis rate rather than accumulating fibre, as suggested by Sheppard et al. (2008). Aragonés et al. (2006) observed an increase in the leaves and whole-plant fibres of *H. ovalis* under simulated grazing, yet this observation requires further confirmation as there were limited studies that show similar pattern to that study. In general, the range of fibre concentration for the four species of seagrass in this study, with some exceptions on *C. serrulata*, were considered relatively lower compared to other seagrass species such as *H. spinulosa*, *E. acoroides* and *Zostera capricorni* which are more seldomly selected by dugongs (Lanyon, 1991; Yamamuro & Chirapat, 2005; Sheppard et al., 2007).

In contrast, whole-plant carbon and C:N ratios were significantly lower in the feeding areas compared to the non-feeding areas, could be an indication of the plant's response to light reduction in the environment (McMahon et al., 2013). The causes of possible low light condition in the feeding areas were not known as light was not measured in this study, but physiological stress under a prolonged period of light reduction would affect the leaf growth and morphology, and also the species diversity of the meadow.

Nutritional variations between species and implications to dugong feeding

The four species of seagrasses (whole plant) were significantly different between each other for all quality variables except nitrogen, indicating that feeding preferences of dugongs in terms of specific seagrass species were less influenced by their nitrogen content. This finding is similar with the results of Sheppard et al. (2008) where they detected significant differences in terms of starch and soluble carbohydrates, organic matter, fibre and lignin among the four dominant tropical species, *H. ovalis*, *H. spinulosa*,

C. serrulata and *S. isoetifolium*, except for nitrogen content. However, dugongs were frequently observed to selectively feed on *H. ovalis* and *H. uninervis* among the other tropical seagrass species even though each species was 'equally' nutritious for dugongs in terms of nitrogen content, as shown in this study and Sheppard et al. (2008). The argument is further supported by observations that dugongs did not selectively feed on seagrass species with high nitrogen (i.e., *H. ovalis* and *H. uninervis*) in tropical north Queensland, Australia, but fed more on *T. hemprichii*, which has lower nitrogen content (Tol et al., 2016). These potentially show that dugongs in tropics might not be selecting seagrass species based on their nitrogen content alone.

Halodule uninervis was considered as the most nutritious seagrass species for dugongs in the meadows of the Sibutu Archipelago, attributing to its greater starch content (average $1.74 \pm 0.31\%$) compared to *H. ovalis* (average $1.53 \pm 0.23\%$). Although starch data for *C. serrulata* and *S. isoetifolium* are lacking in this study, others have shown that starch content in these species are lower than in *H. uninervis* and *H. ovalis* (Sheppard et al., 2007; 2008), while Lanyon (1991) ranked the soluble carbohydrate content in the belowground component of *C. serrulata* to be lower than *H. uninervis* but higher than *H. ovalis*.

Halophila ovalis had the lowest fibre levels among the four encountered species, rendering it as the most digestible food species for dugongs. The results here agreed with Sheppard et al. (2007) in demonstrating that *H. uninervis* has a higher fibre content than *H. ovalis*, and also in agreement with Sheppard et al. (2008) in demonstrating that *C. serrulata* has a higher fibre content than *H. ovalis*, followed by *S. isoetifolium*. Despite the variation, Sheppard et al. (2007) showed similar in vitro dry matter digestibility (IVDMD) for *H. ovalis* and *H. uninervis*, indicating both species are equally digestible for dugongs. If digestibility is an important driving factor, then this difference in fibre may be sufficient to support the finding of this study which is that dugong feeding was

more associated to *H. ovalis* than *H. uninervis*. Nonetheless, the results confirmed previous findings (Preen, 1992; Aragones, 1996; Sheppard et al., 2008) that dugongs may be selecting *H. uninervis* and *H. ovalis* over other seagrasses due to their overall nutritional superiority (high starch and low fibre content).

The significant variation in fibre levels among the four seagrass species only occurred in the non-feeding areas but not in the feeding areas, suggesting that different levels of herbivory intensity occurred in both areas. The fibre content among seagrass species is not always consistent and presumably depends on the age of the plants that have been sampled (Marsh et al., 2011). Therefore, in the feeding areas, the lack of interspecies difference in fibre levels is probably because there were more young shoots and leaves of each species that grew after grazing, compared to the non-feeding areas in which dugong grazing was absent.

The variation in carbon content was only significant in the non-feeding areas. Among all species, *H. ovalis* had the least carbon content which was consistent with the observations of Yamamuro and Chirapat (2005). The larger difference in the non-feeding areas was attributed to greater carbon content that were found in the *H. uninervis* in those areas. Meanwhile, the interspecies differences for C:N ratios were only significant in the feeding areas, particularly between *H. ovalis* and *H. uninervis*, as well as *H. ovalis* and *C. serrulata*, which could be due to the growth of more young shoots and leaves of *H. ovalis* and *H. uninervis* after being grazed by dugongs. The variation in terms of carbon and C:N ratios in feeding areas and non-feeding areas suggests that herbivory may induce different effects on the production of young leaves and in turn the elemental composition in different seagrass species.

The phosphorus levels were significantly different among species in both feeding areas and non-feeding areas. *Halophila ovalis* had considerably more phosphorus content than the other three species, which may reflect high phosphorus-uptake efficiency of this

species. The *H. ovalis* plants which occur in the intertidal meadow of Merambong Shoal, Malaysia, also recorded higher phosphorus levels compared to *H. uninervis* and *H. spinulosa* (Wan Hazma et al., 2015). It has been suggested that the success of cultivation grazing depends on whether phosphorus is sufficient for the seagrass (Holzer & McGlathery, 2016). Consequently, *H. ovalis* in the Sibutinggi meadows, which had high phosphorus resources, is likely to respond positively towards repeated grazing by dugongs.

5.5.3 Food quantity vs. food quality vs. sediment size

Of all variables examined, food quantity and particle size of sediment significantly influenced the feeding site selection of dugongs. In terms of food quantity, the results indicated that only the leaf and shoot abundance of *H. ovalis*, i.e., aboveground biomass and ratio of AG:BG biomass, had positive relationships with dugong feeding. This finding agrees with Tol et al. (2016) who found that seagrass biomass primarily affects the feeding site use of dugongs in the tropical Australian region, and that nutritional content (i.e., nitrogen) of seagrass played a lesser role in food selection. More abundance of aboveground biomass (higher fraction of leaves and shoots) of seagrass means that a greater amount of food per bite is available, which in turn provides bulk energy benefit for the dugongs. However, this factor was not prominent in other species of seagrass in the meadows, including *H. uninervis* which is also commonly known as the other preferred food of dugongs (Heinsohn & Birch, 1972; Johnstone & Hudson, 1981). This indicates that there was a strong preference by dugongs feeding on dense *H. ovalis* complex patches in my study site. Dugongs in other tropical and subtropical regions have been observed to demonstrate selective feeding behaviour towards the *H. ovalis* community (Preen, 1992; de Iongh, 1996; Mukai et al., 1999; Zulkifli Poh, 2009; Adulyanukosol, 2010; D'Souza et al., 2015) and this model strongly supports the theory.

Sediment size, on the other hand, affected the feeding preference of dugongs in terms of the proportion of silt-clay in the sediment. The effect of sediment size in influencing feeding site selection is not as clear as how it affects the feeding method of dugongs. Preen (1992) suggested that dugongs may have to constrict their rostral disc in a sandy substrate to push through easier compared to a muddy substrate which implied dugongs feed easier in the fine-sediment substrate. However in that study, the particle size of sediment did not appear to affect the dugongs' choice in selecting feeding areas within their range of sediment. It is worth mentioning that both substrates in the feeding areas and non-feeding areas in Moreton Bay, Australia were dominated by sand while silt only constituted less than 1% of the substrata (Preen, 1992). Separately, de Iongh et al. (1995) suggested a preference of dugong feeding on sandy substrate, as their study found most of the feeding trails (64 – 73% of the total number of feeding trails) in sandy sediment and less feeding trails (15 – 31%) in muddy and mixed (sand and mud) sediments. While the hypothesis seems debatable due to the different nature of particle sizes present in the different study areas, my results suggest that there is a potential tendency for dugongs to establish feeding activity in areas with relatively less fine-sediment substrate. Fine sediment particles would be easily disturbed during feeding, creating sediment clouds in the water column which can obscure the dugong's vision to scan for their predators (Wirsing et al., 2007a). Moreover, the poor water clarity caused by the suspended fine sediment might act to limit the growth of seagrass by reducing the amount of light for photosynthesis. The negative effect has been said to be more prominent in small, colonising species such as *H. ovalis* and *H. uninervis*, which are suggested to be less tolerant to prolonged low light conditions (Longstaff & Dennison, 1999; Freeman et al., 2008; Collier et al., 2012). Therefore, the effect of silt-clay component could be indirectly consequential to the dugongs by affecting the density and productivity of the animals' food plants in the meadows.

Together with the study of Tol et al. (2016), the results of this study suggest seagrass biomass as the most influential factor for dugongs to choose their feeding areas. It is known and accepted that dugongs prefer feeding on *H. ovalis* and *H. uninervis*, considering both species' high nitrogen concentrations, which particularly fit the dugong's dietary requirements (Lanyon, 1991; Preen, 1992; Sheppard et al., 2010). This study's results still support the aforementioned theory because the nitrogen levels in the feeding areas were found to be relatively higher, yet the regression models showed higher likelihood for dugongs to feed in denser *H. ovalis* areas. This suggests that feeding patterns of dugongs may be less influenced by the limitation in nitrogen in meadows dominated by seagrass species that are generally rich in nitrogen, but are more affected by the quantity of food resources available, especially that of *H. ovalis*.

5.6 Conclusion

The dugongs in the Sibutu Archipelago potentially fed on all four species of seagrass that were available in the meadows. The quantity and quality of seagrasses varied between the feeding areas and the non-feeding areas at the community and species levels. In terms of food quantity, dugong feeding areas were associated with high shoot density and aboveground biomass of *H. ovalis* and *H. uninervis*, in which those parameters were the ones that made the patches look dense from a visual perspective. This supported the hypothesis that feeding site selections were influenced by food quantity. Dugongs preferred to feed in areas with higher abundance of *H. ovalis* followed by *H. uninervis*, but did not seem to prefer areas with high abundance of *C. serrulata* and *S. isoetifolium*. The GLM showed that the occurrence of dugong feeding was mostly influenced by the aboveground biomass and the ratio of aboveground to belowground biomass of *H. ovalis*, reflecting the importance of food quantity in driving the feeding preferences of dugongs in these subtidal tropical meadows that appear to be dynamic in space and time.

In terms of food quality, dugong feeding areas were occupied by seagrasses with high nitrogen, starch and fibre concentrations, and seagrasses with low carbon and C:N ratios. This supported the hypothesis that feeding site selections were influenced by food quality as well. The high starch and low fibre content of *H. uninervis* and *H. ovalis* make them the most nutritious food species to dugongs within the meadow, in addition to their high nitrogen content, although the latter parameter was not significantly different when compared to *C. serrulata* and *S. isoetifolium*. Despite *H. uninervis* and *H. ovalis* having different fibre concentrations, both species probably have similar digestibility for dugongs, as suggested by Aragonés (1996) and Sheppard et al. (2007, 2008). Hence with meadow composition that mainly consists of *H. ovalis* and *H. uninervis*, seagrass nutritional quality to dugongs can be considered from nitrogen and starch alone. If dugongs were limited by protein and energy sources, the quality ranking from the most to least nutritional food for dugongs in the Sibutu Archipelago was *Halodule uninervis* = *Halophila ovalis* > *Cymodocea serrulata* > *Syringodium isoetifolium* (hierarchy of *C. serrulata* and *S. isoetifolium* was based on nitrogen content alone as their starch content was not determined in this study). If dugongs were also limited by fibre on top of protein and energy sources, the ranking would be *Halophila ovalis* > *Halodule uninervis* > *Cymodocea serrulata* > *Syringodium isoetifolium*.

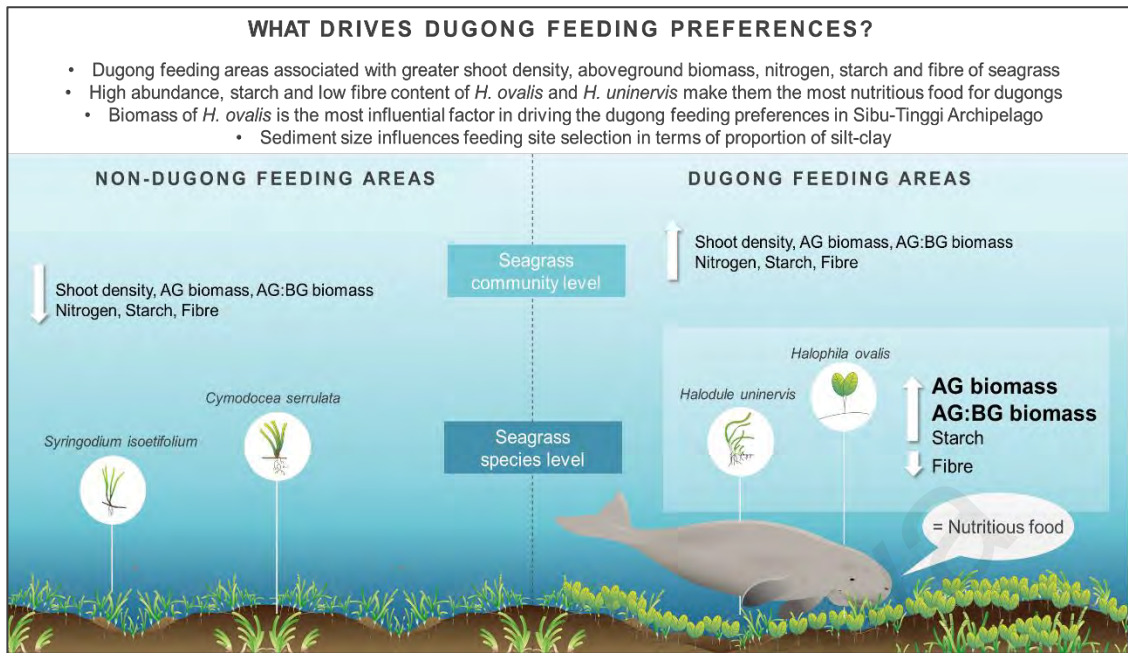


Figure 5.18 Schematic diagram summarising the main factors that drive feeding preferences of dugongs. Images used to create this illustration are attributed to the Dugong and Seagrass Conservation Project – Indonesia

CHAPTER 6: CONCLUSION

Despite their unique life history as the only extant large marine mammalian herbivore in the Family Dugongidae and their capability in ecologically engineering an ecosystem by playing the role of a primary consumer (Bakker et al., 2016; Scott et al., 2018), information about the interactions between dugongs and their food plants, i.e., feeding behaviours and the spatial-temporal relationship with the distributions and characteristics of seagrass communities varies from site to site. Thus, our understanding of dugong feeding preferences remains unresolved. Given the limited information on dugong feeding habitats in Malaysia, this study appears to be the first in-depth study of its kind in the country, investigating the spatial and feeding ecology of the species. This thesis generated scientific knowledge on dugong feeding ecology in three connected levels. First, the distribution of the subtidal seagrass meadow in the Sibul Archipelago, being one of the most significant dugong habitats in Peninsular Malaysia which lacked habitat baseline information, was assessed and mapped. Second, this research characterised the distribution of dugong feeding trails and described spatial feeding patterns of dugongs under three different levels of seagrass cover in the meadows, and identified feeding hotspots and coldspots in the meadow of the Sibul Archipelago. Finally, the thesis suggested potential drivers of dugong feeding preferences and ranked the most influential factors which affect habitat selection of dugongs at the Sibul Archipelago as well as neighbouring Pulau Tinggi. The following sub-sections concluded the key findings of each objective (also see **Figure 6.1**), future applications and limitations of this study.

6.1 The largest seagrass bed in Malaysia experienced high cover changes

The seagrass meadow in the Sibul Archipelago is the single largest meadow recorded for Malaysia. At 12.88 km², it is far more extensive than other better-known meadows in

the country such as Pulau Tinggi (3.00 km²) and Tanjung Adang-Merambong Shoal (0.90 km²) (Ooi et al., 2011b; Hossain et al., 2015a). By growing in the forereef region of continental islands, the seagrasses occupied the shallow water shelf from 2 m to 10 m depth which made the whole meadows always accessible to herbivores. From 2016 to 2017, the meadow size shrank from the inter-monsoon to the pre-monsoon by 7 % and was left with approximately 75 % of its original size by the post-monsoon. Presumably because of the reduced light intensity and broad-scale sediment burial associated with the northeast monsoon, seagrass cover showed a drastic decline throughout the meadow (from 76 – 100% to 0 – 5%), with the highest reduction of seagrass cover occurring at the meadow edge. The meadow interior, which sustained the highest seagrass cover in each season, possibly serves as a recovery area for the whole meadow after large-scale disturbances. The diminishing trend of the meadow's extent and coverage suggests that this subtidal meadow is exposed to high gradients of change caused by broad environmental processes which require further investigation to confirm the causal factors. In *Chapter 3: Spatial and Temporal Distribution Patterns of Seagrass Habitats*, I obtained fine-scale biogeographical information of the spatial extent of the seagrass meadow in the Sibul Archipelago, one that was inhabited and utilised regularly by the local dugong population.

6.2 Dugongs are strategic feeders with feeding patterns influenced by seagrass cover

The spatial patterns of feeding trails at the local scale showed that dugongs were strategic feeders when utilising their seagrass habitat to obtain food, even if a subtidal environment meant that the animals had constant access to their food source. As hypothesised, dugongs fed in a spatially structured pattern in all seasons, where clusters of high/low feeding trail densities were present within the meadow. Feeding patches

which ranged from 1.4 - 4.2 km² suggested that dugongs maintain local-scale feeding clusters within the meadow. It was likely that the dugongs' spatial feeding patterns were influenced by food quantity, i.e., seagrass cover, with two main feeding strategies detected: (1) a dispersed feeding pattern, resulting in large feeding patches with low feeding trail density, and (2) a concentrated feeding pattern, resulting in smaller feeding patches with high feeding trail density. In ***Chapter 4: Spatial and Temporal Distribution Patterns of Dugong Feeding Trails***, a conceptual model on the dugongs' feeding patterns in relation to seagrass quantity was proposed. When seagrass coverage is moderate (mode 26 – 75%), dugongs feed in a spatially concentrated manner while when seagrass coverage is relatively low (mode 0 – 25% cover) and high (mode 76-100% cover), dugongs switch to feeding in a dispersed pattern. The proposed model intended to suggest, under the assumption that food availability was the major driver of dugong feeding patterns, that dugongs, like other terrestrial mammalian herbivores, tend to maximise their net intake rate by concentrating their feeding in patches with a moderate level of food quantity. In other words, a concentrated feeding pattern could be a more efficient strategy when food resources are neither too high nor too low.

Despite both favoured plant species, i.e., *Halophila ovalis* and *Halodule uninervis*, being widely distributed across the meadow of the Sibu Archipelago, the dugongs maintained some most-favoured feeding areas (feeding hotspots) which had clusters of high number of feeding trails and some least-favoured feeding areas (feeding coldspots) which had clusters of low number of feeding trails. Throughout all seasons, the feeding hotspots were formed in areas with moderate seagrass cover while feeding coldspots were formed in areas with low seagrass cover, indicating that dugongs strategically selected and visited areas with relatively higher food quantity to feed in a consistent manner. It appeared that dugongs in the Sibu Archipelago, besides exhibiting high site fidelity by returning to the same feeding patches, were possibly practicing cultivation grazing

behaviour by maintaining patches with higher food biomass compared to the other patches within the multi-specific meadow. Such grazing behaviour has been observed in dugongs elsewhere in its range (Preen, 1995b; de Iongh et al., 1998) .

6.3 Seagrass quantity primarily affects dugong feeding site selection

Of all the potential factors that were examined to investigate the manner in which dugongs chose to feed, the feeding site selection by dugongs was primarily influenced by seagrass quantity. The generalised linear model revealed a significant association of feeding areas with higher aboveground biomass and ratio of AG:BG biomass of *Halophila ovalis*. Sediment size was selected by the final model in which the proportion of silt-clay explained relatively well for the feeding site selection. Although seagrass quality also showed significant variations between feeding areas and non-feeding areas, particularly for nitrogen, starch and fibre, the nutrient compositions of the seagrasses explained relatively little of the feeding site selection by dugongs in the Sibutu Archipelago. *Chapter 5: What Drives Dugong Feeding Preferences* concluded that seagrass biomass had the strongest influence on the feeding site selection compared to other variables, thus emphasising the relative importance of food quantity as a driving factor for the feeding preferences of dugongs living in a subtidal meadow environment.

In contrast to the theory in which food quality or nutritional status can outweigh food quantity in a herbivore's diet (Owen-Smith & Novellie, 1982), the result of this study showed that food quantity is the more prominent currency in determining the food and habitat choices of dugongs. This result also corroborated the ideas in *Chapter 4* in which the animals consistently selected and fed in areas with relatively higher abundance of food resources (as shown by significantly higher seagrass coverage in the feeding hotspots) and that feeding patterns of dugongs seemed to be influenced by the seagrass quantity at a local scale. However, by dugongs preferring areas with higher aboveground

biomass of *H. ovalis*, it is difficult to posit if dugongs were at all quantity-seekers rather than quality-seekers, as *H. ovalis* was the most nutritious seagrass species within the dugong habitat, if fibre and nitrogen are the limiting nutrients. However, if starch and nitrogen are the limiting nutrients, then dugongs would be expected to select patches with higher biomass of *H. uninervis* attributed to their higher starch content. Nevertheless, the animals' affinity for *H. uninervis* was not evident in this study. To understand the relative importance of each nutrient parameter to the herbivores, the information of apparent digestibility based on energy, protein and fibre of each seagrass species by dugongs needs to be considered.

Overall, the results were consistent with my hypothesis that feeding site preferences of dugongs are influenced by food quantity and food quality, but did not support the hypothesis of feeding site preferences being more influenced by the whole seagrass community as opposed to individual seagrass species. Instead, the results support the influence of food quantity and quality factors more at the species level. The greater explanatory power of individual species variables compared to whole community variables in the GLM suggested that the species assemblages in the seagrass meadows play an important role in drawing or deterring the animals from feeding, adding to the evidence that dugongs are species-selective feeders, even in meadows that are dominated by both favourite food species, *H. ovalis* and *H. uninervis*. Sediment particle size unexpectedly appeared to be one of the main drivers of feeding site selection, suggesting that the proportion of silt-clay in dugong habitats may help explain patterns of habitat selection by way of directly or indirectly affecting the feeding efficiency of dugongs.

6.4 Future research and applications

The current knowledge on patterns of dugong feeding appear to be scale-specific and linked to the local meadow characteristics that are usually unique to the particular areas

of study. Hence, understanding the complex interactions between dugongs and their food plants in a tropical, subtidal and multi-specific seagrass meadow is likely to generate a different perspective on the feeding ecology of this large herbivore, which are typically informed from intertidal meadows. The existing survey techniques can be used effectively to identify key feeding grounds and to monitor seagrass spatial distribution as part of the habitat management plans in the Sibutinggi Archipelago. Additionally, the knowledge on the animals' feeding patterns and drivers of feeding preferences contributes to a wider understanding of the habitat utilisation patterns and processes that shape the survival and adaptation of the local dugong population in a highly dynamic seagrass habitat.

Moving forward, future dugong-seagrass interaction studies should be conducted at least in the same study site across another monsoon cycle and using a multiple spatial scales approach (e.g., across landscape-scale (10 – 10,000 km²) and local-scale (< 10 km²) to assess the consistency in the seasonal patterns of seagrass and its effects on the spatial feeding patterns of dugongs. The seagrass and feeding trail mapping (*Chapters 3 and 4*) should also be extended from the current site of Pulau Sibutinggi to Pulau Tinggi, whereby I was unable to cover the latter in this study due to the time and financial constraints. The similarity and differences of spatial feeding patterns and feeding hotspots-coldspots between Pulau Sibutinggi and Pulau Tinggi may provide further insights to the habitat use by dugongs. In terms of selection factors, the role of sediment particle size in driving the dugongs' feeding site selection requires further examination.

The sampling methodology in this study was carried out with some limitations and assumptions noted. As mentioned in *Chapter 4*, I used a towed video method to accurately collect fine-scale geographical data of seagrass and dugong feeding trails, however the results might have been underestimated due to potential biases such as undetected feeding trails caused by substandard appearance of the feeding trails. The habitat use patterns interpreted in *Chapters 4 and 5* were related primarily to feeding factors and not other

non-feeding factors such as behaviours that are associated with predator avoidance, large-scale movements or human disturbances (see Wirsing et al., 2007a, 2007b; Sheppard et al., 2006; Hodgson et al., 2007). Other limiting aspects of this study were insufficient amount of samples from individual seagrass species for the nutrient analysis which resulted in missing data, e.g., starch data in this study. I recommend that collectors weigh the wet weight of the seagrass samples on site to make sure that the minimum weight required for laboratory analyses are met before ending the field sampling.

At the fundamental level, our current knowledge gaps of dugong spatial ecology and feeding behaviour specific to the Sibutu Archipelago, Malaysia, were filled. The ecological information obtained via this study provides important scientific data which can aid in evidence-based decision-making critical for the conservation and management of dugongs and their habitats in the area, which is now internationally designated as an IUCN Important Marine Mammal Area (IMMA). To the best of my knowledge, this is the first in-depth study of its kind for dugongs in Asia, where such information on dugong spatial and feeding ecology lacks, particularly in a subtidal environment.

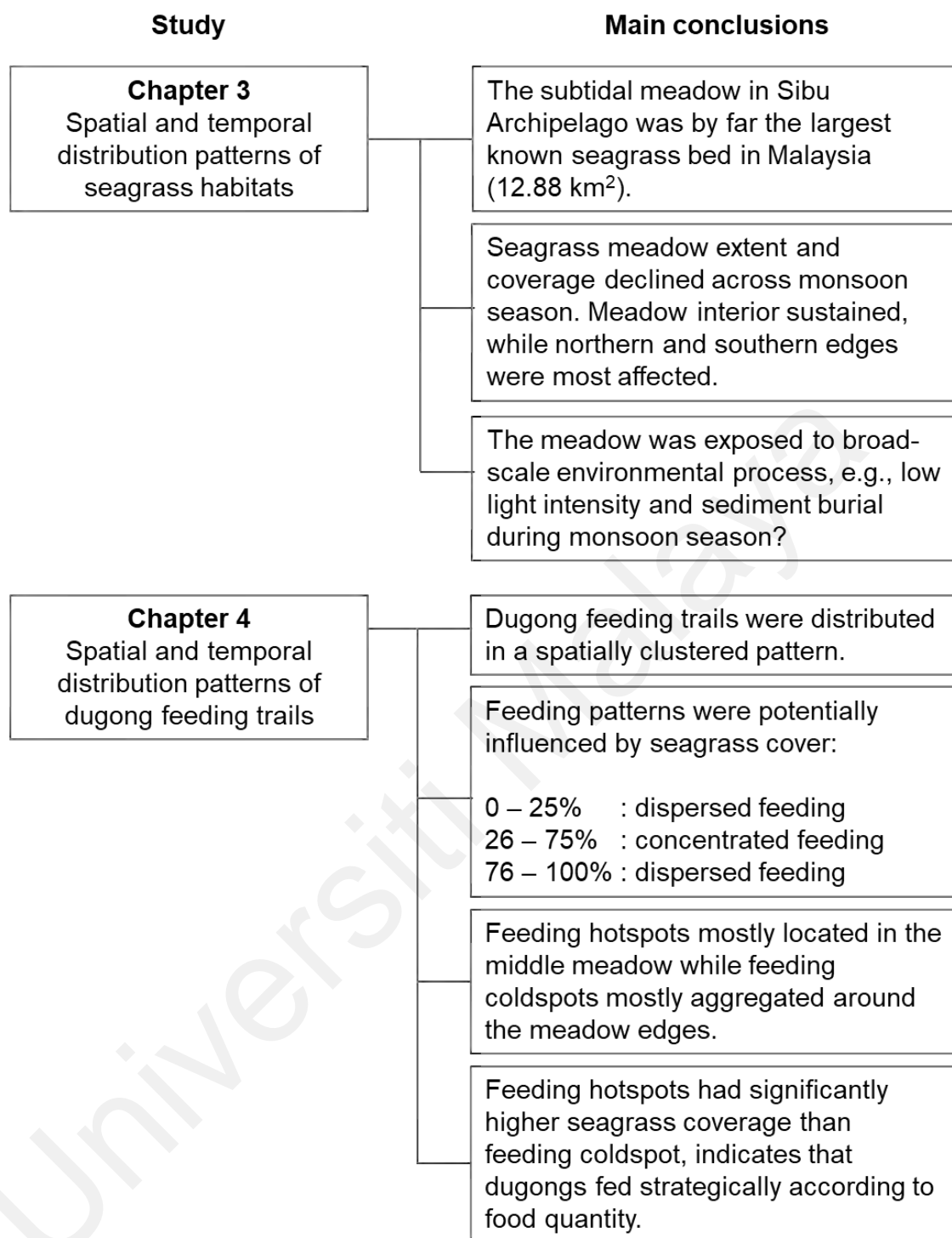


Figure 6.1 The summary of conclusions of each chapter in this study. Figure continued on next page

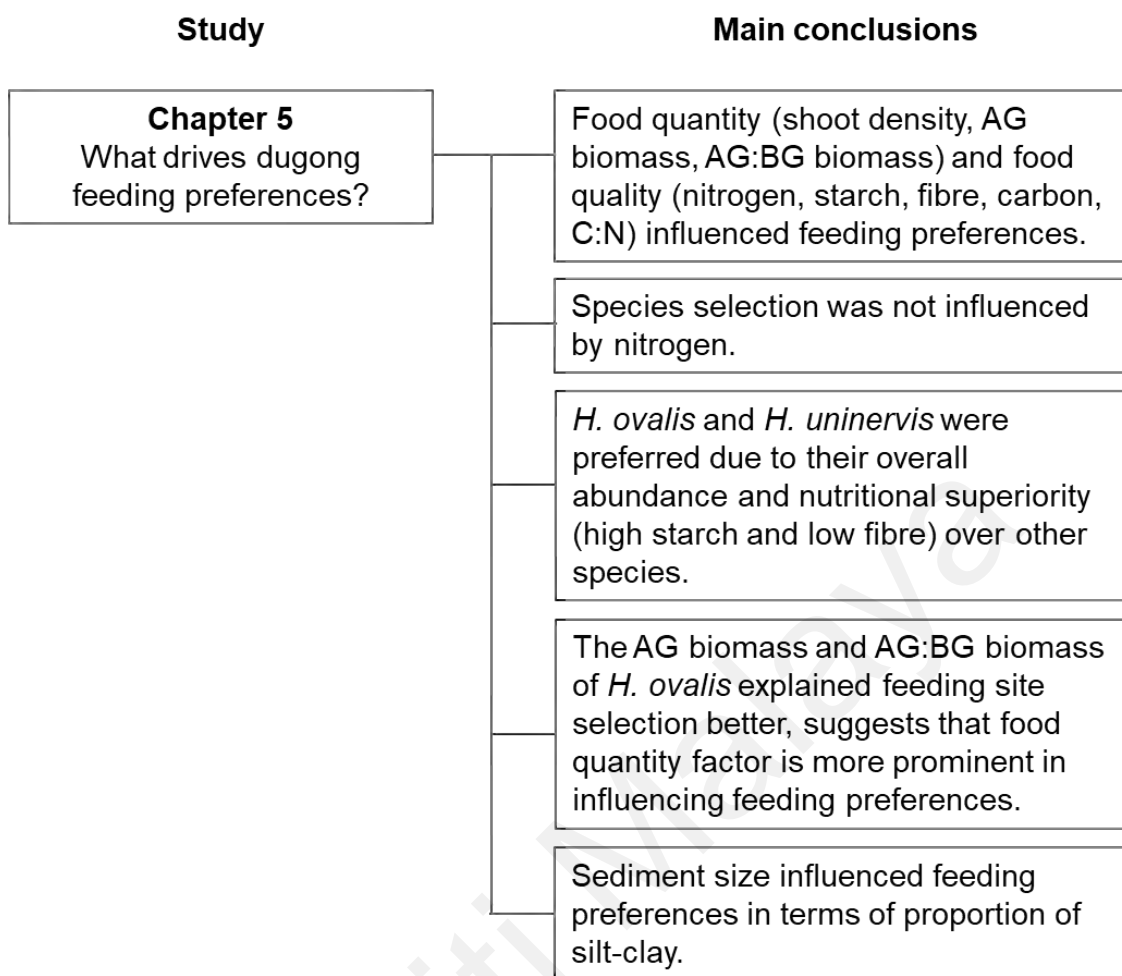


Figure 6.1 (Cont.)...The summary of conclusions of each chapter in this study.

LIST OF PUBLICATIONS AND PAPERS PRESENTED

Publications:

Technical Report

Heng, W.K., Ooi, J.L.S. & Ponnampalam, L.S. (2019) GEF DSCP Project MY4 Final Report, Attachment 3: External Report – Seagrass Mapping & Dugong Feeding Ecology Surveys. In: A Multi-Pronged Approach in Overcoming Knowledge Barriers on the Ecology and Status of Dugongs in Johor – Towards Critical Habitat Protection (MY4-2114). Final report submitted to the Global Environment Facility (GEF) Dugong and Seagrass Conservation Project (DSCP). eds. L.S. Ponnampalam and J.S. Fairul Izmal), p. 38.

Peer-reviewed Article

Heng, W.K., Ooi, J.L.S., Affendi, Y.A., Kee Alfian, A.A. & Ponnampalam, L.S. (*in review*). Dugong Feeding Grounds and Spatial Patterns in Subtidal Seagrass: A case study at Sibu Archipelago, Malaysia. *Estuarine, Coastal and Shelf Science*. (**Chapter 3 and 4**)

Presentations:

1. Poster Presentation “**MAPPING DUGONG HABITAT AND UNDERSTANDING DUGONG FEEDING HABITS IN THE JOHOR EAST COAST ISLANDS**”: Sustainability Science Research Cluster (SuSci) Symposium 2016, 21st April 2016, University of Malaya, Kuala Lumpur, Malaysia
2. Oral Presentation “**MAPPING SEAGRASS HABITAT AND UNDERSTANDING FEEDING PREFERENCES OF ENDANGERED DUGONGS (*DUGONG DUGON*) IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: 10th WESTPAC International Scientific Conference, 19th April 2017, Qingdao, P. R. China
3. Poster Presentation “**MAPPING SEAGRASS HABITAT AND UNDERSTANDING FEEDING PREFERENCES OF ENDANGERED DUGONGS (*DUGONG DUGON*) IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: Institute of Ocean and Earth Sciences (IOES) HICoE Seminar 2017, 12th September 2017, University of Malaya, Kuala Lumpur, Malaysia

4. Oral Presentation “**MAPPING SEAGRASS HABITAT AND UNDERSTANDING FEEDING PREFERENCES OF ENDANGERED DUGONGS (*DUGONG DUGON*) IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: MPA Seminar "Holistic Approach to Marine Protected Areas - Towards Sustenance and Conservation Success", 10th October 2017, Johor, Malaysia
5. Poster Presentation “**MAPPING SEAGRASS HABITAT AND UNDERSTANDING FEEDING PREFERENCES OF ENDANGERED DUGONGS (*DUGONG DUGON*) IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: 2nd Toba Symposium of Dugongs “30th Anniversary of SERENA”, 22 February 2018, Toba City, Mie Prefecture, Japan
6. Poster Presentation “**STRATEGIC OR OPPORTUNISTIC? SUBTIDAL SEAGRASS USE BY DUGONGS IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: 4th Asia-Pacific Coral Reef Symposium (APCRS), 8 June 2018, Cebu, Philippines
7. Oral Presentation “**STRATEGIC OR OPPORTUNISTIC? SUBTIDAL SEAGRASS USE BY DUGONGS IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: World Seagrass Conference 2018, 12 June 2018, Singapore
8. Oral Presentation “**HABITAT USE BY DUGONGS IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: Rufford Small Grants Conference – Vietnam 2018, 19 October 2018, Hanoi, Vietnam
9. Poster Presentation “**STRATEGIC OR OPPORTUNISTIC? SUBTIDAL SEAGRASS USE BY DUGONGS IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: Universiti Malaya Research Carnival (UMRC), 15 November 2018, Kuala Lumpur, Malaysia
10. Oral Presentation “**STRATEGIC OR OPPORTUNISTIC? SUBTIDAL SEAGRASS USE BY DUGONGS IN THE SIBU-TINGGI ARCHIPELAGO, JOHOR, MALAYSIA**”: 3rd South China Sea Conference (SCS 2019), 25 June 2019, Kuala Lumpur, Malaysia


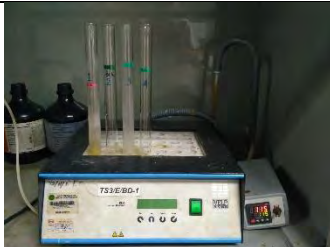
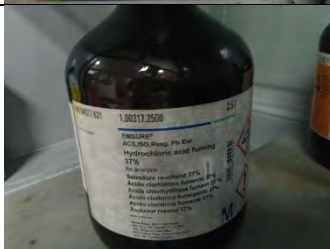
APPENDIX A



Full protocol for chemical analyses in Chapter 5.

A. Determination of Carbon (% C) and Nitrogen (%N)





1. Homogenize the aboveground and belowground samples of seagrass
2. Dry the samples $100 \pm 10^\circ\text{C}$ for 1 hour prior for sample loading using CN analyzer
3. Nitrogen and Carbon freed by combustion at high temperature ($900\text{-}1000^\circ\text{C}$) in pure oxygen is measured by thermal conductivity detection.





B. Determination of Phosphorus (% P)

No.	Procedure	Picture
1	Pour 10 ml of 65% nitric acid into each 100 ml tube which contained samples and leave overnight	
2	Place tubes in the digester in 115°C for two hours	
3	Pipette 5 ml of 37% hydrochloric acid into each tube and leave it for two hours	
4	Add distilled water into each tube and top up to 100 ml	
5	Put a stopper/cock on each tube and overturn the tube to mix well all solutions	

6	Filter each sample solutions by using filter paper into a small bottle	
7	Send sample to ICP-OES. The intensity of characteristic light emitted by each excited element is proportional to its concentration.	



C. Determination of Starch (% S)





No.	Procedure	Picture
1	Weigh about 5-10 g of sample by using 250 ml beaker.	
2	Wash the sample with cold water and filter with filter paper. Wash and filter around three times.	
3	Place the filter paper with sample inside a 500 ml beaker and spray the sample down into the beaker by using 0.5 N hydrochloric acid. Top up to 250 ml with HCl.	
4	Equip the beaker with a reflux condenser. Apply the heat until it boiled. Cool to room temperature.	

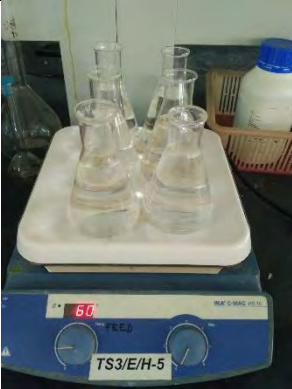

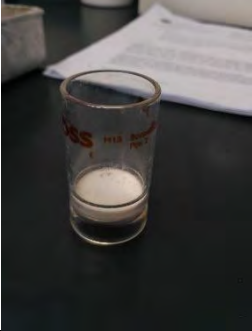

5	Neutralize the sample by adding 20% NaOH until pH 5.1-5.2 using distilled water bottle (adjust with 0.5 N HCl if too alkaline).	
6	Filter the sample again through Whatman no.541 filter paper into a 250 ml volumetric flask. Dilute to the mark of 250 ml with distilled water. Discard the filter paper.	
7	Continue with analysis of sugar using method of Lane-Eynon. Pipette 5 ml of Fehling A + 5 ml of Fehling B solutions into new 250 ml conical flask.	
8	Titrate (50 ml burette) first 15 ml of sample first into the Fehling solution. If colour changes to brick red, perform dilution (10X) of sample followed by titration. If colour has not change within the first 15 ml, continue titrate with no dilution needed. Note: beaker has to put on a hotplate magnetic stirrer with stir bar inside.	
9	Add one drop of methylene blue to confirm the colour has changed to red. If the colour has not changed to red after finished titrate 50 ml sample in the burette, perform spiking to confirm the absence of sugar.	
10	Calculate total starch based on the formula below: $\% \text{ Starch} = \frac{C \times B \times 100}{(A \times 1000) \times 0.9}$ A = sample (g) mL B = Dilution factor = 5 (if do spiking) C = Table reading	




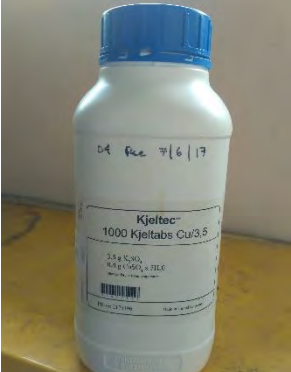
TOTAL REDUCING SUGAR REQUIRED FOR COMPLETE REDUCING OF 10mL SOXHLET SOLN TO BE USED IN CONNECTION WITH LANE-EYNON GENERAL VOLUMETRIC METHOD				
Titre	After Inversion		Before Inversion	
	Invert sugar no sucrose	1 gm sucrose per 100mL invert sugar	5 gm sucrose per 100mL invert sugar	10 gm sucrose per 100mL invert sugar
15	50.5 (336)	49.9	47.6	46.1
16	50.6 (316)	50.0	47.6	46.1
17	50.7 (298)	50.1	47.6	46.1
18	50.8 (282)	50.1	47.6	46.1
19	50.8 (267)	50.2	47.6	46.1
20	50.9 (254.5)	50.2	47.6	46.1
21	51.0 (242.9)	50.2	47.6	46.1
22	51.0 (231.9)	50.3	47.6	46.1
23	51.1 (222.2)	50.3	47.6	46.1
24	51.2 (213.3)	50.3	47.6	46.1
25	51.2 (204.8)	50.4	47.6	46.0
26	51.3 (197.4)	50.4	47.6	46.0
27	51.4 (190.4)	50.4	47.6	46.0
28	51.4 (183.7)	50.5	47.7	46.0
29	51.5 (177.6)	50.5	47.7	46.0
30	51.5 (171.6)	50.5	47.7	46.0
31	51.6 (166.3)	50.6	47.7	45.9
32	51.6 (161.2)	50.6	47.7	45.9
33	51.7 (156.6)	50.6	47.7	45.9
34	51.7 (152.2)	50.6	47.7	45.8
35	51.8 (147.9)	50.7	47.7	45.8
36	51.8 (143.7)	50.7	47.7	45.8
37	51.9 (140.2)	50.7	47.7	45.7
38	51.9 (136.6)	50.7	47.7	45.7
39	52.0 (133.3)	50.8	47.7	45.7
40	52.0 (130.1)	50.8	47.7	45.6
41	52.1 (127.1)	50.8	47.7	45.6
42	52.1 (124.2)	50.8	47.7	45.6
43	52.2 (121.4)	50.8	47.7	45.5
44	52.2 (118.7)	50.9	47.7	45.5
45	52.3 (116.1)	50.9	47.7	45.4
46	52.3 (113.7)	50.9	47.7	45.4
47	52.4 (111.4)	50.9	47.7	45.3
48	52.4 (109.2)	50.9	47.7	45.3
49	52.5 (107.1)	50.1	47.7	45.2
50	52.5 (105.1)			



C. Determination of Total Dietary Fibre (% TDF)

No.	Procedure	Picture
1	Cut the seagrass sample into small pieces.	
2	Weigh duplicate 1 g sample, accurate to 0.1 mg (0.0001 g), into 400 mL tall-form beakers. Sample weights should differ by less than 20 mg from each other.	
3	Prepare blank sample (without sample) to measure any contribution from reagents to residues.	
4	Add 50 mL phosphate buffer to each beaker by using pipette and check pH with pH meter.	

5	Add 100 μ L heat-stable α -amylase solution to remove carbohydrate.	
6	Cover beaker with aluminium foil and place in boiling water bath (85 $^{\circ}$ C for 15 min & 100 $^{\circ}$ C for 15 min, total 30 min). Turn on the shake setting.	
7	Cool solutions to room temperature (to 60 $^{\circ}$ C is sufficient).	
8	Adjust to pH 7.5 \pm 0.1 by adding 10 mL 0.275 N NaOH solution.	
9	Add 100 μ L protease solution to remove protein.	
10	Cover beaker with aluminium foil and incubate at 60 $^{\circ}$ C water bath with continuous agitation for 30 min.	
11	Cool to 60 $^{\circ}$ C and add 10 mL 0.325 N HCl solution to adjust pH to 4.5 \pm 0.2.	

12	Prepare 280 mL 95% EtOH and preheat on hotplate to 60 °C.	
13	Add 100 μL amyloglucosidase, cover with aluminium foil, and incubate 20 min at 60 °C with continuous agitation.	
14	Once the EtOH reaches 60 °C, pour it into the beakers (which also in 60 °C). Let precipitate form at room temperature.	
15	Weigh crucible (use only P2 crucible) containing Celite (~0.5 g to nearest 0.1 mg), then wet and distribute bed of Celite in crucible by using stream of 78% EtOH from wash bottle.	
16	Use filtration by applying suction. Transfer precipitate solution to crucible and filter. Wash residue with three times 20 mL 78% EtOH (total is 60 mL), and two times 10 mL 95% EtOH (total is 20 mL). Finally wash the crucible two times with 10 mL acetone.	

17	Dry crucible containing residue overnight in an oven at 105 °C for 5 hours.	
18	Cool in desiccator and weigh. Subtract crucible and Celite weights to determine residue weight (r).	
19	Use first duplicate for ash determination. Incinerate for 5 hr at 525 °C. Cool in desiccator and weigh. Subtract crucible and Celite weights to determine ash.	
20	Use another replicate for protein determination using N x 6.25 as conversion factor.	
21	Scrape the sample, Celite and residue into a 250 mL digestion tube.	
22	Prepare 0.15 g Glycine into a 250 mL digestion tube as well.	
23	Add one piece of Kjeltec catalyst Cu 3.5 (or 7 gm K ₂ SO ₄ + 0.8 gm CuSO ₄ x 5 H ₂ O) into digestion tubes.	

24	Add 13 mL concentrated H ₂ SO ₄ (95-98%) into digestion tubes.	
25	Place the digestion tubes in the digestion block. Digest the sample at 420 °C until the solution turns clear then leave to cool.	

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APPENDIX B

Summary of species present in the feeding areas and non-feeding areas.

Feeding areas		Non-feeding areas	
Site	Species	Site	Species
1	HO, HU	1	HO, HU, CS, SI
2	HO, HU, CS	2	HO, HU
3	HO, HU, CS	3	HO, HU, CS
4	HO, HU, CS	4	HO, HU, CS, SI
5	HO, HU, CS	5	HU
6	HU	6	HO, HU, CS
7	HO, HU	7	HO, HU, CS, SI
8	HO, HU	8	HU
9	HO, HU	9	HO, HU
10	HO, HU	10	HO, HU
11	HO, HU	11	HO
12	HO	12	HO, HU
13	HO, HU	13	HO, HU, CS, SI
14	HO, HU	14	HO, HU, CS, SI
15	HO, HU	15	HO, HU, CS
16	HO, HU	16	HO, HU, CS
17	HO	17	HO, HU, CS
18	HO, HU, CS, SI	18	HO, HU, CS, SI
19	HO, HU	19	HO, HU
20	HO, HU	20	HO, HU
21	HO, HU, CS	21	HO, HU, CS
22	HO, HU	22	HO, HU, CS
23	HO, HU	23	HO, HU, SI
24	HO, HU	24	HO, HU, CS
25	HO, HU, CS, SI	25	HO, HU, CS
26	HO, HU	26	HO, HU
27	HO, HU	27	HO, HU
28	HO, HU, CS, SI	28	HO, HU, CS
29	HO, HU, CS, SI	29	HO, HU, CS
30	HO, HU, SI	30	HO, HU, CS, SI
31	HO, HU, SI		
32	HO, HU, CS		
33	HO, HU		
34	HO, HU		
35	HO		
36	HO, HU		
37	HO, HU, CS		
38	HO, HU		

REFERENCES

- Adulyanukosol, K. (2010). *Ecology of the dugong (Dugong dugon) in Thailand : Population characteristics , feeding habits and conservation* (Doctoral dissertation, University of the Ryukyus, Japan).
- Adulyanukosol, K., Boukaew, P., & Prasitthipornkul, A. (2004). Analysis of stomach contents of dugongs (*Dugong dugon*) from Gulf of Thailand. *Proceedings of the International Symposium on SEASTAR2000 and Bio-logging Science (The 5th SEASTAR2000 Workshop)* (pp. 45–51). <https://doi.org/10.1071/WR9820055>
- Affendi, Y. A., Ooi, J. L. S., Phang, S. M., Azhar, H. H., Faedzul, R. R., & Rosmadi, F. (2005). *Dugongs In Peril: The Conservation and Protection of Dugongs in Johor, Malaysia*. Report to the United Nations Development Programme (UNDP), Kuala Lumpur, Malaysia.
- Ahmad-Kamil, E. I., Ramli, R., Jaaman, S. A., Bali, J., & Al-Obaidi, J. R. (2013). The effects of water parameters on monthly seagrass percentage cover in lawas, East Malaysia. *The Scientific World Journal*, 2013, 892746. <https://doi.org/10.1155/2013/892746>
- Aketa, K., Asano, S., Wakai, Y., & Kawamura, A. (2003). Apparent digestibility of eelgrass *Zostera marina* by captive dugongs *Dugong dugon* in relation to the nutritional content of eelgrass and dugong feeding parameters. *Mammal Study*, 28, 23–30. <https://doi.org/10.3106/mammalstudy.28.23>
- Aketa, K., & Kawamura, A. (2001). Digestive functions in Sirenians (Review). *The Bulletin of the Faculty of Bioresources, Mie University*, 27, 85–103.
- Alves-Stanley, C. D., Worthy, G. A. J., & Bonde, R. K. (2010). Feeding preferences of West Indian manatees in Florida, Belize, and Puerto Rico as indicated by stable isotope analysis. *Marine Ecology Progress Series*, 402, 255–267. <https://doi.org/10.3354/meps08450>
- Amamoto, N., Ichikawa, K., Arai, N., Akamatsu, T., Shinke, T., & Adulyanukosol, K. (2009). The depth of water effects the feeding ground selection by dugongs in dry season. *Journal of Advanced Marine Science and Technology Society*, 15(2), 149–157.
- Amamoto, N., Ichikawa, K., Arai, N., Akamatsu, T., Shinke, T., Hara, T., & Adulyanukosol, K. (2009). Seasonal characterization of dugong feeding and biomass utilization on selected sites in Talibong Island. *Proceedings of the 4th International Symposium on SEASTAR2000 and Asian Bio-Logging Science (The 8th SEASTAR2000 Workshop)*, 41–43.
- Anderson, P. K. (1982). Studies of dugongs at Shark Bay, Western Australia. II. Surface and subsurface observations. *Australia Wildlife Research*, 9, 85–99.
- Anderson, P. K. (1989). Deliberate foraging on macroinvertebrates by dugongs. *National Geographic Research*, 5, 4–6
- Anderson, P. K. (1998). Shark Bay dugongs (*Dugong dugon*) in summer. II: Foragers in a Halodule-dominated community. *Mammalia*, 62(3), 409–425. <https://doi.org/10.1515/mamm.1998.62.3.409>
- Anderson, P. K., & Birtles, A. (1978). Behaviour and ecology of the Dugong, *Dugong*

- dugon* (Sirenia): Observations in shoalwater and cleveland bays, Queensland. *Wildlife Research*, 5(1), 1–23. <https://doi.org/10.1071/WR9780001>
- André, J., Gyuris, E., & Lawler, I. R. (2005). Comparison of the diets of sympatric dugongs and green turtles on the Orman Reefs, Torres Strait, Australia. *Wildlife Research*, 32(1), 53. <https://doi.org/10.1071/WR04015>
- Anselin, L. (2005). *Exploring Spatial Data with GeoDa: A Workbook*. Center for Spatially Integrated Social Science. Retrieved from <https://www.geos.ed.ac.uk/~gisteac/fspat/>
- Apte, D., Parasharya, D., & Patel, B. (2019). Feeding trails of Dugong *Dugong dugon* (Müller, 1776) (Mammalia: Sirenia: Dugongidae) in the Gulf of Kachchh, western coast of India. *Journal of Threatened Taxa*, 11(1), 13151–13154. <https://doi.org/10.11609/jott.4315.11.1.13151-13154>
- Aragones, L. V., Lawler, I., Marsh, H., Domning, D., & Hodgson, A. (2012). The Role of Sirenians in Aquatic Ecosystems. In Hines, E. M., Reynolds III, J. E., Aragones, L. V., Mignucci-Giannoni, A. A., & Marmontel, M. (Eds.) *Sirenian conservation: issues and strategies in developing countries* (pp. 1–11). Gainesville, FL: University Press of Florida
- Aragones, L., & Marsh, H. (2000). Impact of Dugong grazing and turtle cropping on tropical seagrass communities. *Pacific Conservation Biology*, 5(4), 286–288. <https://doi.org/10.1071/PC000277>
- Aragones, L. V. (1994). Observations on dugongs at Calauit Island, Busuanga, Palawan, Phillipines. *Wildlife Research*, 21(6), 709. <https://doi.org/10.1071/WR9940709>
- Aragones, L. V. (1996). *Dugongs and green turtles: grazers in the tropical seagrass ecosystem* (Doctorate dissertation, James Cook University, Australia). Retrieved from <https://researchonline.jcu.edu.au/44323/>
- Aragones, L. V., Lawler, I. R., Foley, W. J., & Marsh, H. (2006). Dugong grazing and turtle cropping: grazing optimization in tropical seagrass systems? *Oecologia*, 149(4), 635–647. <https://doi.org/10.1007/s00442-006-0477-1>
- Bailey, D. W., Gross, J. E., Laca, E. A., Rittenhouse, L. R., Coughenour, M. B., Swift, D. M., & Sims, P. L. (1996). Mechanisms that result in large herbivore grazing distribution patterns. *Journal of Range Management*, 49(5), 386–400. <https://doi.org/10.2307/4002919>
- Bakker, E. S., Pagès, J. F., Arthur, R., & Alcoverro, T. (2016). Assessing the role of large herbivores in the structuring and functioning of freshwater and marine angiosperm ecosystems. *Ecography*, 39(2), 162–179. <https://doi.org/10.1111/ecog.01651>
- Bakker, E. S., Wood, K. A., Pagès, J. F., Veen, G., Christianen, M. J., Santamaría, L., ... Hilt, S. (2016). Herbivory on freshwater and marine macrophytes: A review and perspective. *Aquatic Botany*, 135, 18–36. <https://doi.org/10.1016/j.aquabot.2016.04.008>
- Bentley, B. L., & Johnson, N. D. (1991). Plants as food for herbivores: the roles of nitrogen fixation and carbon dioxide enrichment. In Price, P. W., Lewinsohn, T. M., Fernandes, G. W., & Benson, W. W. (Eds.), *Plant–Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions* (pp. 257–272). New York: John Wiley and Sons.

- Best, R. C. (1981). Foods and feeding habits of wild and captive Sirenia. *Mammal Review*, 11(1), 3–29. <https://doi.org/10.1111/j.1365-2907.1981.tb00243.x>
- Bicknell, A. W. J., Godley, B. J., Sheehan, E. V., Votier, S. C., & Witt, M. J. (2016). Camera technology for monitoring marine biodiversity and human impact. *Frontiers in Ecology and the Environment*. <https://doi.org/10.1002/fee.1322>
- Birch, W. R. (1975). Some Chemical and Calorific Properties of Tropical Marine Angiosperms Compared with Those of Other Plants. *The Journal of Applied Ecology*, 12(1), 201. <https://doi.org/10.2307/2401729>
- Bjorndal, K. A. (1980). Nutrition and Grazing Behavior of the Green Turtle *Chelonia mydas*. *Marine Biology*, 56, 147–154.
- Boonprakob, U., Chantrapornsyl, S., & Bhatia, O. (1983). Occurrence of dugong (*Dugong dugon*) in coastal waters of Phuket Island and the attempt to keep dugongs in captivity. In *A symposium on marine mammals of the Indian Ocean*.
- Braun-Blanquet, J. (1972). *Plant sociology: the study of plant communities*. Hafner, New York, USA.
- Briscoe, D. K., Hiatt, S., Lewison, R., & Hines, E. (2014). Modeling habitat and bycatch risk for dugongs in Sabah, Malaysia. *Endangered Species Research*, 24(3), 237. <https://doi.org/10.3354/esr00600>
- Burkholder, D. A., Heithaus, M. R., Fourqurean, J. W., Wirsing, A., & Dill, L. M. (2013). Patterns of top-down control in a seagrass ecosystem: Could a roving apex predator induce a behaviour-mediated trophic cascade? *Journal of Animal Ecology*, 82(6), 1192–1202. <https://doi.org/10.1111/1365-2656.12097>
- Carlton, J. T., Vermeij, G. J., Lindberg, D. R., Carlton, D. A., & Dudley, E. C. (1991). The first historical extinction of a marine invertebrate in an ocean basin: the demise of the eelgrass limpet *Lottia alveus*. *Biological Bulletin*, 180(1), 72–80. <https://doi.org/10.2307/1542430>
- Castelblanco-Martínez, D. N., Morales-Vela, B., Hernández-Arana, H. A., & Padilla-Saldivar, J. (2009). Diet of the manatees (*Trichechus manatus manatus*) in Chetumal Bay, Mexico. *Latin American Journal of Aquatic Mammals*, 7(1–2), 39–46. <https://doi.org/10.5597/lajam00132>
- Cebrián, J., & Duarte, C. M. (1998). Patterns in leaf herbivory on seagrasses. *Aquatic Botany*, 60(1), 67–82. [https://doi.org/10.1016/S0304-3770\(97\)00070-3](https://doi.org/10.1016/S0304-3770(97)00070-3)
- Cebrián, J., Duarte, C. M., Nona, N. S., & Merino, M. (1998). Leaf growth response to simulated herbivory: A comparison among seagrass species. *Journal of Experimental Marine Biology and Ecology*, 220(1), 67–81. [https://doi.org/10.1016/S0022-0981\(97\)00084-1](https://doi.org/10.1016/S0022-0981(97)00084-1)
- Charoll, A., Althaus, F., Beaman, R., Friedman, A., Lerodiasconou, D., Ingleton, T., ... Tyndall, A. (2018). *Marine sampling field manual for towed underwater camera systems* In Przeslawski, R., & Foster, S. (Eds.), *Field Manuals for Marine Sampling to Monitor Australian Waters* (pp. 131-152). National Environmental Science Programme (NESP). <https://doi.org/10.11636/9781925297669>
- Chilvers, B. L., Delean, S., Gales, N. J., Holley, D. K., Lawler, I. R., Marsh, H., & Preen, A. R. (2004). Diving behaviour of dugongs, *Dugong dugon*. *Journal of Experimental Marine Biology and Ecology*, 304(2), 203–224. <https://doi.org/10.1016/j.jembe.2003.12.010>

- Chow, P. S., & Landhäuser, S. M. (2004). A method for routine measurements of total sugar and starch content in woody plant tissues. *Tree Physiology*, 24(10), 1129–1136. <https://doi.org/10.1093/treephys/24.10.1129>
- Christianen, M. J. A., Herman, P. M. J., Bouma, T. J., Lamers, L. P. M., Van Katwijk, M. M., Van Der Heide, T., ... Van De Koppel, J. (2014). Habitat collapse due to overgrazing threatens turtle conservation in marine protected areas. *Proceedings of the Royal Society B: Biological Sciences*, 281(1777). <https://doi.org/10.1098/rspb.2013.2890>
- Christianen, M. J. A., Smulders, F. O. H., Engel, M. S., Nava, M. I., Willis, S., Debrot, A. O., ... Becking, L. E. (2018). Megaherbivores may impact expansion of invasive seagrass in the Caribbean. *Journal of Ecology*, 107(1), 45–57. <https://doi.org/10.1111/1365-2745.13021>
- Christianen, M. J. A., van Belzen, J., Herman, P. M. J., van Katwijk, M. M., Lamers, L. P. M., van Leent, P. J. M., & Bouma, T. J. (2013). Low-Canopy Seagrass Beds Still Provide Important Coastal Protection Services. *PLoS ONE*, 8(5). <https://doi.org/10.1371/journal.pone.0062413>
- Cleguer, C. (2015). *Informing dugong conservation at several spatial and temporal scales in New Caledonia*. (Doctoral dissertation, Université Pierre et Marie Curie, Paris and James Cook University, Australia). Retrieved from <http://hal.ird.fr/tel-01320505>
- Colares, I. G., & Colares, E. P. (2002). Food plants eaten by Amazonian manatees (*Trichechus inunguis*, Mammalia: Sirenia). *Brazilian Archives of Biology and Technology*, 45(1), 67–72. <https://doi.org/10.1590/S1516-89132002000100011>
- Collier, C., Waycott, M., & McKenzie, L. J. (2012). Light thresholds derived from seagrass loss in the coastal zone of the northern Great Barrier Reef, Australia. *Ecological Indicator*, 23:211–219
- Demment, M. W., & Van Soest, P. J. (1985). A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. *The American Naturalist*, 125, 641–672. <https://doi.org/10.1086/284369>
- Den Hartog. (1970). The seagrasses of the world. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde Tweede Reeks*, dell 59, No. 1. North Holland Pub. Co. Amsterdam, 275pp.
- D'Souza, E., Patankar, V., Arthur, R., Alcoverro, T., & Kelkar, N. (2013). Long-Term Occupancy Trends in a Data-Poor Dugong Population in the Andaman and Nicobar Archipelago. *PLoS ONE*, 8(10). <https://doi.org/10.1371/journal.pone.0076181>
- D'Souza, E., Patankar, V., Arthur, R., Marbà, N., & Alcoverro, T. (2015). Seagrass herbivory levels sustain site-fidelity in a remnant dugong population. *PLoS ONE*, 10(10). <https://doi.org/10.1371/journal.pone.0141224>
- de Iongh, H. (1996). *Plant-Herbivore Interactions between seagrass and dugongs in a Tropical Small Island Ecosystem* (Doctoral dissertation, University of Nijmegen).
- De Iongh, H. H., Kiswara, W., Kustiawan, W., & Loth, P. E. (2007). A review of research on the interactions between dugongs (*Dugong dugon* Müller 1776) and intertidal seagrass beds in Indonesia. *Hydrobiologia*, 591(1), 73–83. <https://doi.org/10.1007/s10750-007-0785-4>

- de Iongh, H. H., Wenno, B. J., & Meelis, E. (1995). Seagrass distribution and seasonal biomass changes in relation to dugong grazing in the Moluccas, East Indonesia. *Aquatic Botany*, 50(1), 1–19. [https://doi.org/10.1016/0304-3770\(94\)00438-R](https://doi.org/10.1016/0304-3770(94)00438-R)
- De Iongh, H. H., Langeveld, P., & Van Der Wal, M. (1998). Movement and Home Ranges of Dugongs Around the Lease Islands, East Indonesia. *Marine Ecology*, 19(3), 179–193.
- Distel, R. A., Laca, E. A., Griggs, T. C., & Demment, M. W. (1995). Patch selection by cattle: maximization of intake rate in horizontally heterogeneous pastures. *Applied Animal Behaviour Science*, 45(1–2), 11–21. [https://doi.org/10.1016/0168-1591\(95\)00593-H](https://doi.org/10.1016/0168-1591(95)00593-H)
- Domning, D. P. (1994). A Phylogenetic Analysis of the Sirenia. *Proceedings of the San Diego Society of Natural History* (pp. 177–189). Retrieved from <https://www.biodiversitylibrary.org/bibliography/3595>
- Domning, D. P. (2001). Sirenians, seagrasses, and Cenozoic ecological change in the Caribbean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 166(1–2), 27–50. [https://doi.org/10.1016/S0031-0182\(00\)00200-5](https://doi.org/10.1016/S0031-0182(00)00200-5)
- Domning, D. P., & Beatty, B. L. (2007). Use of tusks in feeding by Dugongid Sirenians: Observations and tests of hypotheses. *Anatomical Record*, 290(6), 523–538. <https://doi.org/10.1002/ar.20540>
- Duarte, C. M. (1990). Seagrass nutrient content. *Marine Ecology Progress Series*, 67, 201–207–207. <https://doi.org/10.3354/meps067201>
- Duarte, C. M. (1992). Nutrient concentration of aquatic plants: Patterns across species. *Limnology and Oceanography*, 37(4), 882–889. <https://doi.org/10.4319/lo.1992.37.4.0882>
- Duarte, C. M. (2002). The future of seagrass meadows. *Environmental Conservation*, 29(02). <https://doi.org/10.1017/S0376892902000127>
- Duarte, C. M., & Kirkman, H. (2001). Chapter 07 - Methods for the measurement of seagrass abundance and depth distribution. In Short, F. T., & Coles, R. G. (Eds.), *Global Seagrass Research Methods* (pp. 141–153). Elsevier B.V. <https://doi.org/10.1016/B978-0-444-50891-1.50008-6>
- Duarte, C. M., Losada, I. J., Hendriks, I. E., Mazarrasa, I., & Marbà, N. (2013). The role of coastal plant communities for climate change mitigation and adaptation. *Nature Climate Change*. <https://doi.org/10.1038/nclimate1970>
- Eigeland, K. A., Lanyon, J. M., Trott, D. J., Ouwerkerk, D., Blanshard, W., Milinovich, G. J., ... Klieve, A. V. (2012). Bacterial community structure in the hindgut of wild and captive dugongs (*Dugong dugon*). *Aquatic Mammals*, 38(4), 402–411. <https://doi.org/10.1578/AM.38.4.2012.402>
- Ertfemeijer, P. L., & Koch, E. W. (2001). Chapter 18 – Sediment geology methods for seagrass habitat. In Short, F. T., & Coles, R. G. (Eds.), *Global Seagrass Research Methods* (pp. 345–367). <https://doi.org/10.1016/B978-044450891-1/50019-0>
- Ertfemeijer, P. L. A., & Middelburg, J. J. (1993). Sediment-nutrient interactions in tropical seagrass beds - A comparison between a terrigenous and a carbonate sedimentary environment in south Sulawesi (Indonesia). *Marine Ecology Progress Series*, 102(1–2), 187–198. <https://doi.org/10.3354/meps102187>

- Erfstemeijer, P. L. A., & Herman, P. M. J. (1994). Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. *Oecologia*, *99*(1–2), 45–59. <https://doi.org/10.1007/BF00317082>
- Ferdie, M., & Fourqurean, J. W. (2004). Responses of seagrass communities to fertilization along a gradient of relative availability of nitrogen and phosphorus in a carbonate environment. *Limnology and Oceanography*, *49*(6), 2082–2094. <https://doi.org/10.4319/lo.2004.49.6.2082>
- Fletcher, R., Fortin, M.-J., Fletcher, R., & Fortin, M.-J. (2018). Introduction to Spatial Ecology and Its Relevance for Conservation. In Fletcher, R., & Fortin, M.-J. (Eds.). *Spatial Ecology and Conservation Modeling* (pp. 1–13). Springer International Publishing. https://doi.org/10.1007/978-3-030-01989-1_1
- Fonseca, M. S., & Bell, S. S. (1998). Influence of physical setting on seagrass landscapes near Beaufort, North Carolina, USA. *Marine Ecology Progress Series*, *171*, 109–121. <https://doi.org/10.3354/meps171109>
- Fortes, M. D., Ooi, J. L. S., Tan, Y. M., Prathep, A., Japar Sidik, B., & Yaakub, S. M. (2018). Seagrass in Southeast Asia : a review of status and knowledge gaps , and a road map for conservation. *Botanica Marina*, *61*(3), 269–288. <https://doi.org/10.1515/bot-2018-0008>
- Fourqurean, J., Moore, T., Fry, B., & Hollibaugh, J. (1997). Spatial and temporal variation in C:N:P ratios, $\delta^{15}\text{N}$, and $\delta^{13}\text{C}$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. *Marine Ecology Progress Series*, *157*, 147–157. <https://doi.org/10.3354/meps157147>
- Fourqurean, J. W., Willsie, A., Rose, C. D., & Rutten, L. M. (2001). Spatial and temporal pattern in seagrass community composition and productivity in south Florida. *Marine Biology*, *138*(2), 341–354. <https://doi.org/10.1007/s002270000448>
- Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., ... Serrano, O. (2012). Seagrass ecosystems as a globally significant carbon stock. *Nature Geoscience*, *5*(7), 505–509. <https://doi.org/10.1038/ngeo1477>
- Fourqurean, J. W., Manuel, S., Coates, K. A., Kenworthy, W. J., & Smith, S. R. (2010). Effects of excluding sea turtle herbivores from a seagrass bed: Overgrazing may have led to loss of seagrass meadows in Bermuda. *Marine Ecology Progress Series*, *419*, 223–232. <https://doi.org/10.3354/meps08853>
- Fourqurean, J. W., Zieman, J. C., & Powell, G. V. N. (1992). Phosphorus limitation of primary production in Florida Bay: Evidence from C: N: P ratios of the dominant seagrass *Thalassia testudinum*. *Limnology and Oceanography*, *37*(1), 162–171. <https://doi.org/10.4319/lo.1992.37.1.0162>
- Frair, J. L., Merrill, E. H., Beyer, H. L., Morales, J. M., Visscher, D. R., Fortin, D., Beyer, H. L., & Morales, J. M. (2005). Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landscape Ecology*, *20*, 273–287. <https://doi.org/10.1007/s10980-005-2075-8>
- Frank, D. A., McNaughton, S. J., & Tracy, B. F. (1998). The ecology of the earth's grazing ecosystems: profound functional similarities exist between the Serengeti and Yellowstone. *Bioscience*, *48*, 513–521. <https://doi.org/10.2307/1313313>
- Freeman, A. S., Short, F. T., Isnain, I., Razak, F. A., & Coles, R. G. (2008). Seagrass on

- the edge: Land-use practices threaten coastal seagrass communities in Sabah, Malaysia. *Biological Conservation*, 141(12), 2993–3005.
<https://doi.org/10.1016/j.biocon.2008.09.018>
- Getis, A., & Ord, J. K. (1992). The Analysis of Spatial Association by Use of Distance Statistics. *Geographical Analysis*, 24(3), 189–206. <https://doi.org/10.1111/j.1538-4632.1992.tb00261.x>
- Gohar, H. A. F. (1957). *The Red Sea dugong*. Publications of the Marine Biological Station Al Ghardaqa (Red Sea), Institute of Oceanography, University of Cairo, 9:3–49
- Goto, M., Ito, C., Yahaya, M. S., Wakamura, K., Asano, S., Wakai, Y., ... Kataoka, T. (2004). Effects of age, body size and season on food consumption and digestion of captive dugongs (*Dugong dugon*). *Marine and Freshwater Behaviour and Physiology*, 37(2), 89–97. <https://doi.org/10.1080/1023624042000199935>
- Goto, M., Watanabe, A., Karita, S., Tokita, N., Yamamoto, Y., Wakaki, Y., ... Furuta, M. (2008). Nutrient and energy consumption of captive mature dugong (*Dugong dugon*) consuming eelgrass at the Toba Aquarium. *Marine and Freshwater Behaviour and Physiology*, 41(3), 169–177.
<https://doi.org/10.1080/10236240802284445>
- Green, E. P., & Short, F. (2003). *World Atlas of Seagrasses*. *Botanica Marina* (Vol. 47).
<https://doi.org/10.1515/BOT.2004.029>
- Gross, J. E., Zank, C., Hobbs, N. T., & Spalinger, D. E. (1995). Movement rules for herbivores in spatially heterogeneous environments: responses to small scale pattern. *Landscape Ecology*, 10(4), 209–217. <https://doi.org/10.1007/BF00129255>
- Harasti, D. (2016). Declining seahorse populations linked to loss of essential marine habitats. *Marine Ecology Progress Series*, 546, 173–181.
<https://doi.org/10.3354/meps11619>
- Harris, N. L., Goldman, E., Gabris, C., Nordling, J., Minnemeyer, S., Ansari, S., Lippmann, M., Bennett, L., Raad, M., Hansen, M., & Potapov, P. (2017). Using spatial statistics to identify emerging hot spots of forest loss. *Environmental Research Letters*, 12, 024012. <https://doi.org/10.1088/1748-9326/aa5a2f>
- Hashim, M., Ito, S., Numata, S., Hosaka, T., Hossain, M. S., Misbari, S., ... Ahmad, S. (2017). Using fisher knowledge, mapping population, habitat suitability and risk for the conservation of dugongs in Johor Straits of Malaysia. *Marine Policy*, 78, 18–25. <https://doi.org/10.1016/j.marpol.2017.01.002>
- Hebblewhite, M., Merrill, E., McDermid, G. (2008). A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecological Monographs*, 78, 141-166
- Heck, K. L., & Valentine, J. F. (2006). Plant-herbivore interactions in seagrass meadows. *Journal of Experimental Marine Biology and Ecology*, 330(1), 420–436.
<https://doi.org/10.1016/j.jembe.2005.12.044>
- Heinsohn, G. E., Wake, J., Marsh, H., & Spain, A. V. (1977). The dugong (*Dugong dugon* (Müller)) in the seagrass system. *Aquaculture*, 12(3), 235–248.
[https://doi.org/10.1016/0044-8486\(77\)90064-3](https://doi.org/10.1016/0044-8486(77)90064-3)
- Heinsohn, G. E., & Birch, W. R. (1972). Foods and Feeding Habits of the Dugong, *Dugong dugon* (Erxleben), in Northern Queensland, Australia. *Mammalia*, 36(3),

- Hemminga, M. A., & Duarte, C. M. (2000). *Seagrass Ecology*. Cambridge University Press. [https://doi.org/10.1016/S0304-3770\(01\)00171-1](https://doi.org/10.1016/S0304-3770(01)00171-1)
- Hines, E., Ponnampalam, L., Junchompoo, C., Peter, C., Vu, L., Huynh, T., ... Verutes, G. (2020). Getting to the bottom of bycatch: a GIS-based toolbox to assess the risk of marine mammal bycatch. *Endangered Species Research*, 42, 37–57. <https://doi.org/10.3354/esr01037>
- Hines, E. M., Reynolds III, J. E., Aragones, L. V., Mignucci-Giannoni, A. A., & Marmontel, M. (2012). *Sirenian conservation: Issues and strategies in developing countries*. University Press of Florida. Gainesville. FL.
- Hines, E. M., Adulyanukosol, K., Poochaviranon, S., Somany, P., Ath, L. S., Cox, N., ... Solanki, P. (2012). Dugongs in Asia. In Hines, E. M., Reynolds III, J. E., Aragones, L. V., Mignucci-Giannoni, A. A., & Marmontel, M. (Eds.), *Sirenian Conservation: Issues and strategies in developing countries* (pp. 58-76). University Press of Florida. Gainesville. FL.
- Ho, N. A. J., Ooi, J. L. S., Affendi, Y. A., & Chong, V. C. (2018). Influence of habitat complexity on fish density and species richness in structurally simple foreereef seagrass meadows. *Botanica Marina*. <https://doi.org/10.1515/bot-2017-0115>
- Hodgson, A. J., & Marsh, H. (2007). Response of dugongs to boat traffic: The risk of disturbance and displacement. *Journal of Experimental Marine Biology and Ecology*, 340(1), 50–61. <https://doi.org/10.1016/j.jembe.2006.08.006>
- Hodgson, A. J. (2004). *Dugong behaviour and responses to human influences* (Doctorate dissertation, James Cook University, Australia). Retrieved from <http://www.helenmarsh.com/publications/Unpublished/HodgsonPhDThesis.pdf>
- Holley, D. K. (2006). *Movement patterns and habitat usage of shark bay dugongs* (Doctorate dissertation, Edith Cowan University, Australia).
- Holyoak, M., Leibold, M. A., & Holt, R. D. (2005). *Metacommunities: Spatial Dynamics and Ecological Communities*. The University of Chicago Press. <https://doi.org/10.1111/j.1442-9993.2006.01687.x>
- Holzer, K. K., & McGlathery, K. J. (2016). Cultivation grazing response in seagrass may depend on phosphorus availability. *Marine Biology*, 163(4), 88. <https://doi.org/10.1007/s00227-016-2855-5>
- Hossain, M. S., Bujang, J. S., Zakaria, M. H., & Hashim, M. (2015). Application of Landsat images to seagrass areal cover change analysis for Lawas, Terengganu and Kelantan of Malaysia. *Continental Shelf Research*, 110, 124–148. <https://doi.org/10.1016/j.csr.2015.10.009>
- Hossain, M. S., Japar Sidik, B., & Muta Harah, Z. (2015). Landsat image enhancement techniques for subtidal and intertidal seagrass detection and distribution mapping in the coastal waters of Sungai Pulai estuary, Malaysia. *Coastal Marine Science*, 38(1), 27–41. Retrieved from <http://repository.dl.itc.u-tokyo.ac.jp/dspace/bitstream/2261/57167/1/CMS380105.pdf>
- Ismail, N. (1993). Preliminary Study of the Seagrass Flora of Sabah , Malaysia. *Pertanika J. Trop. Agric. Sci.*, 16(2), 111–118.
- Jackson, J. B. C., Kirby, M. X., Berger, W. H., Bjorndal, K. A., Botsford, L. W.,

- Bourque, B. J., ... Warner, R. R. (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*. <https://doi.org/10.1126/science.1059199>
- Japar Sidik, B., Arshad, A., Hishamuddin, O., Muta Harah, Z., & Misni, S. (1996). Seagrass and macroalgal communities of Sungai Pulai estuary, south-west Johore, Peninsular Malaysia. pp. 3–12. In Kuo, J., Walker, D. I., & Kirkman, H. (Eds.), *Seagrass Biology*. Scientific Discussion from an International Workshop, 1996 January 25-29.: Rottneest Island, Western Australia. University of Western Australia, Nedlands, Western Australia
- Japar Sidik, B., Lamri, A., Muta Harah, Z., Muhamad Saini, S., Mansoruddin, A., Josephine, G., & Fazrullah Rizally, A. R. (1997). *Halophila decipiens* (Hydrocharitaceae), A new seagrass for Sabah. *Sandakaniana*, 9, 67–75
- Japar Sidik, B., & Muta Harah, Z. (2003). Seagrasses in Malaysia. In Green, E. P., & Short, F. T. (Eds.), *World Atlas of Seagrasses* (pp. 152-160). University of California Press, Berkeley, Los Angeles, London.
- Japar Sidik, B., Muta Harah, Z., & Aziz, A. (2006). Distribution and significance of seagrass ecosystems in Malaysia. *Aquatic Ecosystem Health & Management*, 9(2), 203–214. <https://doi.org/10.1080/14634980600705576>
- Japar Sidik, B., Muta Harah, Z., Fazrullah Rizally, A. R., & Kamin, B. (2000). New observations on *Halophila spinulosa* in Neumayer, Malaysia. *Biologia Marina Mediterranea*, 7(2), 75–78.
- Japar Sidik, B., Muta Harah, Z., Kanamoto, Z., & Mohd Pauzi, A. (2001). Seagrass communities of the Straits of Malacca. In Japar Sidik, B., Arshad, A., Tan, S. G., Daud, S. K., Jambari, H. A., & Sugiyama, S. (Eds.), *Aquatic Resource and Environmental Studies of the Straits of Malacca: Current Research and Reviews*, pp. 81-98. Malacca Straits Research and Development Centre (MASDEC), Universiti Putra Malaysia, Serdang.
- Japar Sidik, B., Muta Harah Z., Lamri Ali, Liew, F., Gumpil, J., Rizally F., & Razak, A. (1999b). *Halophila spinulosa*: An unreported seagrass in Sabah. *Sabah Parks Nature Journal*, 2, 1–9.
- Japar Sidik, B., Muta Harah, Z., Mohd, P. A., & Madhavan, S. (1999). *Halodule* species from Malaysia - Distribution and morphological variation. *Aquatic Botany*, 65(1–4), 33–45. [https://doi.org/10.1016/S0304-3770\(99\)00029-7](https://doi.org/10.1016/S0304-3770(99)00029-7)
- Jeevitha, M., Athiperumalsami, T., & Kumar, V. (2013). Dietary fibre, mineral, vitamin, amino acid and fatty acid content of seagrasses from Tuticorin Bay, Southeast coast of India. *Phytochemistry*, 90, 135–146. <https://doi.org/10.1016/j.phytochem.2013.02.008>
- Johnstone, I. M., & Hudson, B. E. T. (1981). The dugong diet: Mouth sample analysis. *Bulletin of Marine Science*, 31(3), 681–690.
- Kamarruddin, I. (2008). *National report on seagrass in the South China Sea - Malaysia*. Retrieved from http://www.unepscs.org/remository/Download/19_-_Technical_Publications_and_Guidelines/National_Reports/03_National_Reports_on_Seagrass.html
- Kataoka, T., Mori, T., Wakai, Y., Palma, J., Yaptinchay, A.A., de Veyra, R. & Trono, R. (1995). *Dugongs of the Philippines: A Report of the Joint Dugong Research and Conservation Programme*. May 1995. Toba Aquarium and the Pawikan

Conservation Project, Japan. 267 pp.

- Kendrick, G. A., Waycott, M., Carruthers, T. J. B., Cambridge, M. L., Hovey, R., Krauss, S. L., ... Verduin, J. J. (2012). The Central Role of Dispersal in the Maintenance and Persistence of Seagrass Populations. *BioScience*, 62(1), 56–65. <https://doi.org/10.1525/bio.2012.62.1.10>
- Kilminster, K., McMahon, K., Waycott, M., Kendrick, G. A., Scanes, P., McKenzie, L., ... Udy, J. (2015). Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment*, 534, 97–109. <https://doi.org/10.1016/j.scitotenv.2015.04.061>
- Kilminster, K. L., Walker, D. I., Thompson, P. A., & Raven, J. A. (2006). Limited nutritional benefit to the seagrass *Halophila ovalis*, in culture, following sediment organic matter enrichment. *Estuarine, Coastal and Shelf Science*, 68: 675–685
- Kirsch, K., Valentine, J., & Heck, K. (2002). Parrotfish grazing on turtlegrass *Thalassia testudinum*: evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. *Marine Ecology Progress Series*, 227, 71–85. <https://doi.org/10.3354/meps227071>
- Koenig, W. D. (1999). Spatial autocorrelation of ecological phenomena. *Trends in Ecology & Evolution*, 14, 22–26. [https://doi.org/10.1016/s0169-5347\(98\)01533-x](https://doi.org/10.1016/s0169-5347(98)01533-x)
- Kohler, K. E., & Gill, S. M. (2006). Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences*, 32(9), 1259–1269. <https://doi.org/10.1016/j.cageo.2005.11.009>
- Kuo, J., & den Hartog, C. (2001). Chapter 02 – Seagrass taxonomy and identification key. In In Short, F. T., & Coles, R. G. (Eds.), *Global Seagrass Research Methods* (pp. 31–58). <https://doi.org/10.1016/B978-044450891-1/50003-7>
- Kwan, D. (2002). *Towards a sustainable indigenous fishery for dugongs in Torres Strait: a contribution of empirical data analysis and process* (Doctorate dissertation, James Cook University, Australia).
- Laca, E. A., Distel, R. A., Griggs, T. C., Deo, G. P., & Demment, M. W. (1993). Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilization. *XVII International Grassland Congress*, (April 2016), 709–710. Retrieved from <https://www.researchgate.net/publication/284107676>
- Langvatn, R., & Hanley, T. A. (1993). Feeding patch choice by red deer in relation to foraging efficiency: an experiment. *Oecologia*, 95, 164–170. <https://doi.org/10.1007/BF00323486>
- Lanyon, J. (1991). The nutritional ecology of the dugong (*Dugong dugon*) in tropical North Queensland (Doctorate dissertation, Monash University, Australia)
- Lanyon, J. M., Limpus, C. J., & Marsh, H. (1989). Dugongs and turtles - grazers in the seagrass system. *Biology of Seagrasses*, 610–634. Retrieved from <papers2://publication/uuid/90065F1E-9F4E-4072-8AE2-B1AFDD872FFF>
- Lanyon, J. M., & Marsh, H. (1995). Digesta passage times in the Dugong. *Australian Journal of Zoology*, 43(2), 119–127. <https://doi.org/10.1071/ZO9950119>
- Lanyon, J. M., & Sanson, G. D. (2006a). Degenerate dentition of the dugong (Dugong

- dugon), or why a grazer does not need teeth: Morphology, occlusion and wear of mouthparts. *Journal of Zoology*, 268(2), 133–152. <https://doi.org/10.1111/j.1469-7998.2005.00004.x>
- Lanyon, J. M., & Sanson, G. D. (2006b). Mechanical disruption of seagrass in the digestive tract of the dugong. *Journal of Zoology*, 270(2), 277–289. <https://doi.org/10.1111/j.1469-7998.2006.00135.x>
- Lanyon, J. M., & Marsh, H. (1995). Temporal changes in the abundance of some tropical intertidal seagrasses in North Queensland. *Aquatic Botany*, 49(4), 217–237. [https://doi.org/10.1016/0304-3770\(94\)00435-O](https://doi.org/10.1016/0304-3770(94)00435-O)
- Larkum, A. W. D., Kendrick, G. A., & Ralph, P. J. (2018). *Seagrasses of Australia: Structure, ecology and conservation*. Springer International Publishing. <https://doi.org/10.1007/978-3-319-71354-0>
- Larkum, A. W. D., Orth, R. J., & Duarte, C. M. (2006). *Seagrasses: Biology, Ecology, and Conservation*. Springer, Dordrecht, Netherlands.
- Lawler, I. R., Aragones, L., Berding, N., Marsh, H., Foley, W., Lawler, I. R., ... Foley, W. (2006). Near-Infrared Reflectance Spectroscopy is a Rapid, Cost-Effective Predictor of Seagrass Nutrients. *Journal of Chemical Ecology*, 32, 1353–1365. <https://doi.org/10.1007/s10886-006-9088-x>
- Lee, K. S., Park, S. R., & Kim, Y. K. (2007). Effects of irradiance, temperature, and nutrients on growth dynamics of seagrasses: A review. *Journal of Experimental Marine Biology and Ecology*, 350(1–2), 144–175. <https://doi.org/10.1016/j.jembe.2007.06.016>
- Lefebvre, A., Thompson, C. E. L., Collins, K. J., & Amos, C. L. (2009). Use of a high-resolution profiling sonar and a towed video camera to map a *Zostera marina* bed, Solent, UK. *Estuarine, Coastal and Shelf Science*, 82(2), 323–334. <https://doi.org/10.1016/j.ecss.2009.01.027>
- Legendre, P., & Fortin, M. J. (1989). Spatial pattern and ecological analysis. *Vegetatio* 80, 107-138. <https://doi.org/10.1007/BF00048036>
- Lipkin, Y. (1975). Food of the red sea dugong (Mammalia: Sirenia) from Sinai. *Israel Journal of Zoology*, 24(3–4), 81–98. <https://doi.org/10.1080/00212210.1975.10688415>
- Longstaff, B. J., & Dennison, W. C. (1999). Seagrass survival during pulsed turbidity events: the effects of light deprivation on the seagrasses *Halodule pinifolia* and *Halophila ovalis*. *Aquatic Botany*, 65, 105-121
- López, I. G. M., Van Den Akker, M., Walk, L., Van Katwijk, M. M., Van Der Heide, T., & Van Tussenbroek, B. I. (2019). Nutrient availability induces community shifts in seagrass meadows grazed by turtles. *PeerJ*, 2019(9). <https://doi.org/10.7717/peerj.7570>
- Lucero, R. S. (2010). Population Estimate and Foraging Niche of Dugong (*Dugong dugon*) in Davao Gulf. *Proceedings of the 5th International Symposium on SEASTAR 2000 and Asian Bio-logging Science (The 9th SEASTAR 2000 workshop)* (pp. 59–62). Retrieved from https://repository.kulib.kyoto-u.ac.jp/dspace/bitstream/2433/107335/1/9thSeastar_59.pdf
- Mansor, M. I., Ahmad, A., Kushairi, M. R. M., & Marsh, H. (2000). Dugongs in Peninsular Malaysia. *FRI Newsletter Vol. 5 No: 1*.

- Marbà, N., Hemminga, M. A., Mateo, M. A., Duarte, C. M., Mass, Y. E. M., Terrados, J., & Gacia, E. (2002). Carbon and nitrogen translocation between seagrass ramets. *Marine Ecology Progress Series*, 226, 287–300. <https://doi.org/10.3354/meps226287>
- Mariani, S., & Alcoverro, T. (1999). A multiple-choice feeding-preference experiment utilising seagrasses with a natural population of herbivorous fishes. *Marine Ecology Progress Series*, 189, 295–299. <https://doi.org/10.3354/meps189295>
- Marsh, H., Heinsohn, G. E., & Marsh, L. M. (1984). Breeding cycle, life history and population dynamics of the dugong, *Dugong dugon* (Sirenia:Dugongidae). *Australian Journal of Zoology*, 32(6), 721–742. <https://doi.org/10.1071/ZO9840767>
- Marsh, H., Penrose, H., Eros, C., & Hugues, J. (2002). *Dugong Status Report and Action Plans for Countries and Territories. Early Warning and Assessments Report Series, UNEP/DEWA/RS.02-1. UNEP, Kenya.*
- Marsh, H., Channells, P. W., Heinsohn, G. E., & Morrissey, J. (1982). Analysis of Stomach Contents of Dugongs from Queensland. *Aust. Wildl. Res.*, 9, 55–67.
- Marsh, H., De'ath, G., Gribble, N., & Lane, B. (2005). Historical marine population estimates: Triggers or targets for conservation? The dugong case study. *Ecological Applications*, 15(2), 481–492. <https://doi.org/10.1890/04-0673>
- Marsh, H., Eros, C., Corkeron, P., & Breen, B. (1999). A conservation strategy for dugongs: Implications of Australian research. *Marine and Freshwater Research*. CSIRO. <https://doi.org/10.1071/MF99080>
- Marsh, H., O'Shea, T. J., & Reynolds III, J. E. (2011). *Ecology and conservation of the Sirenia: Dugongs and Manatees*. Cambridge University Press. <https://doi.org/10.1080/17451000.2012.727231>
- Marsh, H., & Sobotzick, S. (2015). The IUCN Red List of Threatened Species. <https://doi.org/10.2305/IUCN.UK.2015-4.RLTS.T6909A43792211.en>
- Marsh, H., Spain, A. V., & Heinsohn, G. E. (1978). Physiology of the dugong. *Comp. Biochem. Physiol.*, 61A, 159–168.
- Marshall, H. H., Carter, A. J., Ashford, A., Rowcliffe, J. M., & Cowlshaw, G. (2013). How do foragers decide when to leave a patch? A test of alternative models under natural and experimental conditions. *Journal of Animal Ecology*, 82, 892–902. <https://doi.org/10.1111/1365-2656.12089>
- Marshall, C. D., Maeda, H., Iwata, M., Furuta, M., Asano, S., Rosas, F., & Reep, R. L. (2003). Orofacial morphology and feeding behaviour of the dugong, Amazonian, West African and Antillean manatees (Mammalia: Sirenia): functional morphology of the muscular-vibrissal complex. *Journal of Zoology*, 259(3), 245–260. <https://doi.org/10.1017/S0952836902003205>
- Masini, R. J., Anderson, P. K., & McComb, A. J. (2001). A *Halodule*-dominated community in a subtropical embayment: physical environment, productivity, biomass, and impact of dugong grazing. *Aquatic Botany*, 71(3), 179–197. [https://doi.org/10.1016/S0304-3770\(01\)00181-4](https://doi.org/10.1016/S0304-3770(01)00181-4)
- Mathur, M. (2015). *Spatial autocorrelation analysis in plant population: An overview*. *Journal of Applied and Natural Science* (Vol. 7). Retrieved from www.ansfoundation.org

- Mazlan, H., Nurul Nadiah, Y., Samsudin, A., Komatsu, T., Syarifuddin, M., & Md Nadzri, R. (2014). Determination of seagrass biomass at Merambong Shoal in Straits of Johor using satellite remote sensing technique. *Malayan Nature Journal*, 66(JUNE), 20–37.
- McDonald, M. S. (2003). *Photobiology of Higher Plants*. John Wiley and Sons
- McKenzie, L. J. (2003). *Guidelines for the rapid assessment of seagrass habitats in the western Pacific*. Queensland: Department of Primary Industries. Retrieved from http://www.seagrasswatch.org/Methods/Manuals/SeagrassWatch_Rapid_Assessment_Manual.pdf
- McKenzie, L. J., Finkbeiner, M. A., & Kirkman, H. (2001). Chapter 05 – Methods for mapping seagrass distribution. In Short, F. T., & Coles, R. G. (Eds.), *Global Seagrass Research Methods* (pp. 101–121). <https://doi.org/10.1016/B978-044450891-1/50006-2>
- McMahon, K. (2005). *Recovery of subtropical seagrasses from natural disturbance* (Doctorate dissertation, University of Queensland, Australia).
- McMahon, K. M., Evans, R. D., Van Dijk, K. J., Hernawan, U., Kendrick, G. A., Lavery, P. S., ... Waycott, M. (2017). Disturbance is an important driver of clonal richness in tropical seagrasses. *Frontiers in Plant Science*, 8. <https://doi.org/10.3389/fpls.2017.02026>
- McMahon, K., van Dijk, K. -j., Ruiz-Montoya, L., Kendrick, G. A., Krauss, S. L., Waycott, M., ... Duarte, C. (2014). The movement ecology of seagrasses. *Proceedings of the Royal Society B: Biological Sciences*, 281(1795), 20140878–20140878. <https://doi.org/10.1098/rspb.2014.0878>
- McMahon, K., Collier, C., & Lavery, P. S. (2013). Identifying robust bioindicators of light stress in seagrasses: A meta-analysis. *Ecological Indicators*, 30, 7–15. <https://doi.org/10.1016/j.ecolind.2013.01.030>
- McNaughton, S. J. (1984). Grazing lawns: animals in herds, plant form, and coevolution. *The American Naturalists* 124, 863–886.
- Mellors, J. E. (2003). *Sediment and nutrient dynamics in coastal intertidal seagrass of north eastern tropical Australia* (Doctorate dissertation, James Cook University, Australia). Retrieved from <https://www.researchgate.net/publication/277256601>
- Mellors, J., Waycott, M., & Marsh, H. (2005). Variation in biogeochemical parameters across intertidal seagrass meadows in the central Great Barrier Reef region. In *Marine Pollution Bulletin* (Vol. 51, pp. 335–342). <https://doi.org/10.1016/j.marpolbul.2004.10.046>
- Mignucci-Giannoni, A. A., & Beck, C. A. (1998). The diet of the manatee (*Trichechus manatus*) in Puerto Rico. *Marine Mammal Science*, 14(2), 394–397.
- Mohamed, H., Nadaoka, K., & Nakamura, T. (2018). Assessment of machine learning algorithms for automatic benthic cover monitoring and mapping using towed underwater video camera and high-resolution satellite images. *Remote Sensing*, 10(5). <https://doi.org/10.3390/rs10050773>
- Molina Hernández, A., & van Tussenbroek, B. (2014). Patch dynamics and species shifts in seagrass communities under moderate and high grazing pressure by green sea turtles. *Marine Ecology Progress Series*, 517, 143–157. <https://doi.org/10.3354/meps11068>

- Moran, P. A. P. (1948). The Interpretation of Statistical Maps. *Journal of the Royal Statistical Society: Series B (Methodological)*, 10(2), 243–251. <https://doi.org/10.1111/j.2517-6161.1948.tb00012.x>
- Mtwana Nordlund, L., Koch, E. W., Barbier, E. B., & Creed, J. C. (2016). Seagrass ecosystem services and their variability across genera and geographical regions. *PLoS ONE*, 11(10). <https://doi.org/10.1371/journal.pone.0163091>
- Mukai, H., Aioi, K., Lewmanomont, K., Matsumasa, M., Nakaoka, M., Nojima, S., Supanwanid, C., Suzuki, T., & Toyohara, T. (1999). Dugong grazing on *Halophila* beds in Haad Chao Mai National Park, Trang Province, Thailand— How many dugongs can survive? p. 239–254. In Koike, I. (Eds.), *Effects of Grazing and Disturbance by Dugongs and Turtles on Tropical Seagrass Ecosystems*, Ocean Research Institute, University of Tokyo, Tokyo, Japan.
- Muta Harah, Z., Japar Sidik, B., & Fazrullah Rizally, A. R. (2003). Occurrence and Morphological Description of Seagrasses from Pulau Redang, Terengganu, Malaysia. *Jurnal Teknologi*, 38(1), 29–39. <https://doi.org/10.11113/jt.v38.491>
- Muta Harah, Z., & Sidik, B. J. (2013). Occurrence and Distribution of Seagrasses in Waters of Perhentian Island Archipelago, Malaysia. *Journal of Fisheries and Aquatic Science*, 8(3), 441–451. <https://doi.org/10.3923/jfas.2013.441.451>
- Nadarajah, C. (2000). *Breaking The Surface: A Study Of Whales, Dolphins and Dugongs in Peninsular Malaysia*. WWF Malaysia, Malaysia.
- Nakanishi, Y., Adulyanukosol, K., Arai, N., Hosoya, S., Nakanishi, Y., Kotani, K., & Katsukoshi, K. (2008). Dugong grazing scars confirmed in *Enhalus acoroides* meadows. *Journal of Advanced Marine Science and Technology Society*, 14(2), 1–8.
- Nakanishi, Y., Hosoya, S., Arai, N., Katsukoshi, K., & Adulyanukosol, K. (2006). The distribution of seagrass meadows and dugong feeding trails in the dry season around Talibong Island , Trang Province , Thailand. *Proceeding of the 3rd International Symposium on SEASTAR2000 and Asian Biologging Science, Bangkok, Thailand*, 55–62.
- Nakanishi, Y., Hosoya, S., Nakanishi, Y., Arai, N., & Adulyanukosol, K. (2005). The distribution of dugong trenches in the seagrass beds of Libong Island, Thailand. *Journal of Advanced Marine Science and Technology Society*, 11(1), 53–57.
- Nakaoka, M., & Aioi, K. (1999). Growth of seagrass *Halophila ovalis* at dugong trails compared to existing within-patch variation in a Thailand intertidal flat. *Marine Ecology Progress Series*, 184, 97–103. <https://doi.org/10.3354/meps184097>
- Nakaoka, M., Mukai, H., & Chunhabundit, S. (2002). Impacts of dugong foraging on benthic animal communities in a Thailand seagrass bed. *Ecological Research*, 17(6), 625–638. <https://doi.org/10.1046/j.1440-1703.2002.00520.x>
- Nasr, D., Shawky, A. M., & Vine, P. (2019). Status of Red Sea Dugongs. In Rasul, N. M. A., & Stewart I. C. F. (Eds.), *Oceanographic and Biological Aspects of the Red Sea* (pp. 327–354). Springer Oceanography. https://doi.org/10.1007/978-3-319-99417-8_18
- Nuridin, A., Suprayogi, A., Satyaningtjas, A. S., & Darusman, H. S. (2019). Nutrition Value, Feed Efficiency and Species of Seagrass as a Feed of Wild Dugong (*Dugong dugon*) in Lingayan island, Tolitoli, Central Sulawesi. *Journal of the*

- Ooi, J. L. S., Van Niel, K. P., Kendrick, G. A., & Holmes, K. W. (2014). Spatial structure of seagrass suggests that size-dependent plant traits have a strong influence on the distribution and maintenance of tropical multispecies meadows. *PLoS ONE*, 9(1). <https://doi.org/10.1371/journal.pone.0086782>
- Ooi, J. L. S., Affendi, Y. A., & Phang, S. M. (2008). *PHASE II Dugongs in Peril : The Conservation and Protection of Dugongs in Johor , Malaysia Part I : Seagrass Survey Report JULY 2008*. Report to Titan Chemical Corp. Bhd, Pasir Gudang, Malaysia.
- Ooi, J. L. S., Kendrick, G. A., & Van Niel, K. P. (2011a). Effects of sediment burial on tropical ruderal seagrasses are moderated by clonal integration. *Continental Shelf Research*, 31(19–20), 1945–1954. <https://doi.org/10.1016/j.csr.2011.09.005>
- Ooi, J. L. S., Kendrick, G. A., Van Niel, K. P., & Affendi, Y. A. (2011b). Knowledge gaps in tropical Southeast Asian seagrass systems. *Estuarine, Coastal and Shelf Science*, 92(1), 118–131. <https://doi.org/10.1016/j.ecss.2010.12.021>
- Orth, R. J., Carruthers, T. J. B., Dennison, W. C., Duarte, C. M., Fourqurean, J. W., Heck, K. L., ... Williams, S. L. (2006). A Global Crisis for Seagrass Ecosystems. *BioScience*, 56(12), 987. [https://doi.org/10.1641/0006-3568\(2006\)56\[987:agcfse\]2.0.co;2](https://doi.org/10.1641/0006-3568(2006)56[987:agcfse]2.0.co;2)
- Owen-Smith, N., & Novellie, P. (1982). What Should a Clever Ungulate Eat? In *The American Naturalist*, 119, 151–178. https://doi.org/10.5822/978-1-61091-678-3_12
- Perrin, W. F., Reeves, R. R., Dolar, M. L. L., Jefferson, T. a, Marsh, H., Wang, J. Y., & Estacion, J. (2005). *Report of the Second Workshop on The Biology and Conservation of Small Cetaceans and Dugongs of South-East Asia*. UNEP/CMS Secretariat.
- Perry, C. J., & Dennison, W. C. (1999). Microbial nutrient cycling in seagrass sediment. *Journal of Australian Geology & Geophysics*, 17, 227–231.
- Phang, S. M. (2000). *Seagrasses of Malaysia*. Universiti Malaya, Botanical Monographs No. 2. Institute of Biological Sciences, Universiti Malaya, Kuala Lumpur
- Polit, D.F. (2010). *Statistics and Data Analysis for Nursing Research*, 2nd ed. Pearson Education, Upper Saddle River, New Jersey.
- Ponnampalam, L. S. (2014). Medics and Marine Mammals – An Unlikely but Important Connection for Humanity’s Survival. *Malays J Med Sci.*, 21(2), 1–3. Retrieved from http://repository.um.edu.my/37015/1/Ponnampalam_2014_MJMS-21-2-001.pdf
- Ponnampalam, L. S. (2017). *A three-pronged approach for overcoming knowledge barriers on the ecology and status of dugongs in Johor, Malaysia – Towards critical habitat protection*. Narrative Report #3: Year 3 (Final) Progress Report of PEW Fellowship in Marine Conservation (2014 – 2017). Report submitted to The PEW Charitable Trusts.
- Ponnampalam, L. S., Fairul Izmal, J. H., Adulyanukosol, K., Ooi, J. L. S., & Reynolds III, J. E. (2015). Aligning conservation and research priorities for proactive species and habitat management: the case of dugongs *Dugong dugon* in Johor, Malaysia.

- Oryx*, 49(4), 743–749. <https://doi.org/10.1017/S0030605313001580>
- Prado, P., & Heck, K. L. (2011). Seagrass selection by omnivorous and herbivorous consumers: Determining factors. *Marine Ecology Progress Series*, 429, 45–55. <https://doi.org/10.3354/meps09076>
- Preen, A. (1995a). Diet of Dugongs : Are They Omnivores? *Journal of Mammalogy*, 76(1), 163–171.
- Preen, A. (1995b). Impacts of dugong foraging on seagrass habitats: observational and experimental evidence for cultivation grazing. *Marine Ecology Progress Series*, 124(1–3), 201–213. <https://doi.org/10.3354/meps124201>
- Preen, A., & Marsh, H. (1995). Response of dugongs to large-scale loss of seagrass from Hervey Bay, Queensland Australia. *Wildlife Research*, 22(4), 507–519. <https://doi.org/10.1071/WR9950507>
- Preen, A. R. (1992). *Interactions between dugongs and seagrass in a subtropical environment* (Doctorate dissertation, James Cook University, Australia).
- Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal Foraging: A Selective Review of Theory and Tests. *The Quarterly Review of Biology*, 52(2), 137–154. <https://doi.org/10.1086/409852>
- Rajamani, L., & Marsh, H. (2010). Using parallel regional-and local-scale initiatives to inform conservation management of rare wildlife: A case study of the dugong *Dugong dugon* in Sabah, Malaysia. *Endangered Species Research*, 13(1), 17–23. <https://doi.org/10.3354/esr00310>
- Rajamani, L., & Marsh, H. (2015). Mapping seagrass cost-effectively in the Coral Triangle: Sabah, Malaysia as a case study. *Pacific Conservation Biology*, 21(2), 113–121. <https://doi.org/10.1071/PC14908>
- Rasheed, M., O'grady, D., & Scott, E. (2016). *Dugong Feeding Ecology and Habitat Use on Intertidal Banks of Port Curtis and Rodds Bay – Interim Progress Report 2015*. Report produced for the Ecosystem Research and Monitoring Program Advisory Panel as part of Gladstone Ports Corporation's Ecosystem Research and Monitoring Program. Centre for Tropical Water & Aquatic Ecosystem Research (TropWATER) Publication 16/14, James Cook University, Cairns, 30 pp.
- Roguet, C., Dumont, B., & Prache, S. (1998). Selection and use of feeding sites and feeding stations by herbivores: A review. *Animal Research*. <https://doi.org/10.1051/animres:19980401>
- Rossi, R. E., Mulla, D. J., Journel, A. G., & Franz, E. H. (1992). Geostatistical tools for modeling and interpreting ecological spatial dependence. *Ecological Monographs*, 62(2), 277–314. <https://doi.org/10.2307/2937096>
- R Core Team (2018). *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Version 4.0.0
- Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., ... Young, B. E. (2008). The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science*, 322(5899), 225–230. <https://doi.org/10.1126/science.1165115>
- Scott, A. L., York, P. H., Duncan, C., Macreadie, P. I., Connolly, R. M., Ellis, M. T., ... Rasheed, M. A. (2018). The role of herbivory in structuring tropical seagrass

- ecosystem service delivery. *Frontiers in Plant Science*, 9. <https://doi.org/10.3389/fpls.2018.00127>
- Searle, K. R., Thompson Hobbs, N., & Shipley, L. A. (2005). Should I stay or should I go? Patch departure decisions by herbivores at multiple scales. *Oikos*, 111(3), 417–424. <https://doi.org/10.1111/j.0030-1299.2005.13918.x>
- Seidel, D. P., & Boyce, M. S. (2015). Patch-use dynamics by a large herbivore. *Movement Ecology*, 3, 7. <https://doi.org/10.1186/s40462-015-0035-8>
- Senft, R. L., Coughenour, M. B., Bailey, D. W., Rittenhouse, L. R., Sala, O. E., & Swift, D. M. (1987). Large herbivore foraging and ecological hierarchies: Landscape ecology can enhance traditional foraging theory. *BioScience*, 37(789–799), 789–795.
- Serusi, S., Dr. Verhoef, W., Dr. Clevers, J., & Dr. Schlerf, M. (2010). *Estimation of leaves nutrient content in seagrass using spectral data The case of Halodule uninervis*. (Master's Thesis, International Institute for Geo-Information and Earth Observation, Enschede, The Netherlands).
- Shawky, A. M. (2018). Ecological and Behavioural Studies on the Dugong (*Dugong dugon*) Inhabiting Marsa Alam Egyptian Red Sea (Doctorate dissertation, Suez Canal University, Egypt).
- Shawky, A. M. (2019). Evidence of the occurrence of a large dugong in the Red Sea, Egypt. *Egyptian Journal of Aquatic Research*, 45(3), 247–250. <https://doi.org/10.1016/j.ejar.2019.08.001>
- Sheppard, J. K., Lawler, I. R., & Marsh, H. (2007). Seagrass as pasture for seacows: Landscape-level dugong habitat evaluation. *Estuarine, Coastal and Shelf Science*, 71(1–2), 117–132. <https://doi.org/10.1016/j.ecss.2006.07.006>
- Sheppard, J. K., Carter, A. B., McKenzie, L. J., Pitcher, C. R., & Coles, R. G. (2008). Spatial patterns of sub-tidal seagrasses and their tissue nutrients in the Torres Strait, northern Australia: Implications for management. *Continental Shelf Research*, 28(16), 2282–2291. <https://doi.org/10.1016/j.csr.2008.03.033>
- Sheppard, J. K., Jones, R. E., Marsh, H., & Lawler, I. R. (2009). Effects of Tidal and Diel Cycles on Dugong Habitat Use. *Journal of Wildlife Management*, 73(1), 45–59. <https://doi.org/10.2193/2007-468>
- Sheppard, J. K., Marsh, H., Jones, R. E., & Lawler, I. R. (2010). Dugong habitat use in relation to seagrass nutrients, tides, and diel cycles. *Marine Mammal Science*, 26(4), 855–879. <https://doi.org/10.1111/j.1748-7692.2010.00374.x>
- Sheppard, J. K., Preen, A. R., Marsh, H., Lawler, I. R., Whiting, S. D., & Jones, R. E. (2006). Movement heterogeneity of dugongs, *Dugong dugon* (Müller), over large spatial scales. *Journal of Experimental Marine Biology and Ecology*, 334(1), 64–83. <https://doi.org/10.1016/j.jembe.2006.01.011>
- Sheppard, J. K. (2008). *The Spatial Ecology of Dugongs : Applications to Conservation Management* (Doctorate dissertation, James Cook University, Australia). Retrieved from <https://researchonline.jcu.edu.au/2097/>
- Shipley, L. A. (2007). The influence of bite size on foraging at larger spatial and temporal scales by mammalian herbivores. *Oikos*. <https://doi.org/10.1111/j.2007.0030-1299.15974.x>

- Short, F., Dennison, W., & Capone, D. (1990). Phosphorus-limited growth of the tropical seagrass *Syringodium filiforme* in carbonate sediments. *Marine Ecology Progress Series*, 62, 169–174. <https://doi.org/10.3354/meps062169>
- Short, F. T., Coles, R. G., & Pergent-Martini, C. (2001). Chapter 01 - Global seagrass distribution. In Short, F. T., & Coles, R. G. (Eds.), *Global Seagrass Research Methods* (Vol. 33, pp. 5–30). Elsevier B.V. <https://doi.org/10.1017/CBO9781107415324.004>
- Sokal, R. R., & Oden, N. L. (1978). Spatial autocorrelation in biology: 1. Methodology. *Biological Journal of the Linnean Society*, 10(2), 199–228. <https://doi.org/10.1111/j.1095-8312.1978.tb00013.x>
- Sørensen, S. T., Campbell, M. L., Duke, E., & Manley-Harris, M. (2018). A standard, analytical protocol for the quantitation of non-structural carbohydrates in seagrasses that permits inter-laboratory comparison. *Aquatic Botany*, 151, 71–79. <https://doi.org/10.1016/j.aquabot.2018.08.006>
- Stapel, J., Aarts, T. L., van Duynhoven B. H. M., de Groot JD, van den Hoogen PHW, Hemminga MA (1996) Nutrient uptake by leaves and roots of the seagrass *Thalassia hemprichii* in the Spermonde Archipelago, Indonesia. *Marine Ecology Progress Series*, 134:195–206
- Stephens, D. W., & Krebs, J. R. (1986, January). Foraging Theory. *Princeton University Press, Princeton*. Plenum Press. <https://doi.org/10.1046/j.1420-9101.1988.1010086.x>
- Sterner, R. W., & Elser, J. J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, USA
- Supanwanid, C. (1996). Recovery of the seagrass *Halophila ovalis* after grazing by dugong. In: Kuo J, Phillips RC, Walker DI, Kirkman H (ed) *Seagrass Biology: Proceedings of an International Workshop, Rottnest Island, Western Australia*, pp. 315–318.
- Temminghoff, E. J. M., & Houba, V. J. G. (2004). *Plant Analysis Procedures*. [https://doi.org/10.1002/1521-3773\(20010316\)40:6<9823::AID-ANIE9823>3.3.CO;2-C](https://doi.org/10.1002/1521-3773(20010316)40:6<9823::AID-ANIE9823>3.3.CO;2-C)
- Thayer, G. W., Bjorndal, K. A., Ogden, J. C., Willia, S. L., & Zieman, J. C. (1984). Role of larger herbivores in seagrass communities. *Estuaries*, 7(4), 351–376. <https://doi.org/10.2307/1351619>
- Thewissen, J. G. M., & Jo Schneider, B. (2009). Marine Mammal Evolution BT - Encyclopedia of Marine Mammals (Second Edition) (p. 692). <https://doi.org/https://doi.org/10.1016/B978-0-12-373553-9.00160-7>
- The Star (2005). A sanctuary in Johor for dugongs. Retrieved from <https://www.thestar.com.my/news/nation/2005/06/17/a-sanctuary-in-johor-for-dugongs/> (Accessed 22 November 2019)
- The Star (2016). Johor allocates RM1mil to set up dugong sanctuary. Retrieved from <https://www.thestar.com.my/news/nation/2016/05/15/johor-allocates-rm1mil-to-set-up-dugong-sanctuary/> (Accessed 22 November 2019)
- Tol, S. J., Coles, R. G., & Congdon, B. C. (2016). *Dugong dugon* feeding in tropical Australian seagrass meadows: implications for conservation planning. *PeerJ*, 1–17. <https://doi.org/10.7717/peerj.2194>

- Tol, S. J., Jarvis, J. C., York, P. H., Grech, A., Congdon, B. C., & Coles, R. G. (2017). Long distance biotic dispersal of tropical seagrass seeds by marine mega-herbivores. *Scientific Reports*, 7(1), 4458. <https://doi.org/10.1038/s41598-017-04421-1>
- Tsalyuk, M., Kilian, W., Reineking, B., & Getz, W. M. (2019). Temporal variation in resource selection of African elephants follows long-term variability in resource availability. *Ecological Monographs*, 89(2). <https://doi.org/10.1002/ecm.1348>
- Tsutsumi, C., Ichikawa, K., Akamatsu, T., Arai, N., Shinke, T., Hara, T., & Adulyanukosol, K. (2005). Monitoring dugong feeding behavior in a tidal flat by visual and acoustic observation. *Proceedings of the 2nd International symposium on SEASTAR2000 and Asian Bio-logging Science (The 6th SEASTAR2000 Workshop)* (pp. 37–42). Retrieved from https://repository.kulib.kyoto-u.ac.jp/dspace/bitstream/2433/44082/1/6thSEASTAR_37.pdf
- Unsworth, R. K. F., McKenzie, L. J., Collier, C. J., Cullen-Unsworth, L. C., Duarte, C. M., Eklöf, J. S., ... Nordlund, L. M. (2019). Global challenges for seagrass conservation. *Ambio*, 48(8), 801–815. <https://doi.org/10.1007/s13280-018-1115-y>
- Unsworth, R. K. F., Nordlund, L. M., & Cullen-Unsworth, L. C. (2019). Seagrass meadows support global fisheries production. *Conservation Letters*, 12(1). <https://doi.org/10.1111/conl.12566>
- Valentine, J. F., & Heck, K. L. (2020). Herbivory in Seagrass Meadows: an Evolving Paradigm. *Estuaries and Coasts*. <https://doi.org/10.1007/s12237-020-00849-3>
- Valone, T. J. (1991). Bayesian and prescient assessment: foraging with pre-harvest information. *Animal Behaviour*, 41, 569–577. [https://doi.org/10.1016/S0003-3472\(05\)80897-8](https://doi.org/10.1016/S0003-3472(05)80897-8)
- van de Koppel, J. D. E., Huisman, J., van der Wal, R., & Olf, H. (1996). Patterns of herbivory along a productivity gradient: An empirical and theoretical investigation. *Ecology*, 77, 736–745. <https://doi.org/10.2307/2265498>
- van der Wal, R., van de Koppel, J., & Sagel, M. (1998). On the relation between herbivore foraging efficiency and plant standing crop: An experiment with barnacle geese. *Oikos*, 82, 123–130. <https://doi.org/10.2307/3546922>
- Van Soest, P. J. (1994). *Nutritional ecology of the ruminant, 2nd edn*. Comstock, Ithaca
- van Tussenbroek, B., Vonk, J. A., Stapel, J., Erftemeijer, P. L. A., Middelburg, J. J., & Zieman, J. C. (2006). The biology of *Thalassia*: Paradigms and recent advances in research. In Larkum, A. W. D., Orth, R. J., & Duarte, C. M. (Eds.), *Seagrasses: Biology, Ecology and Conservation* (pp. 409–439). Springer Netherlands. https://doi.org/10.1007/978-1-4020-2983-7_18
- Varikoden, H., Preethi, B., Samah, A. A., & Babu, C. A. (2011). Seasonal variation of rainfall characteristics in different intensity classes over Peninsular Malaysia. *Journal of Hydrology*, 404(1–2), 99–108. <https://doi.org/10.1016/j.jhydrol.2011.04.021>
- Vásquez, R. A., Grossi, B., & Márquez, I. N. (2006). On the value of information: studying changes in patch assessment abilities through learning. *Oikos*, 112, 298–310. <https://doi.org/10.1111/j.0030-1299.2006.13530.x>
- Vavra, M., & Ganskopp, D. (1998). Grazing behavior in ungulates: Current concepts and future challenges. *Annals of Arid Zone*, 37, 319–335.

- Vincent, A. C. J., Foster, S. J., & Koldewey, H. J. (2011). Conservation and management of seahorses and other Syngnathidae. *Journal of Fish Biology*, 78(6), 1681–1724. <https://doi.org/10.1111/j.1095-8649.2011.03003.x>
- Vivas, H. J., & Saether, B. E. (1987). Interactions between a generalist herbivore, the moose *Alces alces*, and its food resources: An experimental study of winter foraging behaviour in relation to browse availability. *Journal of Animal Ecology*, 56, 509–520. <https://doi.org/10.2307/5064>
- Vonk, J. A., Pijnappels, M. H. J., & Stapel, J. (2008). In situ quantification of *Tripneustes gratilla* grazing and its effects on three co-occurring tropical seagrass species. *Marine Ecology Progress Series*, 360, 107–114. <https://doi.org/10.3354/meps07362>
- Wagner, H. H., & Fortin, M.-J. J. (2005). Spatial analysis of landscapes: Concepts and statistics. *Ecology*. <https://doi.org/10.1890/04-0914>
- Walker, D. I., Kendrick, G. A., & McComb, A. J. (1988). The distribution of seagrass species in shark bay, Western Australia, with notes on their ecology. *Aquatic Botany*, 30(4), 305–317. [https://doi.org/10.1016/0304-3770\(88\)90063-0](https://doi.org/10.1016/0304-3770(88)90063-0)
- WallisDeVries, M. F. (1996). Effects of resource distribution patterns on ungulate foraging behaviour: A modelling approach. *Forest Ecology and Management*, 88(1–2), 167–177. [https://doi.org/10.1016/S0378-1127\(96\)03822-4](https://doi.org/10.1016/S0378-1127(96)03822-4)
- WallisDeVries, M. F., Laca, E. A., & Demment, M. W. (1999). The importance of scale of patchiness for selectivity in grazing herbivores. *Oecologia*, 121(3), 355–363. <https://doi.org/10.1007/s004420050939>
- Wan Hazma, W. N., Muta Harah, Z., Japar Sidik, B., & Natrah, F. M. I. (2015). Macro and micro nutrients of tropical seagrasses, *Halophila ovalis*, *H. spinulosa* and *Halodule uninervis* in Johore, Malaysia. *Iranian Journal of Fisheries Sciences*, 14(1), 246–261. Retrieved from <https://www.researchgate.net/publication/281858371>
- Waycott, M., Duarte, C. M., Carruthers, T. J. B., Orth, R. J., Dennison, W. C., Olyarnik, S., ... Williams, S. L. (2009). Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proceedings of the National Academy of Sciences*, 106(30), 12377–12381. <https://doi.org/10.1073/pnas.0905620106>
- Westoby, M. (1974). An analysis of diet selection by large generalist herbivores. *The American Naturalist*, 108, 290e304.
- Wilmshurst, J. F., Fryxell, J. M., & Hudson, R. J. (1995). Forage quality and patch choice by wapiti (*Cervus elaphus*). *Behavioural Ecology*, 6, 209–217. <https://doi.org/10.1093/beheco/6.2.209>
- Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007a). Can you dig it? Use of excavation, a risky foraging tactic, by dugongs is sensitive to predation danger. *Animal Behaviour*, 74(4), 1085–1091. <https://doi.org/10.1016/j.anbehav.2007.02.009>
- Wirsing, A. J., Heithaus, M. R., & Dill, L. M. (2007b). Living on the edge: dugongs prefer to forage in microhabitats that allow escape from rather than avoidance of predators. *Animal Behaviour*, 74(1), 93–101. <https://doi.org/10.1016/j.anbehav.2006.11.016>
- Wongsuryrat, M., Chunkao, K., Prabuddham, P., & Daungsavat, M. (2011).

Distribution, Abundance and Conservation Status of Dugong around Koh Talibong, Trang Province, Thailand. *Journal of Sustainable Development*, 4(3), 118–124. <https://doi.org/10.5539/jsd.v4n3p118>

WWF-Indonesia. (2016). *Dugong and seagrass habitat*.

Yamamuro, M., & Chirapart, A. (2005). Quality of the Seagrass *Halophila ovalis* on a Thai Intertidal Flat as Food for the Dugong. *Journal of Oceanography*, 61(1), 183–186. <https://doi.org/10.1007/s10872-005-0030-6>

Zakaria, M. H., & Bujang, J. S. (2011). Disturbances in seagrass ecosystem in Malaysia. In Ogawa, H., Bujang, J. S., Zakaria, M. H. (Eds.), *Resource Status and Trends in Indonesia, Japan, Malaysia, Thailand and Vietnam* (pp. 67–78). Seizando-Shoten Publishing Co., Tokyo, Japan.

Zulkifli Poh, A. N. (2009). *Dugong feeding patterns and food preferences in Sungai Pulai, Johor* (Unpublished BSc Thesis, Universiti Malaysia Terengganu, Malaysia).

Zuur, A. F., Ieno, E. N., & Smith, G. M. (2007). *Analysing Ecological Data*. Springer, New York

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