



## Benthic primary productivity: production and herbivory of seagrasses, macroalgae and microalgae

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## WAMSI Kimberley Marine Research Program

### Final Report

Project 2.2.4

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## **WAMSI Kimberley Marine Research Program**

Initiated with the support of the State Government as part of the Kimberley Science and Conservation Strategy, the Kimberley Marine Research Program is co-invested by the WAMSI partners to provide regional understanding and baseline knowledge about the Kimberley marine environment. The program has been created in response to the extraordinary, unspoilt wilderness value of the Kimberley and increasing pressure for development in this region. The purpose is to provide science based information to support decision making in relation to the Kimberley marine park network, other conservation activities and future development proposals.

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Image 1: Satellite image of the Kimberley coastline

Image 2: Seagrass collection in Bardi Jawi Indigenous Protected Area (Source: Mat Vanderklift CSIRO)

Image 3: Humpback whale breaching, Exmouth (Image: Pam Osborn)

Image 4: Collection of seagrass by Bardi Jawi Ranger and UWA Research Scientist (Source: Mat Vanderklift CSIRO)

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## Executive Summary

This research addressed seagrass, macroalgal and microalgal abundance, biomass and productivity for the Sunday Island Group (in the Buccaneer Archipelago, Western Australia) and also assessed rates of herbivory on seagrass. The main aim was to understand the role of benthic primary producers in the macrotidal fringing reef and terraced lagoon environments which characterize the Sunday Island Group and are common throughout the Kimberley. The information collected in this project is primary data for three other WAMSI Kimberley Marine Research Program (KMRP) projects (1.1.2 – Key ecological processes, 2.2.5 – Mapping productivity and 2.2.8 – Modelling the future of the Kimberley region).

*Thalassia hemprichii* and *Enhalus acoroides* were the most abundant seagrasses recorded in the raised lagoons of the islands in the Bardi Jawi Indigenous Protected Area around One Arm Point and the Sunday Island Group. Other seagrasses recorded included *Thalassodendron ciliatum*, *Halodule uninervis*, *Halophila ovalis* and *Cymodocea serrulata*. The abundance (measured as biomass and shoot density) and growth (measured as leaf extension) of *T. hemprichii* and *E. acoroides* were variable, and did not follow any evident seasonal or temporal pattern, with the exception of seasonal leaf production for *E. acoroides* at Jalan (Tallon Island) and seasonal shoot density for *T. hemprichii* (Jalan and Laanyi). Flowers of both species were only observed in November 2013. It is possible that flowers are predominantly present during the wet season (November to March). Leaf extension rates were high for both species relative to typical seagrass growth rates, with some measurements exceeding several centimetres per leaf per day.

Macroalgae were found to occupy the seaward margins of lagoons and isolated rocky surfaces among the seagrass meadows. Measurements focused on the abundant genus *Sargassum*, for which five species were recorded. The most abundant was *Sargassum polycystum*. This species also yielded the highest growth rates, which at the peak were in the same order as growth rates for seagrass, and among the highest rates of growth recorded for *Sargassum*. *Sargassum* biomass tended to be highest during April surveys, while the fastest growth rates were recorded during the November 2013 survey, when average extension rates exceeded one centimetre per day. These two observations imply that there is a seasonal pattern of growth of *Sargassum*, with highest growth rates occurring during the wet season.

Benthic microalgae (BMA) were dominated by diatoms. The abundance (measured as chlorophyll *a*) and productivity of benthic microalgae did not vary according to any obvious seasonal pattern — indeed, substantial short-term variations (days) in productivity were observed, suggesting that the benthic microalgae respond to local conditions which in turn are influenced by the tide and day-to-day variations in light. BMA were net producers at two sites for the duration of the study, but were also net respirers at some sites during some surveys. Oxygen and hydrogen sulphide profiles of sediment cores showed patterns that implied high oxygen consumption in some surface sediments, which may be credited to bacterial processes and not BMA.

A productive (fast growing) bacterial community was recorded from benthic and pelagic habitats of the region, indicating a potentially important role by microbial cycling of dissolved nutrients in these systems. The results from this research revealed variable but generally high bacterial carbon production rates that were within or above the range previously reported from tropical coastal ecosystems. Measurements also revealed high bacterial carbon utilisation rates, particularly of carbohydrates, amino acids and polymers. There is potentially high connectivity between benthic and pelagic habitats via the flow of Dissolved Organic Carbon (DOC), with pelagic bacterial communities able to use a benthic dissolved organic carbon source.

Consumption of *T. hemprichii* was generally higher than *E. acoroides* and at times was among the highest recorded in the world. At some sites during some surveys consumption appeared to be greater than production. Spatial and temporal variation was high, and no obvious seasonal patterns were evident.

There were distinct differences in  $\delta^{13}\text{C}$  of the main primary producers, with  $\delta^{13}\text{C}$  of mangroves lower than that of seagrasses or macroalgae. The seagrass *Enhalus* and the macroalgae *Turbinaria* yielded the highest  $\delta^{13}\text{C}$ , and probably have unique methods for capture and uptake of carbon. These data will form the basis for food web

studies in other KMRP projects.

Finally, a major outcome of this project was the strong collaborations established between the project team and the Bardi Jawi rangers. These collaborations enabled deeper insights into the ecology of the region, and demonstrated the value of partnerships to exchange and integrate traditional ecological knowledge with scientific knowledge.

## **Implications for management**

The key considerations and recommendations from this research for natural resource managers and other potential end-users are:

- places that support high biomass and diversity of marine plants are likely to be spatially restricted, and because of their importance to the broader ecosystem these places might warrant higher protection and greater effort placed into long-term observations through monitoring, that allow detection of changes. A systematic approach to identify sites with high biomass and diversity by combining multiple sources of information (e.g. existing environmental data, predictive model outputs, and animal tracks) is recommended;
- the importance of marine plants like seagrasses and macroalgae to fauna, and to the people of the Kimberley (either because the animals provide an important food source, or because they are considered vulnerable and so worth protecting) means that any forthcoming management plans for areas with seagrass beds or stands of macroalgae should consider these as Key Performance Indicators;
- the development of standardised methods to monitor seagrasses is likely to aid regional understanding of these important marine plants. Where large-leaved seagrass forms like *Thalassia* and *Enhalus* are present, the methods can follow those we used in this study (see below). Where seagrasses are small-leaved and ephemeral forms, some refinement of methods is still required;
- strong seasonal patterns in biomass or shoot density were not detected for either of the main species of seagrasses (i.e. *Thalassia* and *Enhalus*), but patterns were irregular through time, suggesting that monitoring might be more effective if conducted several times each year — at least during initial surveys;
- shoot density can be an effective metric to detect change in *Thalassia* and *Enhalus* (and is also used for seagrasses with similar morphology in temperate Western Australia). Measurements of seagrass growth were also useful and for *Enhalus* showed strong seasonality;
- it is likely that the highest growth of *Sargassum* in the Kimberley occurs during the wet season, and highest biomass was recorded during surveys after the wet season. Any monitoring of large macroalgae should probably occur during the wet season, noting that this prediction should be verified first;
- some work is still needed to develop methods for monitoring that can be adopted and applied uniformly by indigenous ranger groups for Healthy Country Plan monitoring, and that would also be consistent with methods used for monitoring marine protected areas;
- the importance of seagrasses to large vertebrate herbivore consumers can be easily monitored through simple tethering experiments and can be useful to assess the resilience of the seagrass and its grazers;
- making sense of measurements of seagrasses and macroalgae is difficult without corresponding environmental data. It is recommended that a network of coastal sensors be installed at monitoring sites throughout areas of the Kimberley where ecologically significant primary producer habitats exist. Such sensors would provide data that is relevant beyond their immediate application to marine plants (e.g. water temperature would be broadly relevant); and
- microalgae and sediment-dwelling microbes are vital components of the ecosystem, but tend to be highly variable. As a result, they do not lend themselves to regular ecological monitoring. Nevertheless, occasional measurements can reveal whether the mudflats are net autotrophic.

## Key residual knowledge gaps

This project has significantly increased our understanding of the natural dynamics of seagrasses, macroalgae, benthic microalgae and sediment-dwelling microbes in the Kimberley, it has also highlighted a number of knowledge gaps. Key among those gaps are the following:

- reproductive biology: for seagrasses and macroalgae, our understanding of the periods when, and places where, flowers and seeds (for seagrasses) and zygotes and spores (for macroalgae) are produced remains limited;
- long term trends: we found no clear patterns of temporal change, apart from the likely high growth of *Enhalus* and *Sargassum* during the wet season. Studies elsewhere have shown that trends in patterns of abundance require measurements spanning long periods (up to decades), and that over long periods the abundance of seagrass and macroalgae can change considerably;
- environmental thresholds and determinants of abundance: for most seagrasses and macroalgae, the primary environmental influences are light, temperature and nutrients. The primary producers in the Kimberley live and thrive in extreme environments that appear to be the edge of their tolerances. We do not have a clear understanding of how changes to any of those influences, either alone or in combination, might affect them in the future. The seagrasses are at their limit for temperature tolerance and 1 to 2 degrees Celsius warming threaten their present distribution;
- deeper meadows: our studies were restricted to seagrasses and macroalgae that were accessible at low tide, and we know little about the seagrasses and macroalgae that exist in deeper habitats. Companion work by Gary Kendrick's team indicated strong seasonality in both growth and reproduction with meadows disappearing during the wet season (low light) and re-establishing from seed at the beginning of the following dry season. This work needs to be extended to other places to understand how patterns vary across the Kimberley;
- species composition: the shallow reef platforms host a variety of macroalgae, but their species composition and abundance remain unquantified; and
- benthic microalgae: there is abundant unvegetated sediment that hosts productive assemblages of benthic microalgae, but the role that these play in the broader ecosystem remain poorly understood.



## 1 Introduction

The marine environment of the Kimberley is a unique area characterised by a combination of extreme physical conditions and limited anthropogenic stressors. The Kimberley is part of only 4% of the world's oceans that are classed as "pristine" (Halpern et al. 2008) due to very low population density (1 person per 12.5 km<sup>2</sup>). However, organisms growing in the Kimberley must deal with extreme physical conditions including large tidal ranges (up to 12 m), high temperatures (35 to 40°C in shallow intertidal habitats), and high turbidity during the wet season (Hovey et al. 2015; Pedersen et al. 2016). Benthic primary producers survive and often thrive in the Kimberley despite these extreme conditions, are likely to contribute significantly to primary productivity and ecosystem services, and form the basis of the trophic structure that supports the highly diverse Kimberley marine fauna. However, there is currently limited information on the distribution, biomass and productivity of these benthic primary producers. In this report, we focus on addressing some information gaps for seagrasses, macroalgae and sediment microalgae and bacterial communities within some islands of the Buccaneer Archipelago.

The diversity of seagrass meadows in the Kimberley region is high (12 species, Huisman and Sampey 2014) and comparable to Indonesia, Malaysia and the Philippines (approx. 17 species: Ooi et al. 2011). These are tropical species from the Family Hydrocharitaceae: *Enhalus acoroides* (Linnaeus) Royle, 1839, *Halophila decipiens* Ostenfeld, 1902, *Halophila minor* (Zollinger) den Hartog, 1957, *Halophila ovalis* (Brown) Hooker, 1859, *Halophila spinulosa* (Brown) Ascherson, 1875, *Thalassia hemprichii* (Ehrenberg) Ascherson, 1871, and from the Family: Cymodoceaceae: *Cymodocea angustata* Ostenfeld, 1916, *Cymodocea serrulata* (Brown) Ascherson & Magnus, *Halodule pinifolia* (Miki) den Hartog, 1964, *Halodule uninervis* (Forsskål) Ascherson, 1882, *Syringodium isoetifolium* (Ascherson) Dandy, 1939, *Thalassodendron ciliatum* (Forsskål) den Hartog, 1970 (Huisman and Sampey 2014). Seagrasses provide numerous ecological functions and services in coastal areas, including fisheries production (e.g. nursery habitat provision), sediment stabilisation resulting in coastal protection and carbon sequestration. Seagrass habitat also provides critical habitat to a wide array of fishes and invertebrates, like giant clams (*Tridacna* sp.) and support populations of specially protected species like the dugong (*Dugon dugong*) and marine turtles.

More than 270 species of macroalgae have been recorded in the Kimberley, most of which are red algae (Huisman and Sampey 2014). This is fairly typical of the diversity of macroalgae, and many of these species are small, epiphytic algae. Species of the genus *Sargassum* are abundant in inshore habitats (Huisman and Sampey 2014), and can be important habitat (for example, they shelter juvenile fish) or food. Microalgae are present in the sediment, but prior to this study there had been no investigation into their abundance or ecology in the Kimberley.

The Kimberley has distinct wet (November to March) and dry seasons (April to October). The wet season is characterised by increased freshwater inputs into coastal marine environments, increasing sediment loads and decreasing light availability (Hovey et al. 2015). Low light availability typically reduces the photosynthetic capacity of benthic primary producers, with subsequent effects on productivity and distribution, especially for groups such as seagrasses that typically have high light requirements. Nearshore marine organisms, like seagrasses, live in an environment that is highly dynamic, is macrotidal (>8m spring tides) and periodically exposed to extreme environmental forces (e.g. cyclones) that don't necessarily fit into the seasonal or annual patterns. Understanding the interactions between these environmental influences and biological processes, and how they change over time, will help understand how benthic primary producers are maintained in this region, and provide vital information on the resilience of these marine plants.

There is also a general lack of information about carbon and nitrogen cycling, and the role of microorganisms in nutrient cycling. Microorganisms can strongly influence the generation, transformation, and uptake of carbon and nitrogen in shallow coastal habitats, and can play an important role in connecting coastal habitats (Sävström et al. 2016). Primary producers, both phytoplankton and macrophytes, generate dissolved nutrients which can then be transformed and recycled by microorganisms to allow further uptake by benthic primary producers as bacteria-derived dissolved organic matter.

Benthic primary producer abundance and productivity can also be determined by herbivory. There are a variety of herbivores found in nearshore Kimberley ecosystems that preferentially graze on primary producers such as seagrasses and macroalgae. For example, seagrasses are important food for megafauna such as dugongs (*Dugon dugong*) and green turtles (*Chelonia mydas*), while macroalgae provides a source of food for fish, crabs, turtles and dugongs (Mustoe and Edmunds, 2008). While the importance of primary producers for herbivores in the Kimberley has been established, less is known about the role that grazing by herbivores has on primary producer extent and abundance. In coral reef ecosystems, herbivory by large fish and invertebrates can be the most important control on the distribution and abundance on seaweeds (Hay 1997). Similarly, seagrass meadows in other WA locations such as Shark Bay are strongly influenced by herbivores (Burkholder et al. 2013). Given that herbivory can often have a strong influence on primary producer abundance and diversity, we sought to quantify the rates of herbivory on marine benthic primary producers in the Kimberley.

We aimed to characterise spatial and temporal patterns in the abundance and growth of marine benthic primary producers (seagrass, macroalgae, and benthic microalgae) in the Kimberley. The data presented increases the ability of managers to respond to increasing pressures by informing models of the potential distribution of benthic primary producers in shallow habitats of the Kimberley, and providing first estimates of the rates of primary production, and the major processes controlling primary production in the Kimberley region. The project had three specific objectives:

- to understand the temporal and spatial variations in biomass and productivity of seagrasses, macroalgae and benthic microalgae;
- to investigate the rates and magnitude of microbial carbon and nitrogen cycling processes, and how they influence primary production; and
- to investigate the rates and net effect of herbivory on seagrasses, macroalgae and benthic microalgae.

Specific management implications of this project included:

- improved capacity to assess the likely impact of environmental stress (e.g. through industry development and changing climate) on key biological components of marine environments of the Kimberley marine reserves and indigenous protected areas;
- improved ability to design cost effective monitoring programs; and
- better parameterization of ecosystem models used to predict the likely outcomes of changes to climate and human use patterns.

## **2 Materials and Methods**

### **2.1 Description and survey design**

Our study was focused on the islands and coastline of the Bardi Jawi Indigenous Protected Area (IPA), encompassing Cygnet Bay, One Arm Point, Jalan (Tallon Island) and Iwany (Sunday Island) (Figure 1; Table 1). Five surveys were conducted between November 2013 to November 2015, with three surveys occurring just prior to the wet season (November 2013, October 2014 and October-November 2015) and two surveys just after the wet season (March 2014 and April 2015).

At these locations the following measurements were made during all or most surveys:

1. shoot and flower density, above- and below-ground biomass, and productivity of seagrass (all surveys);
2. biomass and productivity of macroalgae (all surveys);
3. rates of herbivory (three surveys);
4. stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of seagrasses, macroalgae and mangroves (all surveys); and
5. biomass and metabolism of microalgae, concentrations of nutrients in porewater, biomass of



chlorophyll *a* in the sediment, and sediment porosity.

Table 1: The locations and study sites at Tallon Island (Jalan) and in the Sunday Island group (latitude and longitude [decimal degrees]).

| Location | Latitude  | Longitude |
|----------|-----------|-----------|
| Jalan    | -16.40548 | 123.13520 |
| Galadiny | -16.41333 | 123.16991 |
| Laanyi   | -16.42441 | 123.19621 |
| Ngaloon  | -16.39886 | 123.20990 |
| Moyorr   | -16.40441 | 123.22266 |

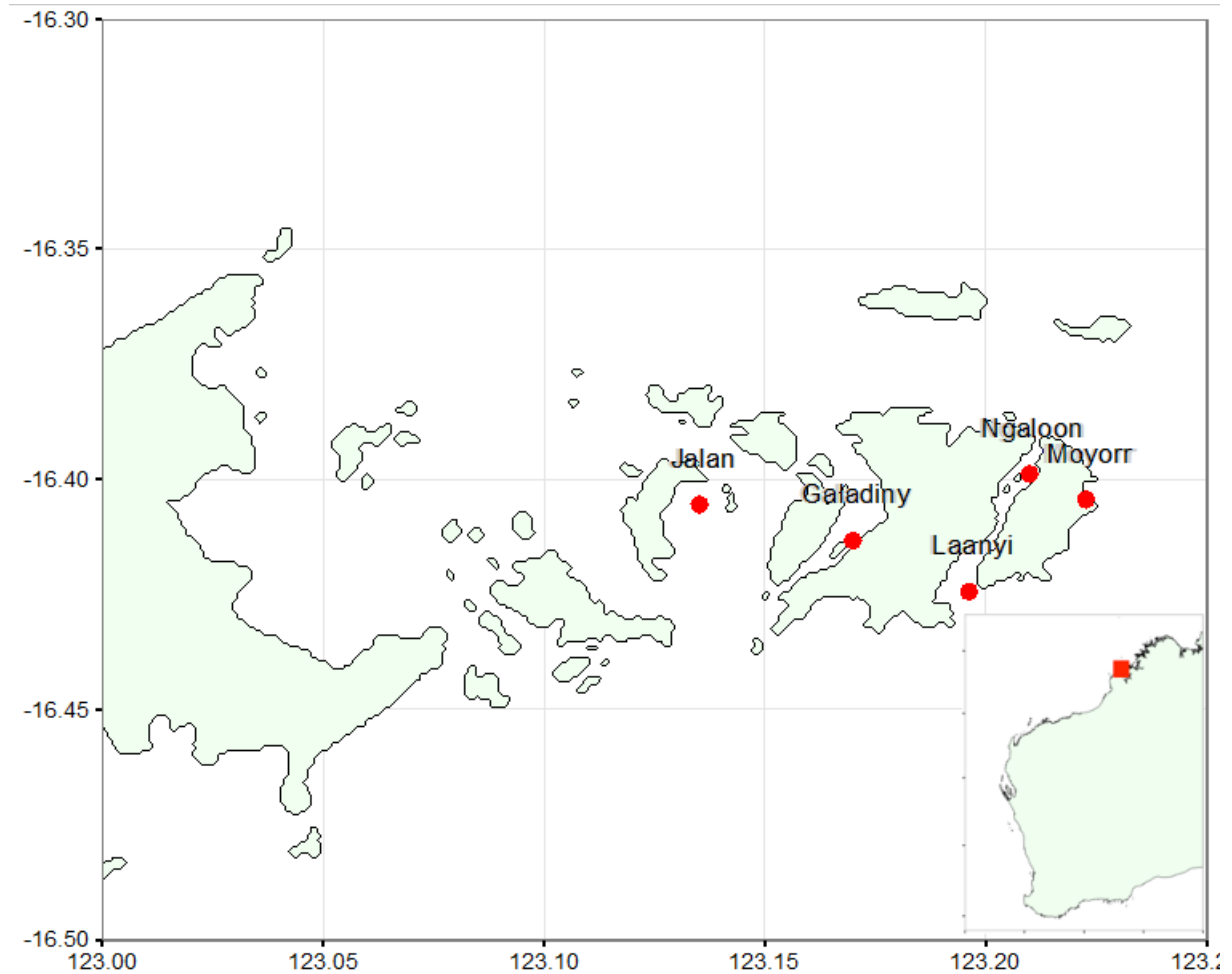


Figure 1: Locations where seagrasses and macroalgae were surveyed during this study.

## 2.2 Seagrass density, biomass and productivity

Five surveys were undertaken to test for spatial and seasonal patterns, in particular differences between the beginning and the end of the wet season (November 2013, April 2014, October 2014, April 2015 and November 2015). These surveys aimed to characterise spatial and temporal variability in the density, biomass and productivity of the region’s two dominant seagrass species (*Thalassia hemprichii* and *Enhalus acoroides*). Five sites were visited during each survey; *Thalassia hemprichii* meadows were sampled at all five sites (Jalan, Laanyi,

Ngaloon, Galadiny and Moyorr) while *E. acoroides* meadows only occurred and were sampled at three of the sites (Jalan, Laanyi and Ngaloon; Figure 1).

Monthly surveys were also conducted by the Bardi Jawi Rangers from April 2014 to April 2015 to characterise monthly variability in the density, biomass and productivity of *T. hemprichii* and *E. acoroides*. Two sites were visited each month; Laanyi (Sunday Island) dominated by *T. hemprichii* and Jalan (Tallon Island) dominated by *E. acoroides*.

During each survey, five 20 cm x 20 cm quadrats were randomly deployed at each site and the number of shoots was counted (shoot density). Three additional quadrats were marked at the corners with flagging tape for subsequent retrieval to measure seagrass biomass and productivity. All seagrass within the quadrats were marked using a standard hole-punching technique (Short and Duarte 2001; Figure 2). After four days, all seagrass within those quadrats was completely extracted using a shovel. Sediment was rinsed off and seagrass was placed into numbered calico bags, frozen and transported to Perth. At the University of Western Australia (UWA) Plant Biology Laboratory, seagrass was thawed and separated into species. Productivity was measured as the distance (in mm) that the hole had moved and this was converted into a growth rate (mm per day). Seagrass was sorted into above ground material (leaves) and below ground material (rhizomes and roots), dried at 60°C for 3 days and weighed (in grams [g]).

The nature and statistical significance of spatial and temporal patterns in seagrass density, biomass and productivity were tested using permutational analysis of variance (PERMANOVA). The model comprised two factors: Survey (fixed) and Site (random). PERMANOVA analyses were based on a Euclidean dissimilarity matrix using a minimum of 9999 permutations of residuals under a reduced model. The PRIMER-E software package (Clarke et al. 2006) and the PERMANOVA + add on for PRIMER (Anderson et al. 2008) were used for PERMANOVA analyses, and R (version 3.0.2; R Development Core Team 2013) with the 'ggplot2' add-on package (Wickham 2009) was used for to produce graphs.



Figure 2: Marking the seagrass *Thalassia hemprichii* for productivity measurements.

### 2.3 Macroalgae productivity

The productivity of five *Sargassum* species (*S. ilicifolium*, *S. marginatum*, *S. oligocystum*, *S. polycystum*, *S. swartzii*) was measured at the same five sites that were used for measurements of seagrass growth (Jalan, Laanyi, Ngaloan, Galadiny and Moyorr; Figure 1) during the same five surveys (November 2013, April 2014, October 2014, April 2015 and November 2015). The longest branch of each individual *Sargassum* was measured *in situ* with a 40 cm ruler and labelled with flagging tape (Figure 3). Individuals were then collected between 2 and 5 days later, frozen and transported to the CSIRO Oceans & Atmosphere laboratories in Floreat, Western Australia.

Approximately 15 to 20 adult individuals were marked at each Galadinyuring each survey, but because identification of *Sargassum* spp. in the field is difficult, the number of individuals per species varied. Only plants greater than 20 grams wet weight were used to ensure that all measurements were comparable. A total of 550 individual *Sargassum* were tagged during the course of the study, of which 358 were relocated and retrieved. Individual *Sargassum* were thawed in the laboratory, epiphytes were removed and the length of all branches measured. The primary meristem of *Sargassum* spp. is located at the tips of the branches, so growth was inferred by change in total length. Relative growth rates ( $\text{mm}^{-1} \text{d}^{-1}$ ; longest branch extension) were calculated by dividing the increase in total length (mm) by the number of days between the initial field measurements and collection. Individual plants were then weighed (wet weight, in grams). Finally, the *Sargassum* were placed into an oven for three days at 60°C and then reweighed to obtain their dry weight (in grams).

To assess the magnitude of variation in productivity among sites, relative to the variation observed among individual *Sargassum*, we determined the relative magnitude of effects ( $\omega^2$ ; Graham & Edwards 2001) calculated as the variance component of each effect, divided by the sum of all variance components (Winer 1971). Because different numbers of individuals were retrieved from each site, the statistical model was unbalanced, so we used a formula for unbalanced models obtained from (Quinn & Keough 2002).

Additional measurements were taken in April 2014 to assess whether growth was uniform across all branches on each individual *Sargassum* or whether each branch grew at an independent rate. Multiple branches were measured and labelled with flagging tape in the field. These individuals were then retrieved and their growth rates assessed using the method described above except for each individual numbered branch rather than the longest branch only. The net growth of the longest branch was compared to the mean of the other branches using a two-sample t-test in SPSS 23.0.



Figure 3: Example of a tagged *Sargassum* plant (April 2014).

## 2.4 Rates of seagrass consumption

Relative rates of consumption of the seagrasses *T. hemprichii* and *E. acoroides* were measured through simple tethering experiments. Shoots of each species were collected, the leaves were cut with scissors at the base above the leaf sheath, and leaves were separated and placed between two sheets of acrylic glass (the top sheet clear and the bottom sheet white), then photographed. Intact (ungrazed and uneroded leaves) were preferred; partially grazed or eroded leaves were discarded. If no intact leaves could be found, they were trimmed with scissors. Leaves were then rebundled and attached to a short piece of sisal rope with clothes pegs. Three shoots from a single species were attached to each piece of rope, which was then placed in a meadow of the matching species (i.e. *Thalassia* was placed in *Thalassia* meadows, *Enhalus* was placed in *Enhalus* meadows). The pieces of rope were firmly secured by inserting tent pegs through each end of the rope into the substrate. After approximately 24 h leaves were collected and photographed. This process was repeated on two separate days during three different surveys (October 2014, April 2015, November 2015) at three different sites: Jalan (Tallon Island), Laanyi and Ngaloan (both on Sunday Island). Fifteen shoots of each species were deployed on each day (n = 540 shoots).

Photographs of leaves before and after deployment were analysed using image analysis software (ImageJ) to calculate surface area, and consumption (% loss) of each shoot was then calculated. The error in area measurements between photographs was up to  $\pm 10\%$  (verified from repeat photographs of leaves with no grazing or erosion), so any change in area  $< 10\%$  was considered to be 0% (see also Vanderklift et al. 2009). Consumption by herbivores was confirmed to be the cause of loss of area, because leaves showed clear evidence of bite marks.

The percent consumption data were analysed by mixed effects ANOVA testing for differences among sites (three levels, random), surveys (three levels, fixed), deployment days (two levels nested in each combination of location and survey, random), and ropes (five levels nested within each combination of location, survey and deployment day, random). Data for *Thalassia* and *Enhalus* were analysed separately. Because there were many zeros in the dataset, the data did not conform to the assumptions of linear models, so statistical significance was tested by permutation, using the PERMANOVA+ (permutational ANOVA) add-on in the PRIMER-E statistical software package. Some tethered shoots could not be relocated, so the degrees of freedom were adjusted as necessary in the analysis.

## 2.5 Patterns in stable isotope ratios

For the main species of seagrasses, mangroves and brown algae that were present at each of the five sites used in the productivity studies, five individual shoots (seagrass), thalli (macroalgae) and leaves (mangroves) were collected by hand. For other species that were present, collections were made opportunistically. Samples were frozen ( $-20^{\circ}\text{C}$ ) and transported to the CSIRO Floreat laboratories, where they were later thawed, cleaned, dried in an oven at  $60^{\circ}\text{C}$ , and ground into a fine powder using a mixer mill (Retsch MM200, Dusseldorf, Germany). Stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were measured at the West Australian Biogeochemistry Centre using a continuous-flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush elemental analyser. A description of the analytical technique can be found in Skrzypek and Paul (2006). Stable isotope ratios are expressed in ‰ using conventional delta ( $\delta$ ) notation  $\delta X (\text{‰}) = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$ ; where X is  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ , and R is the  $^{15}\text{N}/^{14}\text{N}$  (nitrogen) or  $^{13}\text{C}/^{12}\text{C}$  (carbon) ratio in the sample and standards (Vienna PDB equivalent for carbon and the IAEA international standard of atmospheric  $\text{N}_2$  for nitrogen).

Spatial and temporal patterns in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of *T. hemprichii*, *E. acoroides* and *S. polycystum* were analysed by mixed-effects ANOVA testing for differences among sites (four levels, random) and surveys (five levels, fixed). In some cases there were missing samples, so the degrees of freedom were adjusted as necessary in the analysis. Overall patterns of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  among species were visualized through biplots.



## 2.6 Biomass and productivity of benthic microalgae

Benthic chambers (Figure 4) comprising a paired light and dark chamber system, were deployed at four soft sediment sites, two in proximity to the Cygnet Bay Pearl Farm (sites Cygnet Bay South and Cygnet Bay North), one at Jologo Beach near Ardyloon, and one at a known intermittent turtle nesting site (Turtle Beach) on Sunday Island (Figure 5). These sites did not match the macrophyte sites as to effectively deploy the benthic chambers a minimum amount of sediment was required, and many of the seagrass and *Sargassum* sites were too rocky. Also to measure benthic microalgae (BMA) production we needed sites without *Sargassum* and seagrasses. The chambers measured temperature, oxygen evolution (light chamber) and respiration (dark chamber) generated by BMA via Aanderraa® optodes located inside each chamber. Using Redfield's stoichiometric ratios (Redfield et al. 1963) of oxygen:carbon (O<sub>2</sub>:C), production of organic matter by BMA was calculated from linear relationships of oxygen released during the synthesis (photosynthesis) or consumption (respiration) of organic matter over the time of deployment.

Hobo® PAR (photosynthetically active radiation) sensors were also attached to the benthic chambers, to quantify the incident irradiance upon the sediment surface. A RBR Concerto submersible conductivity, temperature and depth (CTD) recorder was attached to collect the physical characteristics of the water column. Deployments typically lasted 2 to 4 hours during the late morning to mid-afternoon (capturing the sun's zenith) with discrete 50 ml water samples collected automatically every 30 minutes from inside the chambers. Water samples were decanted into triplicate 10 ml plastic vials and frozen, later analysed for nitrate, phosphate and silica.

In October 2014 and 2015, the chambers were deployed on three successive days at the same site to investigate the temporal variability of BMA production. During each deployment, a sediment core was collected next to each lander.

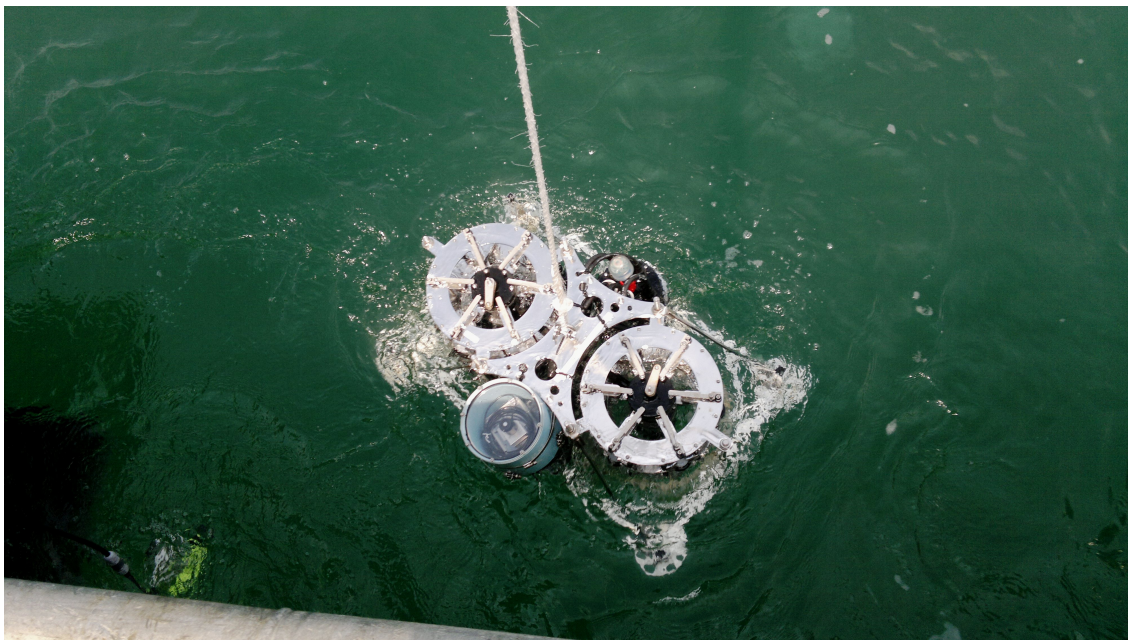


Figure 4: Benthic lander showing paired light and dark chambers used for measure the evolution of oxygen by benthic microalgae in soft sediments.

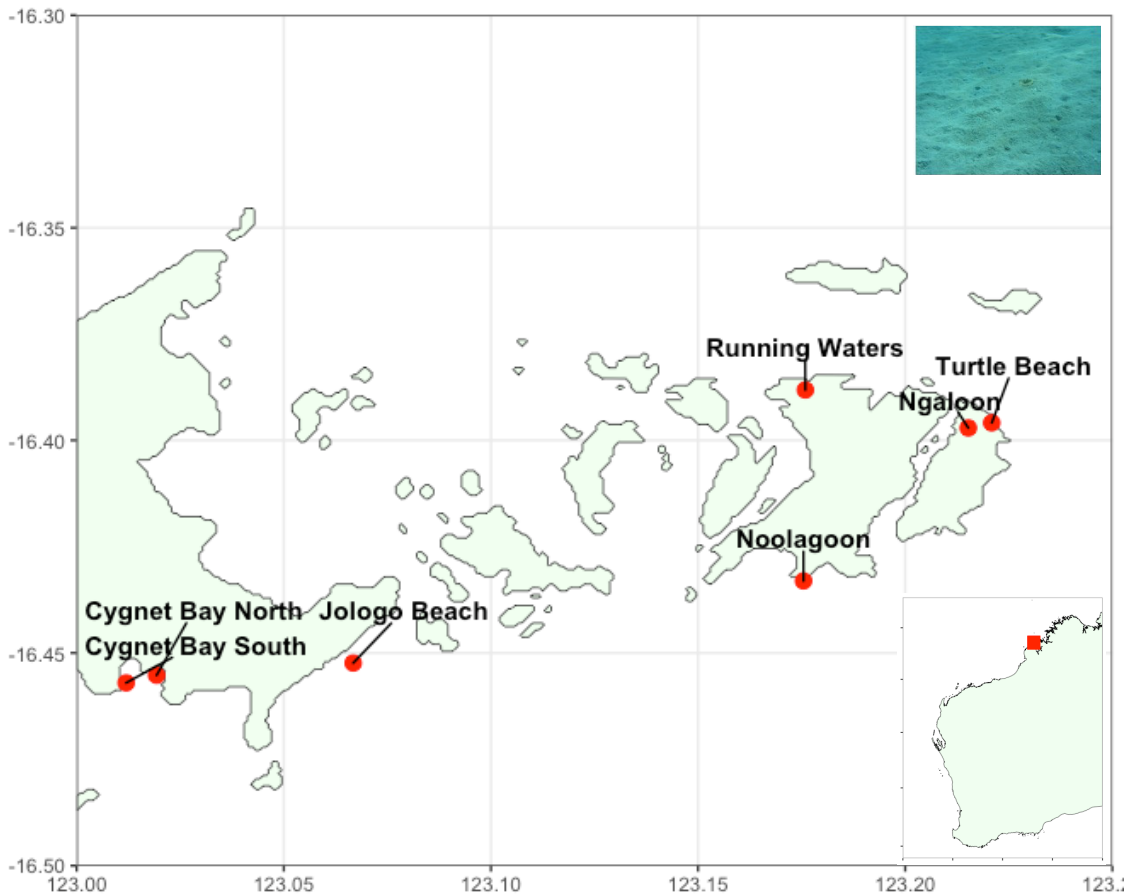


Figure 5: Locations where soft sediments were surveyed during this study.

At each of the sites used for the benthic chamber deployments, as well as additional soft sediment habitat sites on Sunday Island, a low-to-high tide transect was sampled. Along each transect 6 cores (diameter = 10 cm, height = 30 cm) were collected at regular intervals on the incoming tide. In addition, during chamber deployments in areas that were accessible, a sediment core was collected. The sediment cores were frozen and transported to the CSIRO Oceans & Atmosphere laboratories in Floreat, Western Australia.

Estimates of chlorophyll biomass in the cores were taken from scrapes of surface (~ top 1 mm) sediment collected into a 2 mL cryovial and snap frozen in liquid nitrogen. The sample was thawed and decanted into a 20 ml glass vial, weighed, and then 10 ml of 90% acetone added for pigment extraction. Samples were stirred vigorously with a vortexer and placed in the fridge overnight. The extracted pigment was decanted in a glass vial (diluted if required) and measured on a calibrated Turner Designs model 10AU fluorometer. BMA pigments were extracted and analysed by High Performance Liquid Chromatography, for two surveys (April 2014 [post-wet] and October 2014 [post-dry]). Sediment organic carbon (POC), nitrogen (PN) and their stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were also measured from sediment cores collected in April and October 2014. Description of the analytical technique for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  can be found in Skrzypek and Paul (2006) and for POC and PN in Knapp et al. (1996). Sediment porosity was determined by subtracting the mass of a sub-sample of core sediment that had been dried in an oven at 60°C for ~48 hours from its original wet mass.

To determine the concentrations of nutrients within the sediment interstitial spaces a cut off syringe was used to collect ~40 ml of sediment from the cores at each site. Samples were placed in a modified centrifuge tube and frozen. For analysis, samples were thawed and spun in a Sorvall Legend RX centrifuge at 1200 rpm to extract the pore-water from the sediment. Pore-water was then analysed for dissolved inorganic nutrients (nitrate, phosphate and silicate) using an auto-analyser.

## 2.7 Sub-surface sediment chemistry

Microelectrode studies of sediment pore-water dissolved oxygen and hydrogen sulphide were conducted to support *in situ* assessment of productivity by benthic microalgae. Studies of this kind provide sub-millimetre scale information about chemical changes taking place below the sediment surface that are critical to understanding chemical exchange with the overlying water-column. Of particular interest, in this case, was to confirm the impact of benthic microalgae on pore-water oxygen content, and help to understand previously measured variability in oxygen exchange rate between the seabed and water-column.

During October 2015, in addition to the routine collection of sediment cores described above, 10 cm diameter cores were also collected in the close vicinity of the repeat chamber deployment site in Cygnet Bay over the three days of the benthic chamber deployments (27 to 29 October 2016), and on different tidal phases (three on the flood tide, and two on the ebb tide). In each case, three adjacent cores were collected at the site while it was covered with ~5 to 10 cm of overlying water. Following collection, the cores were stored in a flow-through ambient temperature (~30°C) seawater tank, exposed to sunlight, until subsequent sampling. Immediately prior to profiling, ~400 ml of overlying water was carefully removed from each core by siphon, and the cores were transferred to a temperature controlled laboratory (28 ± 0.5°C) to begin micro-profiling.

Oxygen and hydrogen sulphide Unisense® micro-electrodes were calibrated in the laboratory according to manufacturer's instructions before and after each set of profiling. For profiles conducted under light conditions, an LED desk lamp was directed onto the sediment surface to supplement the laboratory over-head fluorescent lighting. Typically the sensors were arranged so that they crossed the sediment-water interface ~400 µm below the starting position. Height adjustments were made manually using a micrometre allowing a total vertical displacement of 37 mm. Depth resolution of measurements was 200 µm, increased to 1 mm resolution below 2 mm depth in some cases where oxygen concentration was observed to reach zero. At each depth interval between 3 and 5 electrode readings were recorded 1 second apart to provide an average. Following completion of the light profiles, the cores were left in the dark for 10 mins, and then profiling was repeated.

## 2.8 Microbial carbon and nitrogen cycling

At each of the five sites included in measurements of seagrass and macroalgae productivity measurements were taken from mangrove, seagrass and unvegetated sediment for bacterial carbon production (BCP) (see Smith & Azam, 1992; Kirchman, 1993 for detailed method) and utilization (estimated via the use of Biolog EcoPlates™, see Sävström et al., 2016 for detailed method), and concentrations of dissolved organic carbon (DOC) and total dissolved nitrogen (TDN). In addition surface water samples were obtained at the edge of the reef flat and bioassays were set up to see how labile and usable the DOC and TDN pool derived from each benthic habitat type was to the pelagic bacterial community. DOC and TDN (0.2 µ filtered water) was analysed on a Shimadzu Total Organic Carbon (TOC) analyser with a Total Nitrogen Unit attachment.

Spatial and temporal patterns in BCP, DOC and TDN were analysed using MANOVA. A principal component analysis was used to analyse spatial and temporal patterns in carbon utilization pattern (estimated via the use of Biolog EcoPlates™). Statistical analyses were performed in R version 2.15.0 GUI 1.51.

Samples for the diversity and abundance of nitrogen cycling bacteria and archaea were collected from surface sediments and water samples from each site. DNA was extracted from sediment samples using the MP Bio FastDNA Soil Extraction kit. DNA from water samples was extracted using the MoBio PowerWater DNA Isolation kit. Ammonia-oxidising bacteria and archaea were enumerated using the quantitative polymerase chain reaction (qPCR), and their structure and function were quantified using functional gene microarray (Abell et al. 2011).

## 2.9 Light, temperature and depth

RBR Concerto submersible conductivity, temperature and depth recorders with a Licor 192SA Photosynthetic Photon Flux Density (PPFD) sensor (fitted with a Zebra-Tech Hydro-Wiper H) were moored approximately 15 cm above the substrate at each site at the beginning of each survey, and were programmed to record data every 30 seconds. At the end each survey, the loggers were retrieved and the data immediately downloaded via the

interface software Ruskin (version 1.10.0). Using the supplied graphical interface of Ruskin, data (conductivity, temperature, pressure, depth, salinity and photosynthetic photon flux density) were briefly checked to verify the instrument had worked correctly during the deployment then archived. Each unit was cleaned and batteries replaced.

Scripts were developed (in the R software) to process the data. Data for each deployment were truncated to whole days starting and finishing at midnight; typically there were 3 to 4 complete days per deployment. Data for each mooring was examined for data quality and bad data removed when relevant (for example the Licor sensor failed and data were removed from two deployments). The data were then binned in 15 minute bins and the average taken for each bin. An “average” day was then created for each deployment by taking average of the corresponding times each day across the deployment.

Using the average day for each deployment, PPFD (the measurement of light intensity that we used) were used to calculate day length using a threshold of  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ . Once day length was calculated, daily values were determined for the daylight period, specifically, the total PPFD, and mean PPFD 30 minutes either side of solar noon.

The mean values of temperature and mooring depth were also calculated. The timing of the tide was an important factor so the mean daytime depth of the mooring was also calculated by taking the mean of the depth values during the daylight hours. This allows some indication of the variation in the tide during daylight hours between the different deployments.

## 2.10 Planktonic microalgae

Seawater samples from surface waters at all sites used in the studies of seagrass and MPB were collected for measurements of chlorophyll-*a* (chl-*a*) and phaeopigments. Samples were size-fractionated by vacuum-filtering onto a Whatman 25 mm diameter GF/F (nominal pore size of  $0.7 \mu\text{m}$ ) for the total chl-*a* fraction (1 L), and a 25 mm diameter,  $5 \mu\text{m}$  Nitex mesh for the  $>5 \mu\text{m}$  fraction (2L) under low light conditions. The filters and screens were snap frozen immediately in liquid nitrogen and stored at  $-80^\circ\text{C}$  until analysis, when pigments were extracted in 90% acetone overnight and measured on a calibrated Turner Designs model 10AU fluorometer utilising the acidification technique of Parsons et al. (1989). The  $<5 \mu\text{m}$  or small fraction is calculated as the difference between the total and  $>5 \mu\text{m}$  or large fraction.

Seawater for measurements of suspended particulate matter (SPM) was collected from the surface water at all sites. Immediately after collection, a known volume (2 L) of sample water was vacuum-filtered onto dried and pre-weighed glass fibre filters (47 mm,  $0.7 \mu\text{m}$ , Whatman GF/F). Filters were then stored in the cool and the dark until analysis. Filters were then dried to constant weight at  $60^\circ\text{C}$  SPM (in  $\text{mg L}^{-1}$ ) calculated by subtraction. Surface water samples (between 1 to 5 L) were also filtered onto a glass fibre filter (25 mm,  $0.7 \mu\text{m}$ , Whatman GF/F) to measure phytoplankton pigments. Once collected, filters were stored in liquid nitrogen until analysis. Pigments were extracted and analysed by High Performance Liquid Chromatography [HPLC] with a Waters-Alliance system following the protocol detailed in Hooker et al. (2009). Particulate organic carbon (POC), particulate nitrogen (PN) and their stable isotopes ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) were also measured. Four-litre water samples were filtered on precombusted Whatman GF/F filters and stored at  $-20^\circ\text{C}$  until analysis by mass spectrometer, following the preparation techniques of Knap et al. (1996).

A 10 mL sample of unfiltered seawater was analysed from surface waters at all sites for dissolved inorganic nutrients (nitrate + nitrite [hereafter nitrate], ammonia, phosphate and silicate) using an auto-analyser (Lachat QuickChem 8000 series flow injection with detection by absorbance at specific wavelengths for silicate [QuikChem Method 31-114-27-1-D], nitrate [Quikchem Method 31-107-04-1-A] and phosphate [QuikChem Method 31-115-01-1-G]), with ammonia measured by a Shimadzu RF-10AxI Fluorescence detector using the CSIRO Method (Watson et al. 2005). Detection limits were  $0.02 \mu\text{M}$  for all inorganic nutrient species, with a standard error of  $<0.7\%$ .



### 3 Results

#### 3.1 Seagrass density, biomass and productivity

##### *Thalassia hemprichii*

Shoot density of *Thalassia hemprichii* varied substantially between sites and surveys, but not in a consistent way, as indicated by a statistically-significant interaction between sites and surveys ( $P=0.0014$ ; Table 2). Shoot density was greatest in November 2015, at the beginning of the wet season (Figure 6). However, shoot density was not always high during early wet season surveys in previous years (November 2013 and April 2014), suggesting that we cannot make simple inferences about seasonal patterns from sampling twice within a year. Indeed, the more frequent surveys at Jalan and Laanyi tended to have higher shoot densities towards the end of the wet season (reaching 1200 shoots/m<sup>2</sup>) and lower densities during mid dry season (as low as 40 shoots/m<sup>2</sup>). Analyses of the data collected during the higher-frequency surveys indicated that shoot density also varied significantly among months (Table 2;  $P=0.048$ ), being highest in April 2014 and April 2015 at Jalan and Laanyi, which implies that this might be when maximum shoot density occurs in these meadows. Both aboveground and belowground biomass of *T. hemprichii* also varied significantly among sites and surveys (Table 2), but unlike shoot density there was no statistically significant interaction, indicating that these patterns were more consistent. Neither aboveground nor belowground biomass varied significantly among months during the higher-frequency surveys (Table 2;  $P=0.24$ ), and neither showed consistent evidence of seasonal differences across years, although both tended to be highest during the November 2015 surveys (except at Laanyi where biomass was greatest in November 2013).

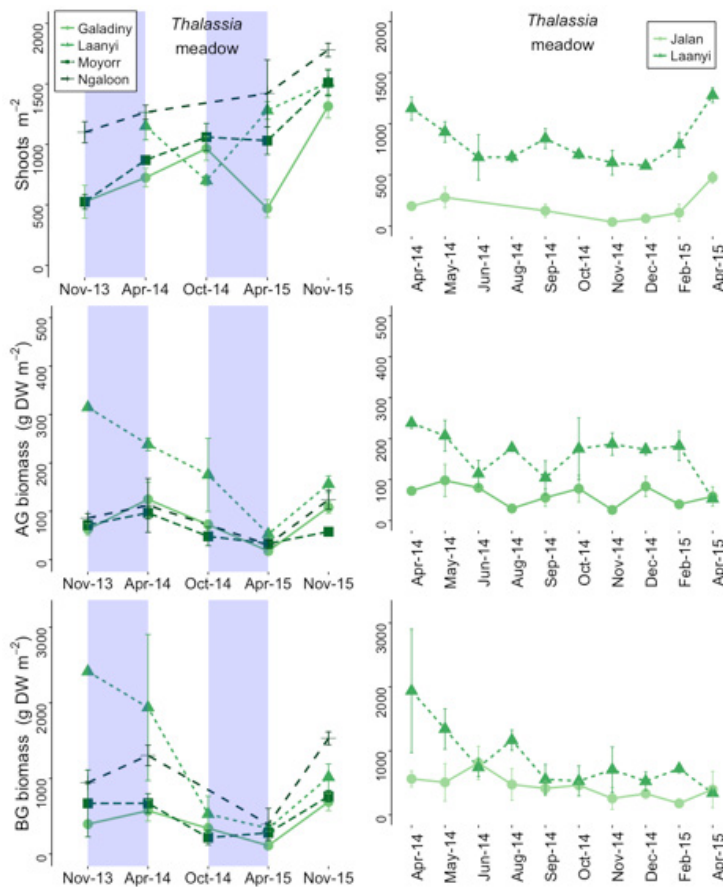


Figure 6: Mean ( $\pm$  SE) shoot densities and above- and belowground biomasses of *Thalassia hemprichii* during biannual (left graphs) and monthly (right graphs) surveys. Blue bars show the wet season.

Table 2: Results of permutational analyses of variances testing for patterns in shoot densities and above- and belowground biomasses of *Thalassia hemprichii* during biannual (left columns) and monthly (right columns) surveys.

|   |     | Seasonal |          |               |    | Monthly |          |               |  |
|---|-----|----------|----------|---------------|----|---------|----------|---------------|--|
| <b><u>Thalassia shoot density</u></b>       |     |          |          |               |    |         |          |               |  |
| Source                                      | df  | MS       | Pseudo-F | P(perm)       | df | MS      | Pseudo-F | P(perm)       |  |
| Time  | 4   | 561.99   | 8.5706   | <b>0.0014</b> | 9  | 169.22  | 4.2708   | <b>0.0487</b> |  |
| Site  | 4   | 873.77   | 33.491   | <b>0.0001</b> | 1  | 5361.7  | 176.97   | <b>0.0001</b> |  |
| Time x Site                                 | 16  | 68.091   | 2.6099   | <b>0.0014</b> | 6  | 37.615  | 1.2416   | 0.296         |  |
| Residual                                    | 142 | 26.089   |          |               | 83 | 30.296  |          |               |  |
| Total                                       | 166 |          |          |               | 99 |         |          |               |  |
| <b><u>Thalassia aboveground biomass</u></b> |     |          |          |               |    |         |          |               |  |
| Source                                      | df  | MS       | Pseudo-F | P(perm)       | df | MS      | Pseudo-F | P(perm)       |  |
| Time  | 4   | 54.062   | 7.1012   | <b>0.0027</b> | 9  | 9.9243  | 1.019    | 0.488         |  |
| Site  | 4   | 49.665   | 7.1878   | <b>0.0002</b> | 1  | 336.61  | 41.151   | <b>0.0001</b> |  |
| Time x Site                                 | 16  | 7.6469   | 1.1067   | 0.3689        | 9  | 9.7388  | 1.1906   | 0.3146        |  |
| Residual                                    | 63  | 6.9097   |          |               | 46 | 8.18    |          |               |  |
| Total                                       | 87  |          |          |               | 65 |         |          |               |  |
| <b><u>Thalassia belowground biomass</u></b> |     |          |          |               |    |         |          |               |  |
| Source                                      | df  | MS       | Pseudo-F | P(perm)       | df | MS      | Pseudo-F | P(perm)       |  |
| Time  | 4   | 618.33   | 12.068   | <b>0.0004</b> | 9  | 108.34  | 1.6288   | 0.2371        |  |
| Site  | 4   | 359.01   | 5.4093   | <b>0.0011</b> | 1  | 972.16  | 12.774   | <b>0.0007</b> |  |
| Time x Site                                 | 16  | 50.508   | 0.76101  | 0.7196        | 9  | 66.517  | 0.87403  | 0.5576        |  |
| Residual                                    | 63  | 66.37    |          |               | 46 | 76.104  |          |               |  |
| Total                                       | 87  |          |          |               | 65 |         |          |               |  |

### *Enhalus acoroides*

*E. acoroides* was present at Jalan, Laanyi and Ngaloon in mixed meadows with *T. hemprichii*. Shoot density significantly differed between sites (Table 3; P=0.0001) and at Jalan over monthly sampling (Table 4; P=0.006), but the statistically-significant interaction between sites and surveys indicates that these differences among locations were not consistent during each survey nor between months at Jalan. Like *T. hemprichii* there was no indication that there were regular seasonal patterns (Figure 7). Shoot densities were highly variable, ranging from 10 to 400 shoots per m<sup>2</sup>. Aboveground and belowground biomass did not vary significantly among sites or surveys, and there was also no indication of interactions between these from biannual surveys (Table 3) although there was significant variation between months during the monthly surveys (Table 4; P=0.002) that was not apparently seasonal.

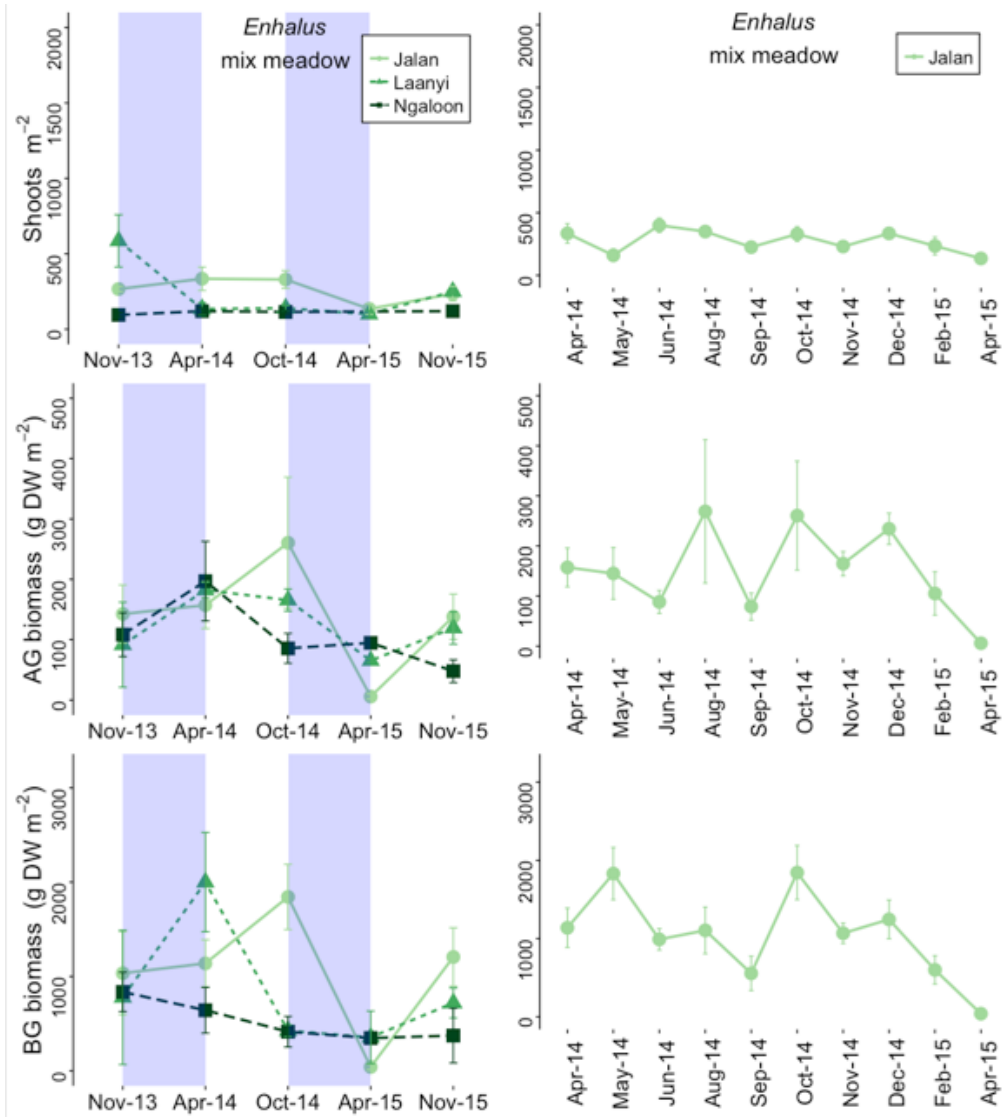


Figure 7: Mean ( $\pm$  SE) shoot densities and above- and belowground biomasses of *Enthalus acoroides* during biannual (left graphs) and monthly (right graphs) surveys. Blue bars show the wet season.

Table 3: Results of permutational analyses of variances testing for patterns in shoot densities and above- and belowground biomasses of *Enhalus acoroides* during biannual and monthly surveys.

|   | Biannual sampling |        |          |               | Monthly sampling |         |          |               |
|---|-------------------|--------|----------|---------------|------------------|---------|----------|---------------|
| <b><u>Enhalus shoot density</u></b>       |                   |        |          |               |                  |         |          |               |
| Source                                    | df                | MS     | Pseudo-F | P(perm)       | df               | MS      | Pseudo-F | P(perm)       |
| Time                                      | 4                 | 84.47  | 1.4654   | 0.3245        | 9                | 45.578  | 0.44555  | 0.8422        |
| Site                                      | 2                 | 216.04 | 9.3424   | <b>0.0001</b> | 1                | 611.21  | 52.172   | <b>0.0001</b> |
| Time x Site                               | 7                 | 57.954 | 2.5061   | <b>0.0257</b> | 3                | 102.29  | 8.7317   | <b>0.0002</b> |
| Residual                                  | 61                | 23.125 |          |               | 56               | 11.715  |          |               |
| Total                                     | 74                |        |          |               | 69               |         |          |               |
| <b><u>Enhalus aboveground biomass</u></b> |                   |        |          |               |                  |         |          |               |
| Source                                    | df                | MS     | Pseudo-F | P(perm)       | df               | MS      | Pseudo-F | P(perm)       |
| Time                                      | 4                 | 38.971 | 2.2339   | 0.1345        | 9                | 41.643  | 1.4357   | 0.4441        |
| Site                                      | 2                 | 2.0563 | 0.20509  | 0.8185        | 1                | 0.83643 | 6.58E-02 | 0.7993        |
| Time x Site                               | 8                 | 17.551 | 1.7506   | 0.1381        | 3                | 25.074  | 1.9717   | 0.1543        |
| Residual                                  | 22                | 10.026 |          |               | 23               | 12.717  |          |               |
| Total                                     | 36                |        |          |               | 36               |         |          |               |
| <b><u>Enhalus belowground biomass</u></b> |                   |        |          |               |                  |         |          |               |
| Source                                    | df                | MS     | Pseudo-F | P(perm)       | df               | MS      | Pseudo-F | P(perm)       |
| Time                                      | 4                 | 286.7  | 1.5693   | 0.2689        | 9                | 243.4   | 0.41438  | 0.8626        |
| Site                                      | 2                 | 158.96 | 1.7545   | 0.1904        | 1                | 246.12  | 5.598    | <b>0.0274</b> |
| Time x Site                               | 8                 | 184.02 | 2.0311   | 0.0846        | 3                | 493.47  | 11.224   | <b>0.0001</b> |
| Residual                                  | 22                | 90.598 |          |               | 23               | 43.965  |          |               |
| Total                                     | 36                |        |          |               | 36               |         |          |               |

Table 4: Results of analyses of variances testing for patterns in shoot densities and above- and belowground biomasses of *Enhalus acoroides* during monthly surveys.

| <b>Monthly sampling</b>                   |    |        |        |          |
|---|----|--------|--------|----------|
| <b><u>Enhalus shoot density</u></b>       |    |        |        |          |
| Source                                    | df | MS     | F      | P        |
| Survey                                    | 9  | 39112  | 3.0996 | 0.006436 |
| Residual                                  | 40 | 12619  |        |          |
| Total                                     | 49 |        |        |          |
| <b><u>Enhalus aboveground biomass</u></b> |    |        |        |          |
| Source                                    | df | MS     | F      | P        |
| Survey                                    | 9  | 19393  | 1.4907 | 0.2213   |
| Residual                                  | 19 | 13010  |        |          |
| Total                                     | 28 |        |        |          |
| <b><u>Enhalus belowground biomass</u></b> |    |        |        |          |
| Source                                    | df | MS     | F      | P        |
| Survey                                    | 9  | 803918 | 4.5275 | 0.00272  |
| Residual                                  | 19 | 177564 |        |          |
| Total                                     | 28 |        |        |          |

### Seagrass productivity

Productivity of *Thalassia* varied from around 0.001 to up 0.005 g per shoot per day (reflecting leaf extension rates from 5 to 26 mm per shoot per day). Spatial and temporal patterns in productivity of *Thalassia* were complex as reflected in the statistically-significant interactions between sites and surveys from both biannual and monthly surveys (Table 5). However, they usually decreased between the beginning and end of the wet season (i.e. between October to November and April). Monthly surveys indicated that the highest productivity occurred between August and February but not consistently between sites (Figure 8).

In contrast, productivity of *Enhalus* tended not to vary interannually among sites or surveys from November 2013 to November 2015 (Table 5). In Jalan, monthly sampling indicated a strong seasonality where growth rates decreased from May until September (dry season; growing as low as 0.0025 g and 6 mm per shoot per day [ $\text{g sh}^{-1} \text{d}^{-1}$ ]) then increased during the wet season from October to February (reaching almost 0.015 g and 30 mm per shoot per day; Figure 9; Table 6). Monthly surveys did not occur at Laanyi so we do not have information on seasonal patterns in growth of *E. acoroides* at that site.

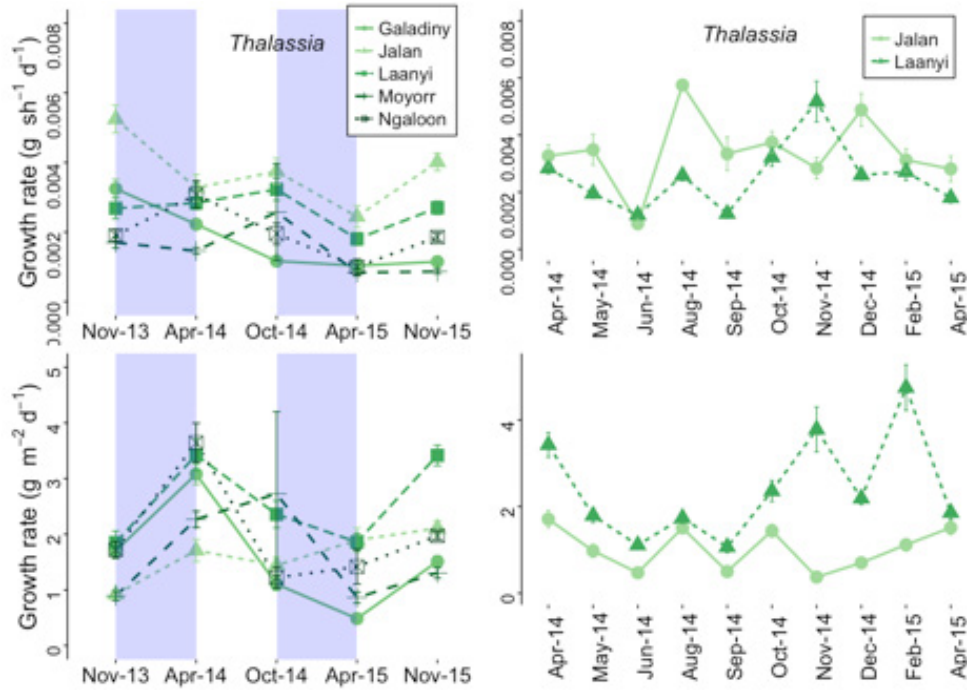


Figure 8: Mean ( $\pm$  SE) leaf growth rates of *Thalassia hemprichii* during biannual (left graphs) and monthly (right graphs) surveys. Blue bars show the wet season.

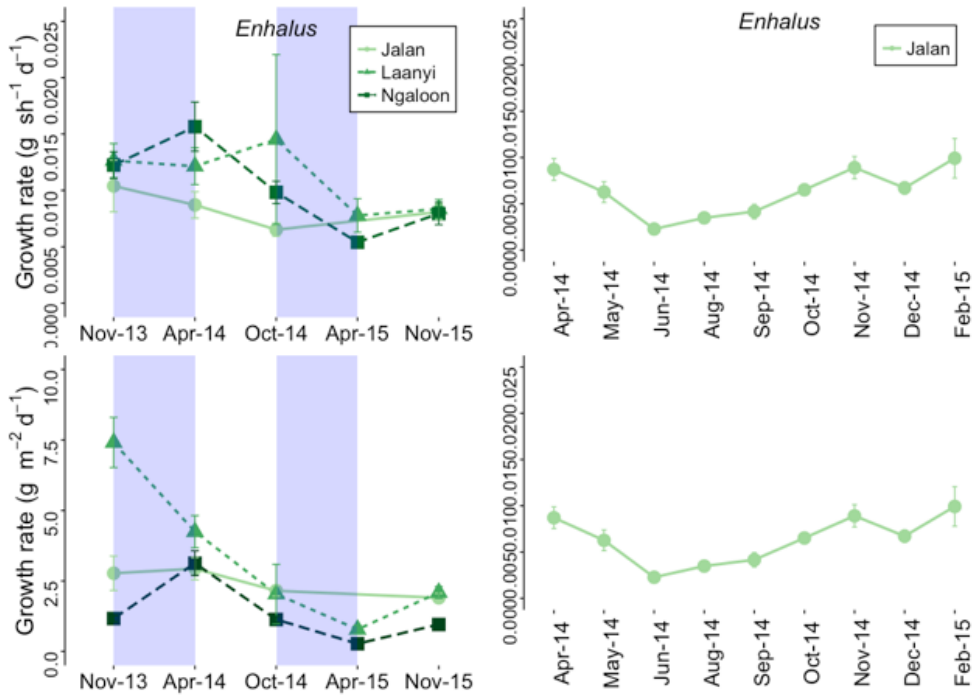


Figure 9: Mean ( $\pm$  SE) leaf growth rates of *Enhalus acoroides* during biannual (left graphs) and monthly (right graphs) surveys. Blue bars show the wet season.

Table 5: Results of permutational analyses of variances testing for growth rates (g. shoot<sup>-1</sup> day<sup>-1</sup>) of *Thalassia hemprichii* and *Enhalus acoroides* during biannual (left columns) and monthly (right columns, only for *T. hemprichii*) surveys.

|                                     |     | Biannual |          |               |     | Monthly  |          |               |  |
|-------------------------------------|-----|----------|----------|---------------|-----|----------|----------|---------------|--|
| <b><u>Thalassia growth rate</u></b> |     |          |          |               |     |          |          |               |  |
| Source                              | df  | MS       | Pseudo-F | P(perm)       | df  | MS       | Pseudo-F | P(perm)       |  |
| Survey                              | 4   | 3.68E-03 | 4.8233   | <b>0.0104</b> | 9   | 1.88E-03 | 2.5559   | 0.0932        |  |
| Site                                | 4   | 9.18E-03 | 50.439   | <b>0.0001</b> | 1   | 3.14E-03 | 15.937   | <b>0.0004</b> |  |
| Survey x                            |     |          |          |               |     |          |          |               |  |
| Site                                | 16  | 8.39E-04 | 4.6106   | <b>0.0001</b> | 9   | 7.36E-04 | 3.7298   | <b>0.0003</b> |  |
| Residual                            | 683 | 1.82E-04 |          |               | 476 | 1.97E-04 |          |               |  |
| Total                               | 707 |          |          |               | 495 |          |          |               |  |
| <b><u>Enhalus growth rate</u></b>   |     |          |          |               |     |          |          |               |  |
| Source                              | df  | MS       | Pseudo-F | P(perm)       |     |          |          |               |  |
| Survey                              | 4   | 2.44E-03 | 4.0317   | 0.068         |     |          |          |               |  |
| Site                                | 2   | 3.09E-03 | 2.9482   | 0.0507        |     |          |          |               |  |
| Survey x                            |     |          |          |               |     |          |          |               |  |
| Site                                | 7   | 5.26E-04 | 0.50161  | 0.8019        |     |          |          |               |  |
| Residual                            | 140 | 1.05E-03 |          |               |     |          |          |               |  |
| Total                               | 153 |          |          |               |     |          |          |               |  |

Table 6: Results of one-way analysis of variance testing significance difference in growth rates (g. shoot<sup>-1</sup> day<sup>-1</sup>) of *Enhalus acoroides* during monthly surveys at Jalan Island.

| Source   | df  | MS       | F      | P        |
|----------|-----|----------|--------|----------|
| Survey   | 8   | 0.013677 | 9.0819 | <0.00001 |
| Residual | 125 | 0.001506 |        |          |
| Total    | 133 |          |        |          |

**Flower densities**

Seagrass flowers were only observed during the November 2013 survey, when flower densities varied between sites for both *Thalassia* and *Enhalus*. At Galadiny four *Thalassia* flowers m<sup>-2</sup> were observed while at Laanyi one *Enhalus* flower m<sup>-2</sup> were observed. No flowers for either species were observed at Jalan or Ngaloan, or during 2014 or 2015 surveys, likely due to the earlier timing of these surveys (October and early November) compared with the 2013 study period (late November 2013).

**3.2 Macroalgae productivity**

Considerable variability in biomass and productivity of *Sargassum* spp. was observed between individuals and between sites. Individual plants tended to be larger in April (9.31 ±4.05 g ind<sup>-1</sup> in April 2014; 8.90 ±4.13 g ind<sup>-1</sup> in April 2015) than October or November (4.71 ±1.45 g ind<sup>-1</sup> in November 2013; 2.04 ±0.92 g ind<sup>-1</sup> in October 2014; 2.79 ±0.98 g ind<sup>-1</sup> in October 2015) (Figure 10).

Despite the higher average plant mass, the productivity observed during April surveys tended to be lower (April 2014: 0.85 ±0.98 mm ind<sup>-1</sup> d<sup>-1</sup>; April 2015: 0.67 ±0.48 mm ind<sup>-1</sup> d<sup>-1</sup>) than November 2013 (11.15 ±15.36 mm ind<sup>-1</sup> d<sup>-1</sup>; Figure 10). However, productivity also tended to be low during October surveys (October 2014: 0.16 ±0.37 mm ind<sup>-1</sup> d<sup>-1</sup>, October 2015: 0.51 ±0.42 mm ind<sup>-1</sup> d<sup>-1</sup>; Figure 11). Generally, Laanyi yielded the highest average relative growth rates (pooled all surveys: 7.93 ±8.16 mm ind<sup>-1</sup> d<sup>-1</sup>) while Jalan tended to have the lowest average relative growth rates (pooled all surveys: 1.36 ±3.63 mm ind<sup>-1</sup> d<sup>-1</sup>).

The November 2013 survey yielded the highest productivity for all species (Figure 12). *S. polycystum* had the highest growth rates during this period (11.92 ±15.86 mm ind<sup>-1</sup> d<sup>-1</sup>) and was the only species that was present at all sites and during each survey, so it was the only species to be included in further statistical analyses.

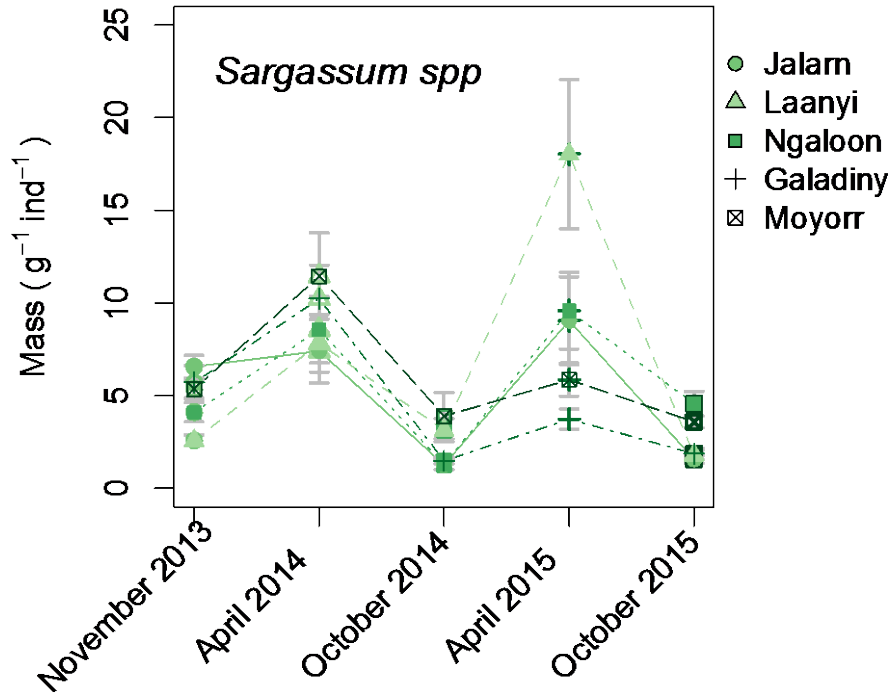


Figure 10: Mean dry weight (grams per individual,  $\pm$  SE) of all *Sargassum* species combined from each survey and each site.

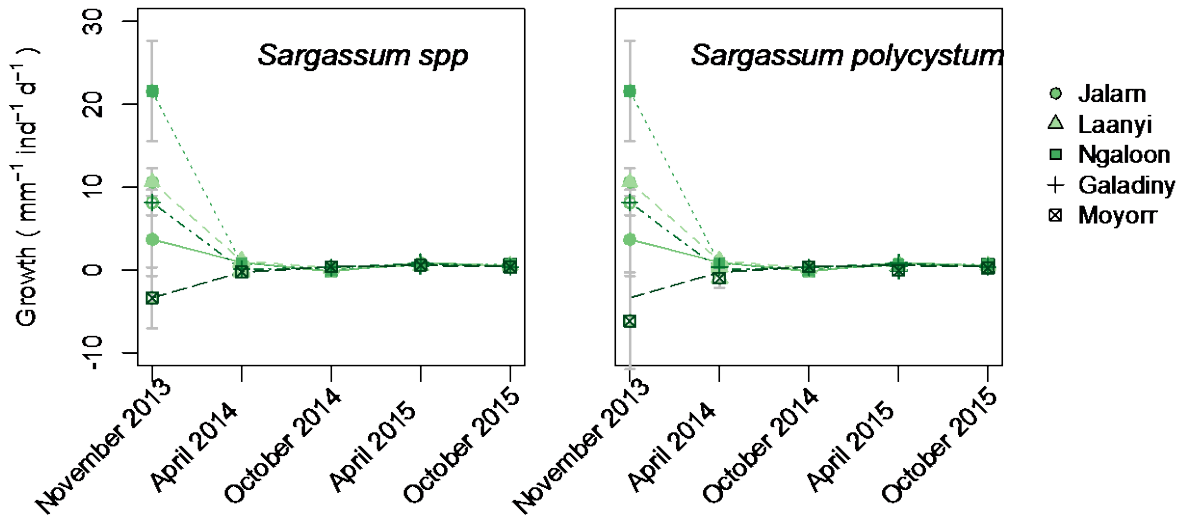


Figure 11: Average growth of *Sargassum* ( $\pm$  SE) in each survey of (a) all *Sargassum* spp. combined, and (b) of *Sargassum polycystum* only.



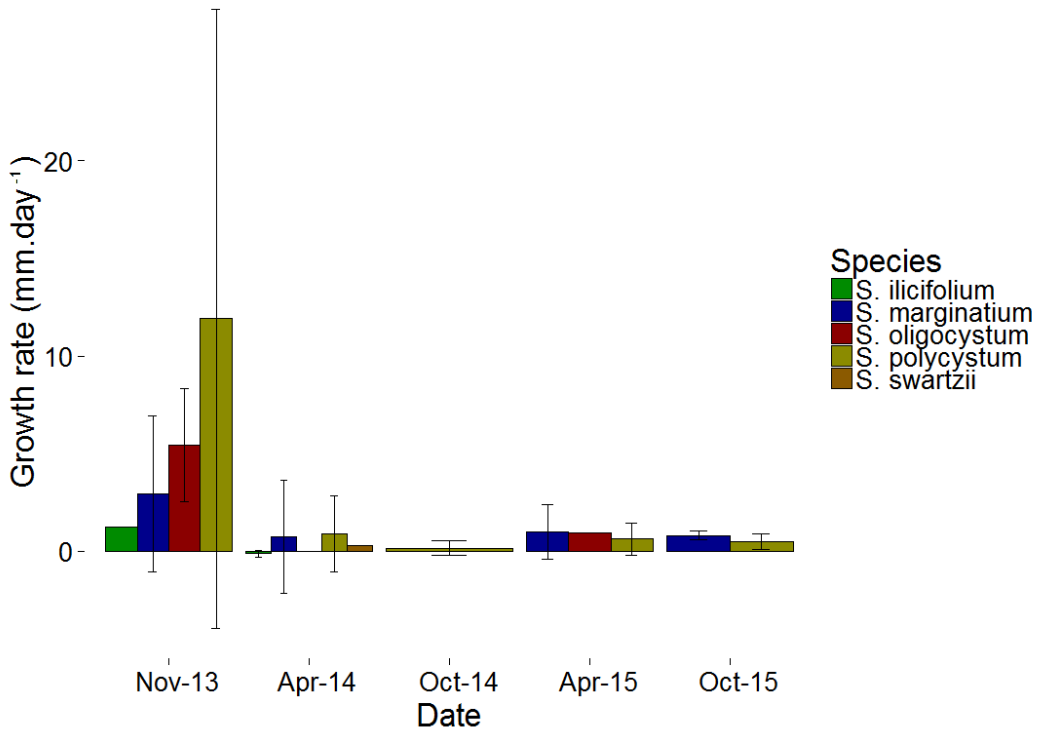


Figure 12: Mean productivity (mm day<sup>-1</sup>; longest branch) of each *Sargassum* spp. during each survey. Error bars represent two standard deviations.

Productivity of *S. polycystum* varied among sites and surveys in complex ways, reflected in a statistically-significant interaction (Table 7). Of the seven individuals for which growth was measured on multiple branches, one indicated a statistically significant difference between the growth of the longest branch and the mean growth of all other measurement branches (Plant C, p=0.04; Table 8). The other six individuals did not produce any evidence of different net growth rates of the longest branch compared to the other branches.

Table 7: Results of analyses of variance testing for differences between and within sites. Two way ANOVA incorporating both site and season.

| <b>Sargassum Growth</b> |           |           |          |            |
|-------------------------|-----------|-----------|----------|------------|
| <b>Two way</b>          | <b>df</b> | <b>MS</b> | <b>F</b> | <b>Sig</b> |
| <b>ANOVA</b>            |           |           |          |            |
| Time                    | 4         | 1596.2    | 29.559   | <0.001     |
| Site                    | 4         | 163.9     | 9.3424   | 0.018      |
| Time x Site             | 16        | 291.5     | 5.399    | <0.001     |
| Residual                | 301       | 53.9      |          |            |
| Total                   | 326       |           |          |            |

Table 8: Results of two-sample T-tests comparing growth of the longest branch on each plant to the mean net growth rate of the other branches. P-value shows results of t-test of hypothesis that longest branch grew at a different rate to that of other branches.

| Sargassum I.D | Species               | Site   | Net growth of longest branch (mm d <sup>-1</sup> ) | Mean net growth of other branches (mm d <sup>-1</sup> ) | p           |
|---------------|-----------------------|--------|--|---|-------------|
| Plant A       | <i>S. polycystum</i>  | Jalan  | 0.49   | 0.99  | 0.29        |
| Plant B       | <i>S. polycystum</i>  | Jalan  | 0.49   | 0.049   | 0.1         |
| Plant C       | <i>S. polycystum</i>  | Laanyi | 0.99   | 0.29  | <b>0.04</b> |
| Plant D       | <i>S. polycystum</i>  | Laanyi | 0.49   | 0   | NA          |
| Plant E       | <i>S. polycystum</i>  | Laanyi | 0.74   | 0.55  | 0.42        |
| Plant F       | <i>S. ilicifolium</i> | Moyorr | 1.00   | 1.96  | 0.34        |
| Plant G       | <i>S. marginatum</i>  | Moyorr | 1.50   | 0.94  | 0.22        |

### 3.3 Rates of seagrass consumption

Overall, *Thalassia* was consumed at greater rates than *Enhalus* (16.1% ±1.7 for *Thalassia* vs 6.7% ±1.1 for *Enhalus*). However, within this broad trend there was substantial variability (Figure 13, Table 9). For both seagrasses, there was significant variation among the sets of tethered shoots attached to different ropes, indicating substantial patchiness in rates of consumption; this accounted for more than a quarter of the total variation for both species. Variation among deployments (i.e. among different places at different times) was also significant for *Enhalus*, but not for *Thalassia*.

Consumption of *Thalassia* was high at Ngaloon in October 2014 and October 2015, but not during April 2015, it is possible that this might indicate a seasonal pattern, but there was no evidence of this at any other locations. High rates of consumption of *Enhalus* occurred only once: at Jalan during October 2014.

Table 9: Results of permutational analyses of variances testing for patterns in the consumption (% per day) of two species of seagrasses: *Thalassia* and *Enhalus*.

| <b><i>Thalassia hemprichii</i></b> |     |       |       |                  |       |               |
|------------------------------------|-----|-------|-------|------------------|-------|---------------|
| Source                             | df  | SS    | MS    | Denominator      | F     | p             |
| Location [L]                       | 2   | 7819  | 3909  | Day (L × S)      | 3.67  | 0.067         |
| Survey [S]                         | 2   | 5817  | 2908  | L × S            | 1.29  | 0.373         |
| L × S                              | 4   | 8984  | 2246  | Day (L × S)      | 2.11  | 0.162         |
| Day (L × S) [D]                    | 9   | 9588  | 1065  | Rope (L × S × D) | 1.98  | 0.053         |
| Rope (L × S × D)                   | 72  | 38280 | 531   | Residual         | 5.67  | <b>0.0001</b> |
| Residual                           | 174 | 16312 | 93    |                  |       |               |
| <b><i>Enhalus acoroides</i></b>    |     |       |       |                  |       |               |
| Source                             | df  | SS    | MS    | Denominator      | F     | p             |
| Location [L]                       | 2   | 33976 | 16988 | Day (L × S)      | 16.96 | <b>0.001</b>  |
| Survey [S]                         | 2   | 13060 | 6529  | L × S            | 0.95  | 0.459         |
| L × S                              | 4   | 27477 | 6869  | Day (L × S)      | 6.88  | <b>0.007</b>  |
| Day (L × S) [D]                    | 9   | 8938  | 993   | Rope (L × S × D) | 1.02  | 0.435         |
| Rope (L × S × D)                   | 69  | 67321 | 975   | Residual         | 3.75  | <b>0.0001</b> |
| Residual                           | 173 | 44972 | 259   |                  |       |               |

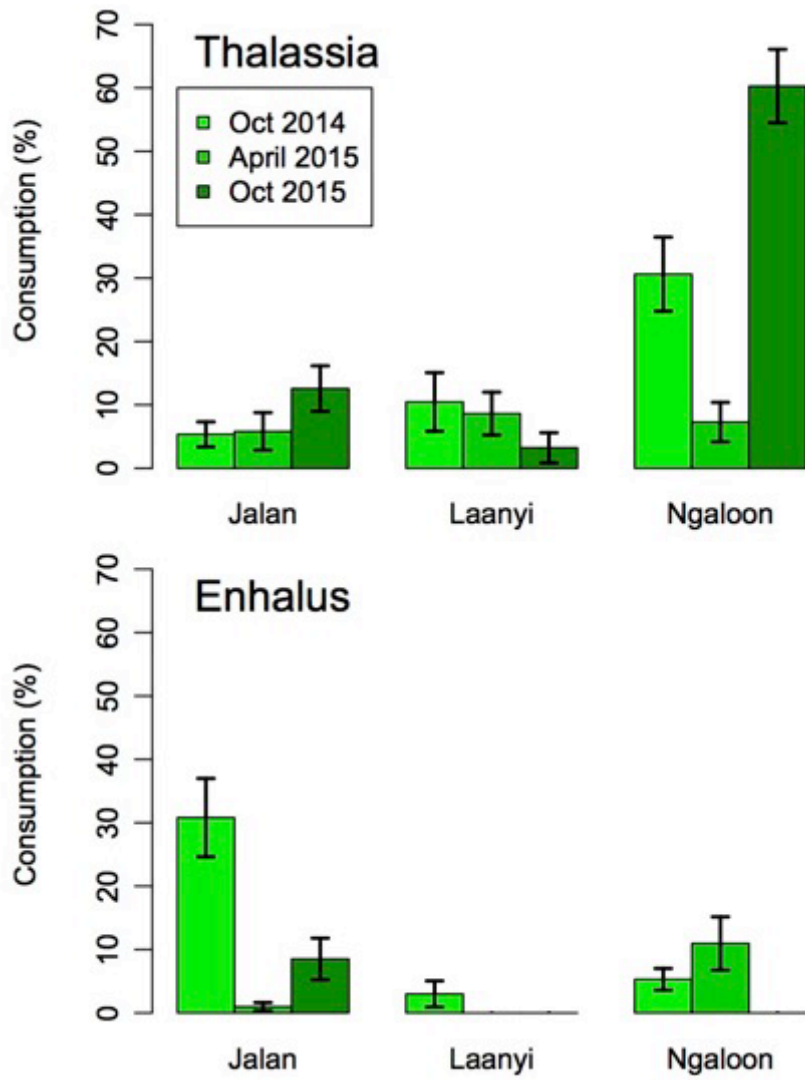


Figure 13: Rates of consumption (% per day) of the seagrasses *Thalassia hemprichii* and *Enhalus acoroides* at three survey locations in the Bardi Jawi IPA.

### 3.4 Patterns in stable isotope ratios

$\delta^{13}\text{C}$  of primary producers encompassed a wide range of values (-32.3 to -6.7: Figure 14), with mangroves tending to yield lower  $\delta^{13}\text{C}$  (-32.3 to -25.0) than seagrasses or macroalgae, which tended to encompass similar ranges (seagrass: -24.9 to -7.6 macroalgae: -24.1 to -6.7).  $\delta^{15}\text{N}$  of primary producers tended to overlap, and varied less than  $\delta^{13}\text{C}$  (-4.2 to 6.1, although most were greater than 0: Figure 14). Seagrasses encompassed the widest range of  $\delta^{15}\text{N}$  of all primary producers (-4.2 to 6.0).

Within these broad trends there were differences among species within major phyla (Figure 15, Figure 16). The mangrove *Rhizophora stylosa* tended to yield lower  $\delta^{13}\text{C}$  than the mangrove *Sonneratia alba*, the seagrasses *T. hemprichii*, *H. ovalis*, *H. uninervis* and *Thalassodendron ciliatum* yielded lower  $\delta^{13}\text{C}$  than the seagrass *E. acoroides*, and the brown algae *S. polycystum*, *Sargassum ilicifolium*, *S. oligocystum*, *H. cuneiformis* and *S. trinodis* yielded lower  $\delta^{13}\text{C}$  than *T. gracilis* and *T. ornata*. Cyanobacteria tended to have lower  $\delta^{15}\text{N}$  than seagrasses or macroalgae, and varied in  $\delta^{13}\text{C}$ .

Spatial and temporal patterns in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of three widespread benthic primary producers (the seagrasses *T. hemprichii* and *E. acoroides*, and the brown alga *S. polycystum*) were variable and somewhat idiosyncratic (Figure 17, Table 10). Some differences among locations were observed, but these differences were not consistent among surveys. In addition, there did not appear to be evidence of regular seasonal patterns in the  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  of any species at any location (Figure 17). In general, these patterns were reflected as highly significant interactions between surveys and locations (5 of 6 tests  $P < 0.05$ , Table 10).

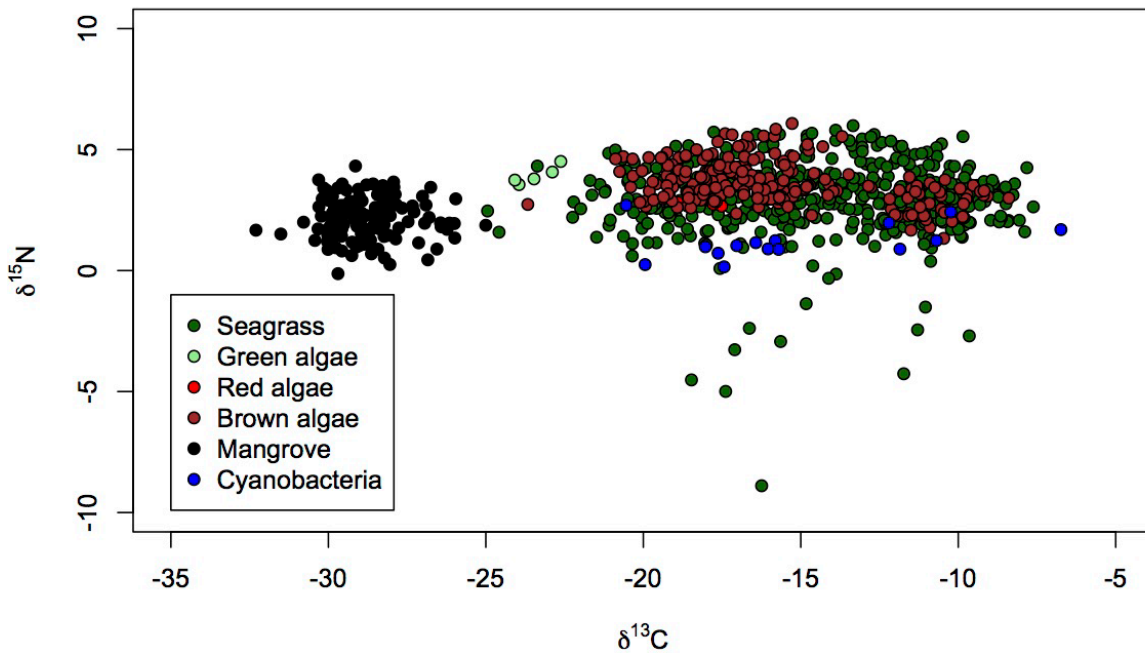


Figure 14: Individual measurements of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of benthic primary producers collected from Sunday Island (Iwany) and Tallon Island (Jalan) in the Bardi Jawi IPA, shown according to major taxonomic group.

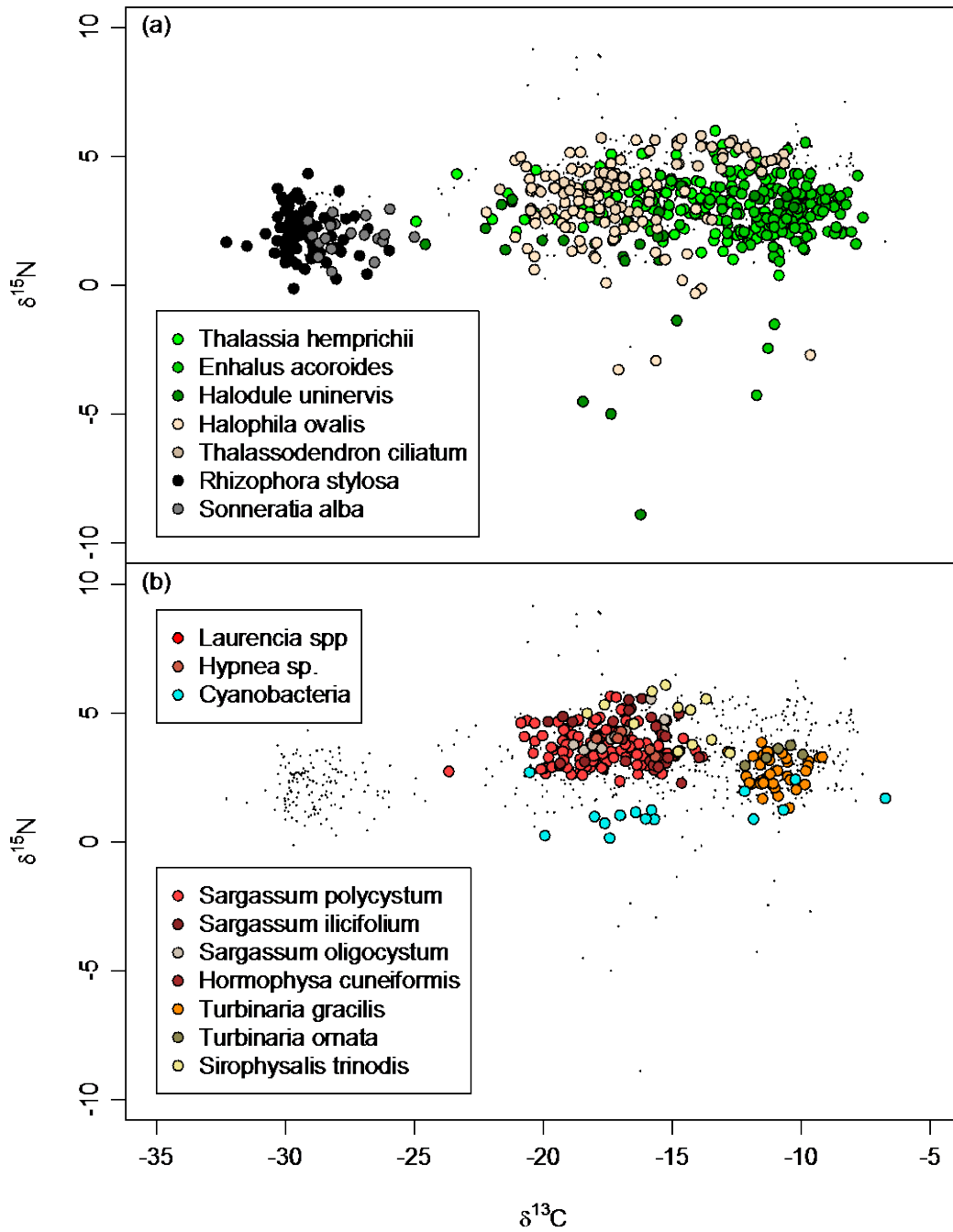


Figure 15: Individual measurements of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of benthic primary producers collected from Sunday Island (Iwany) and Tallon Island (Jalan) in the Bardi Jawi IPA, shown by species: (a) Seagrasses and mangroves, (b) Macroalgae and cyanobacteria. The small black dots indicate data shown in other plots.

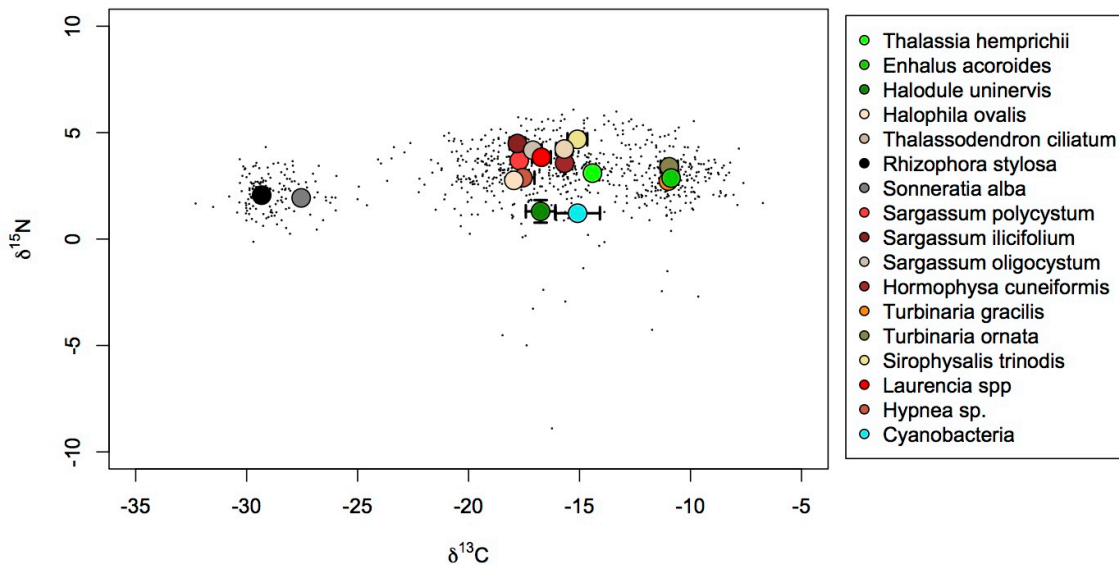


Figure 16: Mean ( $\pm$  SE)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of major species of benthic primary producers collected from Sunday Island (Iwany) and Tallon Island (Jalan) in the Bardi Jawi IPA. Where SE are not visible they are hidden by the symbols.

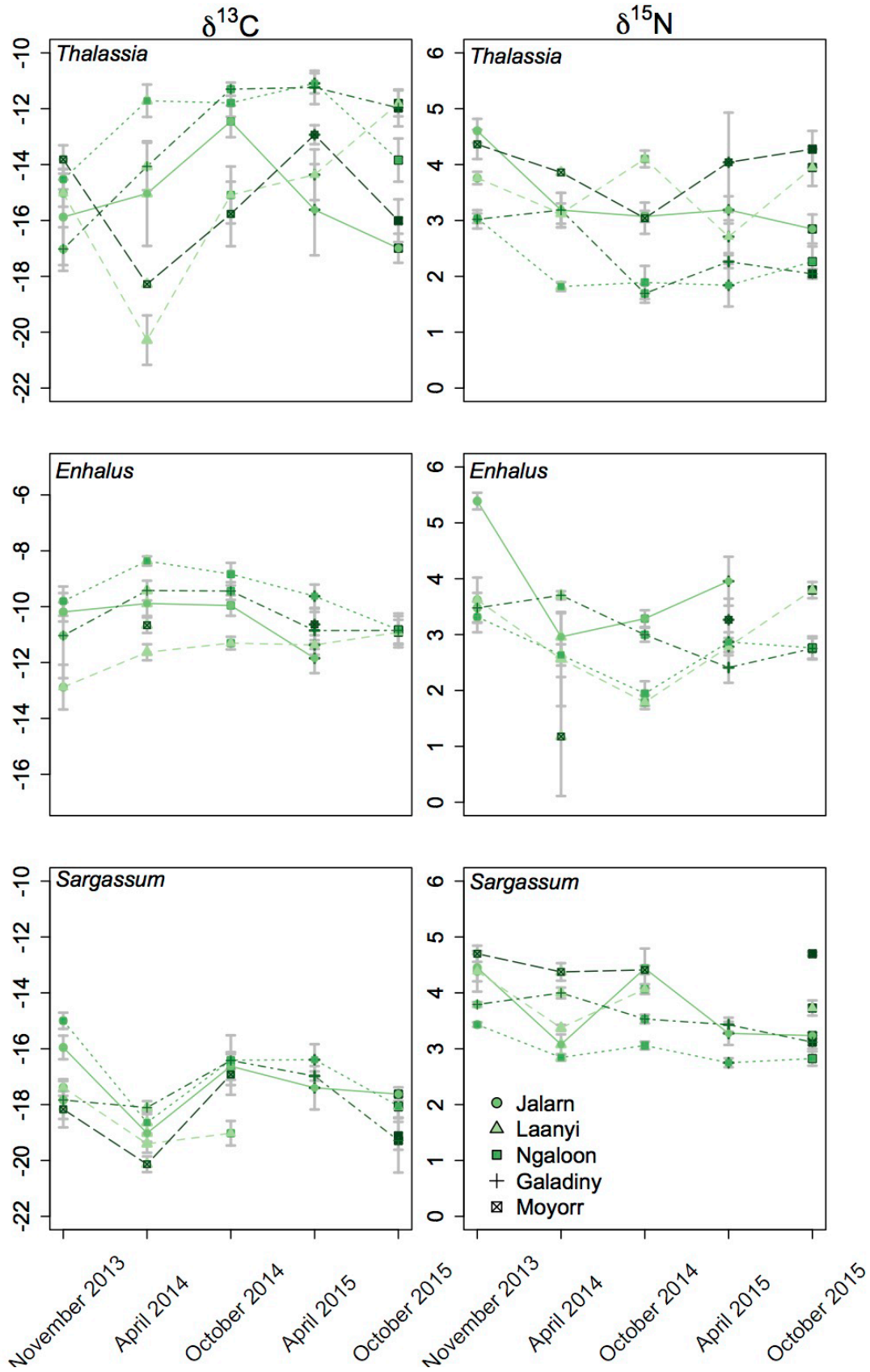


Figure 17: Spatial and temporal patterns in mean ( $\pm$  SE)  $\delta^{13}\text{C}$  (left column) and  $\delta^{15}\text{N}$  (right column) of three major species of benthic primary producers collected from Sunday Island (Iwany) and Tallon Island (Jalan) in the Bardi Jawi IPA.

Table 10: Results of analyses of variances testing for patterns in the stable isotope ratios ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of two species of seagrasses (*Thalassia hemprichii* and *Enhalus acoroides*) and the brown alga *Sargassum polycystum*. Survey was considered a fixed factor, and location was considered a random factor.

| <b><i>Thalassia hemprichii</i></b> |    |       |      |      |                  |                       |      |      |      |                  |
|------------------------------------|----|-------|------|------|------------------|-----------------------|------|------|------|------------------|
| $\delta^{13}\text{C}$              |    |       |      |      |                  | $\delta^{15}\text{N}$ |      |      |      |                  |
| Source                             | df | SS    | MS   | F    | p                | df                    | SS   | MS   | F    | p                |
| Location [L]                       | 3  | 217.1 | 72.3 | 14.2 | <b>&lt;0.001</b> | 3                     | 31.0 | 10.3 | 32.2 | <b>&lt;0.001</b> |
| Survey [S]                         | 4  | 202.1 | 50.5 | 1.8  | 0.193            | 4                     | 14.4 | 3.6  | 2.4  | 0.107            |
| L × S                              | 12 | 323.7 | 26.9 | 5.3  | <b>&lt;0.001</b> | 12                    | 18.4 | 1.5  | 4.7  | <b>&lt;0.001</b> |
| Residual                           | 90 | 456.8 | 5.1  |      |                  | 90                    | 28.8 | 0.3  |      |                  |
| <b><i>Enhalus acoroides</i></b>    |    |       |      |      |                  |                       |      |      |      |                  |
| $\delta^{13}\text{C}$              |    |       |      |      |                  | $\delta^{15}\text{N}$ |      |      |      |                  |
| Source                             | df | SS    | MS   | F    | p                | df                    | SS   | MS   | F    | p                |
| Location [L]                       | 3  | 73.5  | 24.5 | 16.0 | <b>&lt;0.001</b> | 3                     | 12.8 | 4.2  | 7.8  | <b>&lt;0.001</b> |
| Survey [S]                         | 4  | 51.8  | 12.9 | 3.2  | 0.052            | 4                     | 20.5 | 5.1  | 3.1  | 0.057            |
| L × S                              | 12 | 48.1  | 4.0  | 2.6  | <b>0.005</b>     | 12                    | 18.7 | 1.6  | 2.8  | <b>0.002</b>     |
| Residual                           | 85 | 130.4 | 1.5  |      |                  | 85                    | 46.7 | 0.6  |      |                  |
| <b><i>Sargassum polycystum</i></b> |    |       |      |      |                  |                       |      |      |      |                  |
| $\delta^{13}\text{C}$              |    |       |      |      |                  | $\delta^{15}\text{N}$ |      |      |      |                  |
| Source                             | df | SS    | MS   | F    | p                | df                    | SS   | MS   | F    | p                |
| Location [L]                       | 3  | 29.6  | 9.8  | 7.2  | <b>&lt;0.001</b> | 3                     | 10.8 | 3.6  | 27.0 | <b>&lt;0.001</b> |
| Survey [S]                         | 4  | 66.4  | 16.6 | 4.7  | 0.018            | 4                     | 9.6  | 2.4  | 4.0  | 0.031            |
| L × S                              | 11 | 39.3  | 3.5  | 2.6  | 0.006            | 11                    | 6.4  | 0.6  | 4.4  | <b>&lt;0.001</b> |
| Residual                           | 76 | 103.3 | 1.3  |      |                  | 76                    | 10.1 | 0.1  |      |                  |

### 3.5 Biomass and productivity of benthic microalgae (BMA)

Sediment at the sites surveyed for benthic macroalgae (BMA) varied from fine grain sandy sediments at Cygnet Bay South, Cygnet Bay North, Jologo Beach, Noolagoon (Figure 18a) to coarser silica grains intermixed with shell and coral hash at Sunday Island Running Waters and Turtle Beach (Figure 18b). Ngaloon was different from all other study sites; sediment there was dominated by fine mud intermixed with coarse silica grains (Figure 18c).





Figure 18: Site photos depicting the fine grain sediments (a) at Cygnet Bay South (also representative of Cygnet Bay North, Jologo Beach, and Noolagoon), coarse sediments (b) at Sunday Island Running Waters (similar to Turtle Beach), and muddy sediments (c) found at Ngaloon.

The biomass of BMA (as estimated from extracted chlorophyll-*a*) did not show any specific seasonal trends within sites (Figure 19). The mudflats at Ngaloon consistently yielded the highest chl-*a* biomass estimates during the study, but decreased during the course of the study from 11.9  $\mu\text{g g}^{-1}$  in April 2014 to 6.6  $\mu\text{g g}^{-1}$  in October 2015.

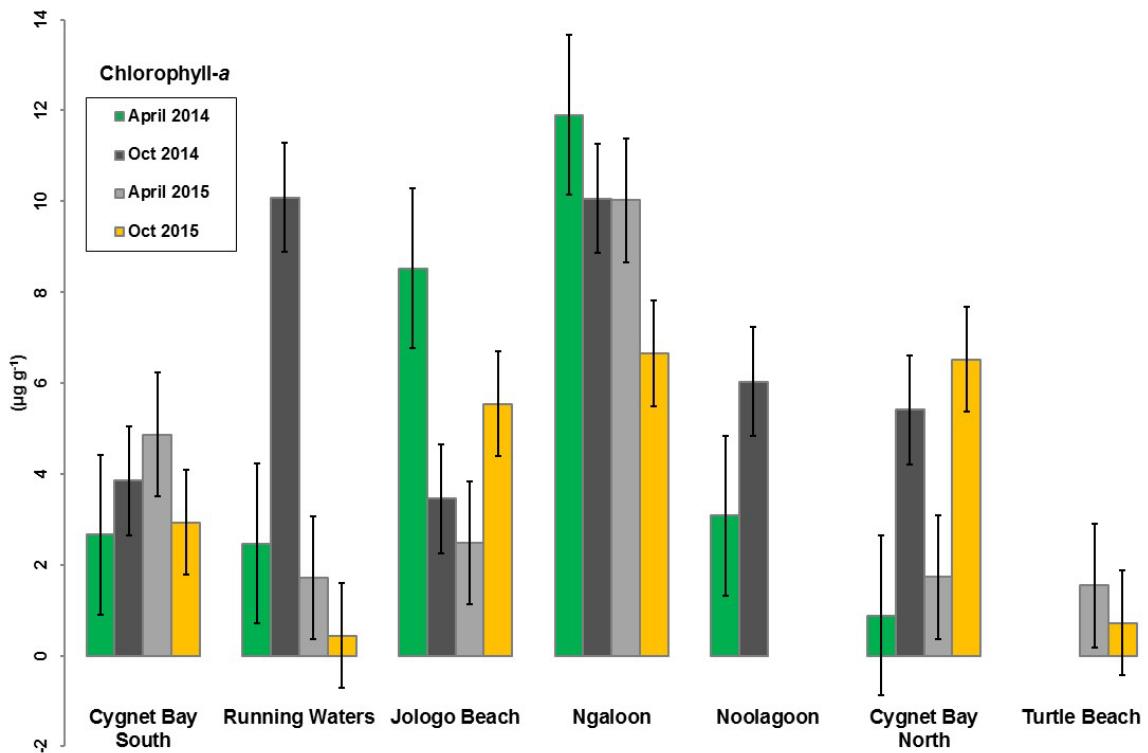


Figure 19: Site average chlorophyll-*a* content ( $\mu\text{g g}^{-1}$ ) of sediments from study sites in proximity to Aardylloon and Sunday Island.

The composition of the BMA assemblage — estimated by HPLC analysis of microalgal accessory pigments in April (Figure 20) and October 2014 (Figure 21) — was dominated by benthic diatoms, usually consisting of free-living motile epipelton (BMA associated with, mud or silt) and epipsammon (BMA attached to, or associated with, sand). The presence of chlorophyll-*b* (chl-*b*) was found only at Ngaloon. Cyanobacteria was observed at all sites but was greater in biomass at Ngaloon and Jologoo Beach (Figures 20 and 21).

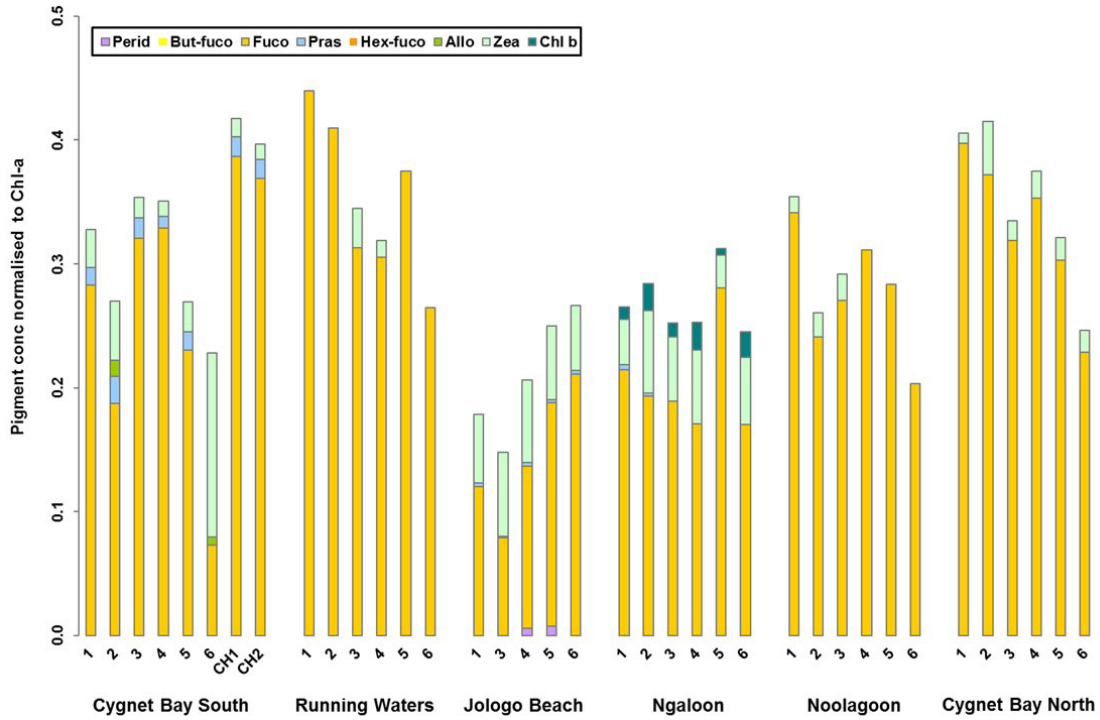


Figure 20: Composition of BMA assemblage in April 2014, estimated from analysis of accessory pigments via HPLC.

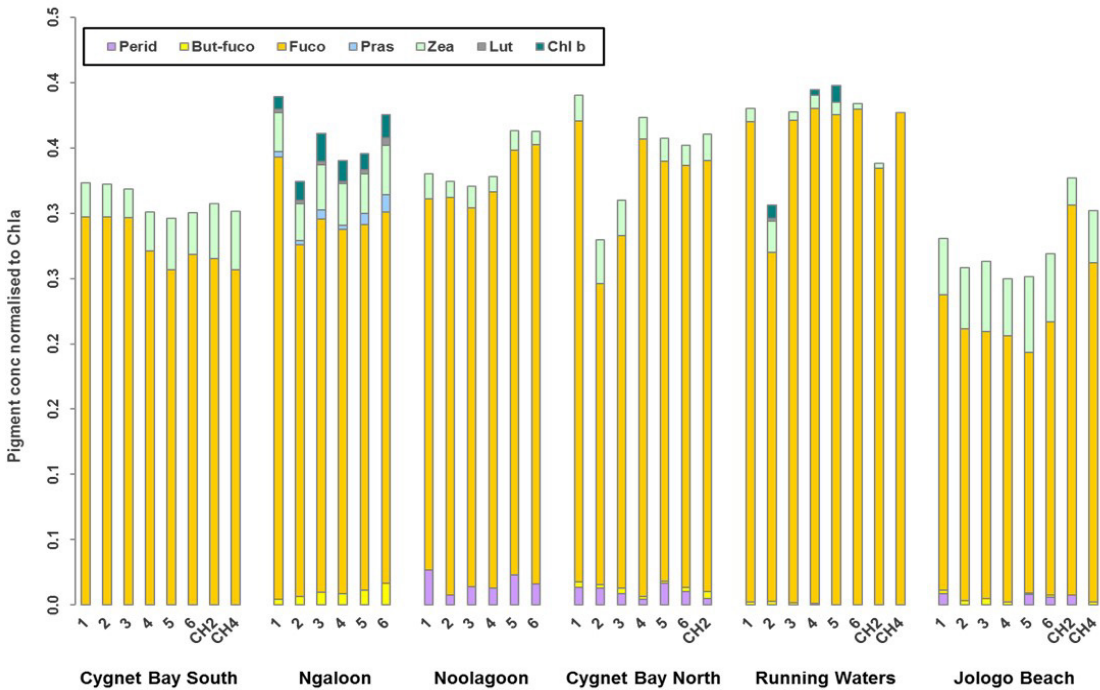


Figure 21: Composition of BMA assemblage in October 2014, estimated from analysis of accessory pigments via HPLC.

Like chl-*a*, nutrients (nitrate, phosphate and silica) extracted from sediment pore water did not show any discernible seasonal trends over the course of the study (Figures 22, 23 and 24). Correlations of chlorophyll-*a* with porewater nutrients did not yield a strong relationship with any of the nutrient species measured ( $R^2 = 0.02$  for  $\text{NO}_x$ , 0.015 for  $\text{PO}_4$ , and 0.023 for Si).

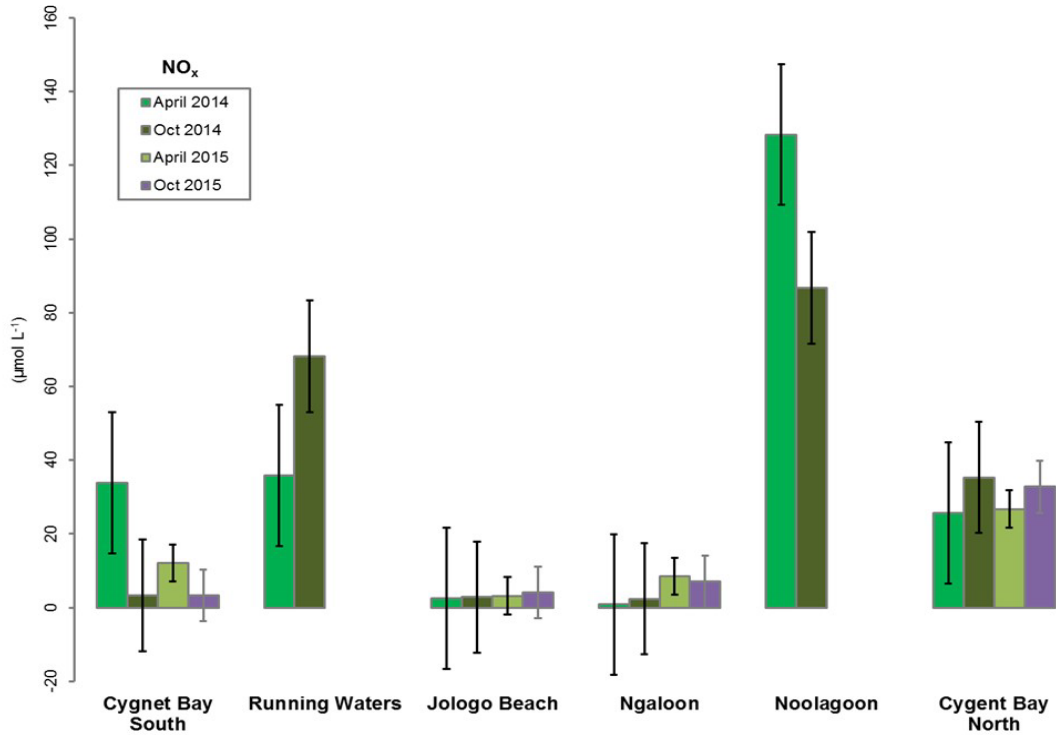


Figure 22: Site average concentration of nitrate ( $\mu\text{mol L}^{-1}$ ) from sediment pore waters (Note: not enough sample collected from Turtle Beach to analyse).

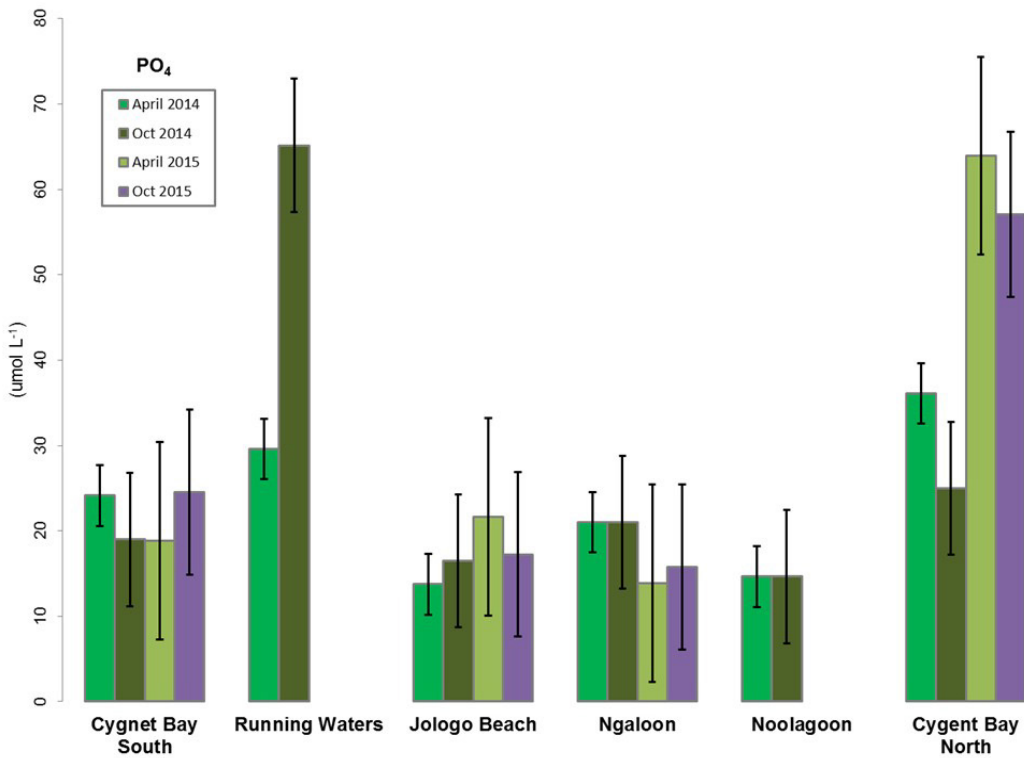


Figure 23: Site average concentration of phosphate ( $\mu\text{mol L}^{-1}$ ) from sediment pore waters (Note: not enough sample collected from Turtle Beach to analyse).

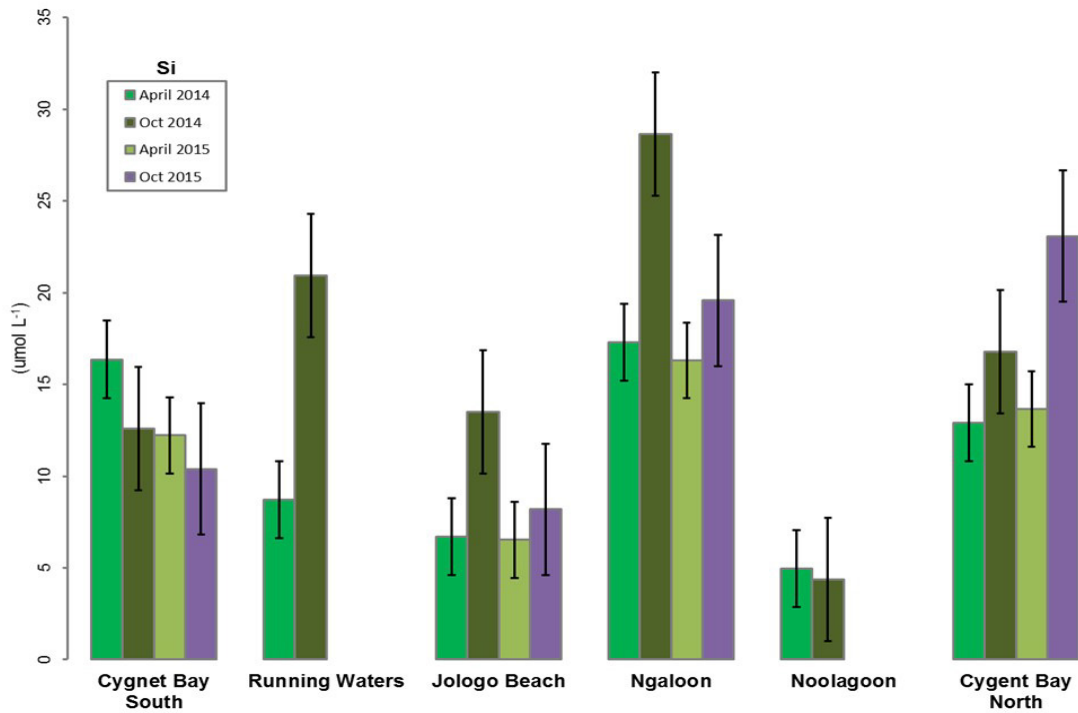


Figure 24: Site average concentration of silica ( $\mu\text{mol L}^{-1}$ ) from sediment pore waters (Note: not enough sample collected from Turtle Beach to analyse).

Using the inverse of the amount of water retention in sediments (i.e. the weight of water as a percent of the total wet weight of sediment) as a proxy for porosity, sites with large sediment particles (Turtle Beach and Sunday Island Running Waters) had sediment water content between 0.4 and 3 %. These had higher porosity than sediments of the other “sandy” sites whose sediment water content ranged between 9 and 18 %. There appears to be a general trend showing an increase in porosity (decrease in water retention) over the course of the study (Figure 25). Porosity was not strongly correlated with chl-*a* biomass yielding an  $R^2$  value of 0.16.

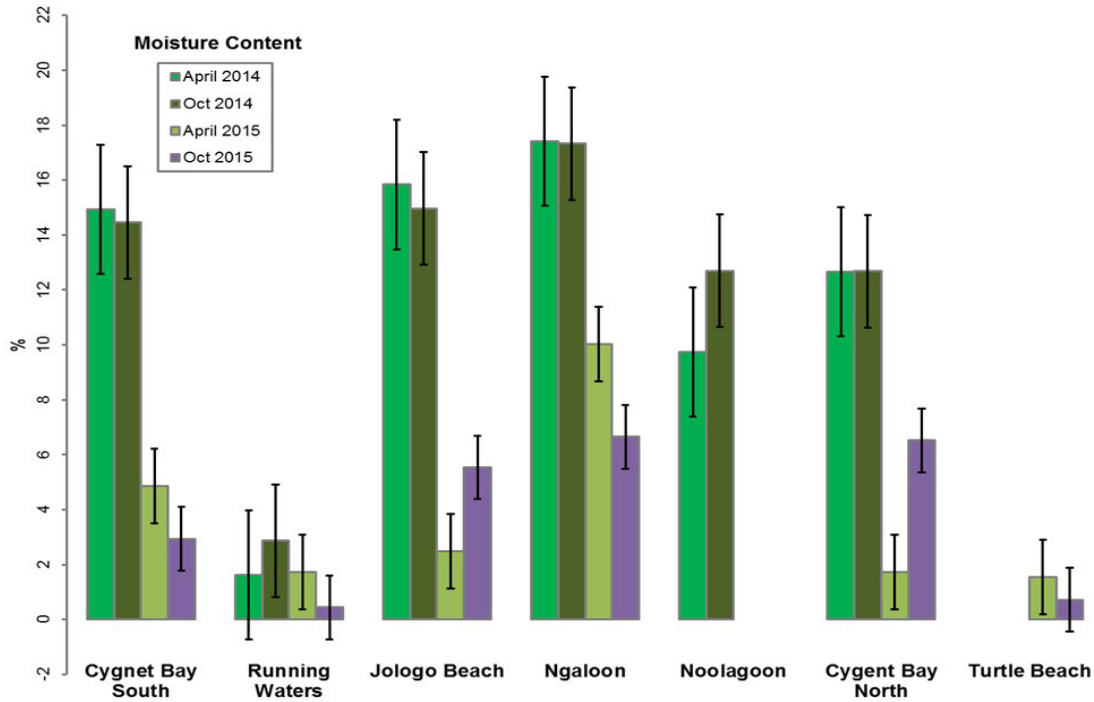


Figure 25: Site average porosity of sediments calculated from water content as a % of the total weight.

Net productivity (uptake of carbon calculated from oxygen via Redfield ratios) of BMA measured in soft sediment habitats by the benthic chambers was positive at Cygnet Bay South (ranging between 350 to 1100 mg C m<sup>-2</sup>d<sup>-1</sup>) and Jologo Beach (ranging between 200 to 600 mg C m<sup>-2</sup>d<sup>-1</sup>) during each survey (Figure 26). However, at Cygnet Bay North, the system shifted from net respiration (-460 mg C m<sup>-2</sup>d<sup>-1</sup> in Nov 2013 and -750 mg C m<sup>-2</sup>d<sup>-1</sup> in April 2014) to net production (ranging between 240 and 730 mg C m<sup>-2</sup>d<sup>-1</sup>) during the last 3 surveys. Observations from cores collected at Cygnet Bay North in Nov 2013 and April 2014 showed very strong and shallow anoxic layer (blackened layers of sediment) compared to observations made after this time. At site Turtle Beach, respiration was dominant (-370 mg C m<sup>-2</sup>d<sup>-1</sup> in April 2015 and -2850 mg C m<sup>-2</sup>d<sup>-1</sup> in Oct 2015) indicating the site as a potential carbon source during surveys in 2015.

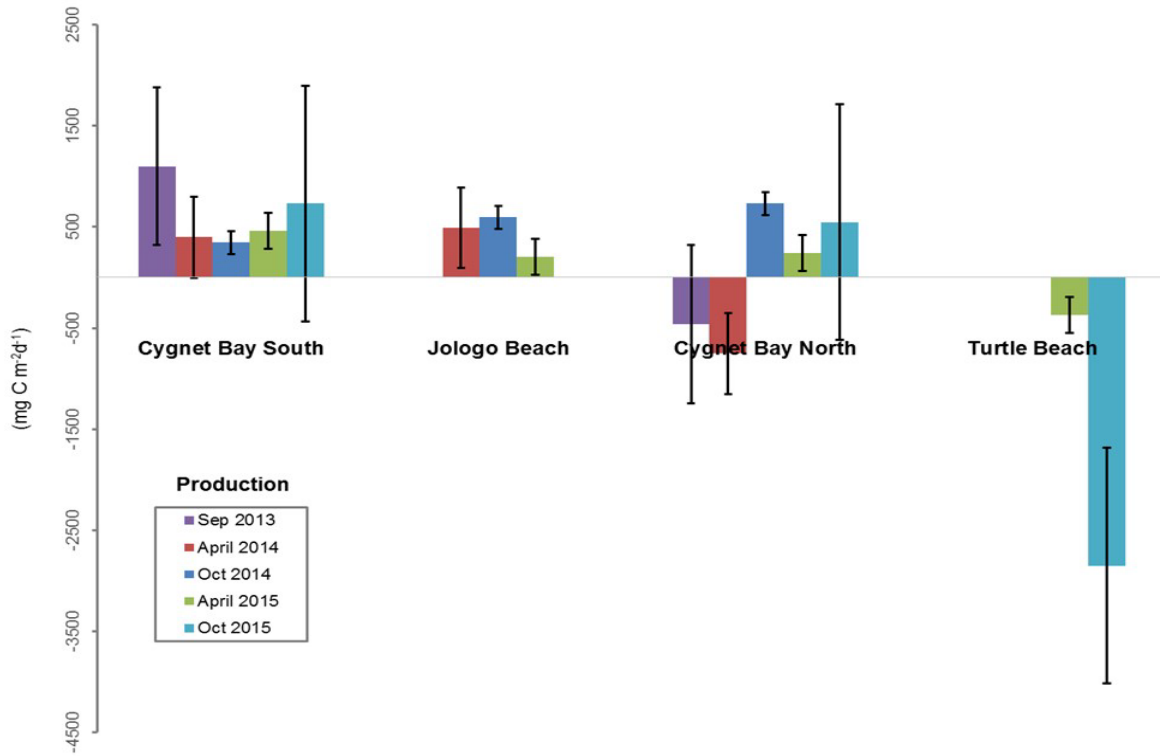


Figure 26: Site net daily production by sediment dwelling benthic micro-algae (mg C m<sup>-2</sup>d<sup>-1</sup>).

Rates of net production over daily temporal scales (measured concurrently over 3 days) at Cygnet Bay South (Figure 27) were highly variable (ranging between 55 – 520 mg C m<sup>-2</sup>d<sup>-1</sup> in Oct 2014, and -55 – 430 mg C m<sup>-2</sup>d<sup>-1</sup> in Oct 2015). This is despite chlorophyll biomass remaining relatively consistent (ranging between 2.72 - 2.98 µg g<sup>-1</sup> in Oct 2014, and 2.00 – 2.69 µg g<sup>-1</sup> in Oct 2015) over the same time period (Figure 27) indicating no correlation between the two ( $R^2 = 0.287$ ).

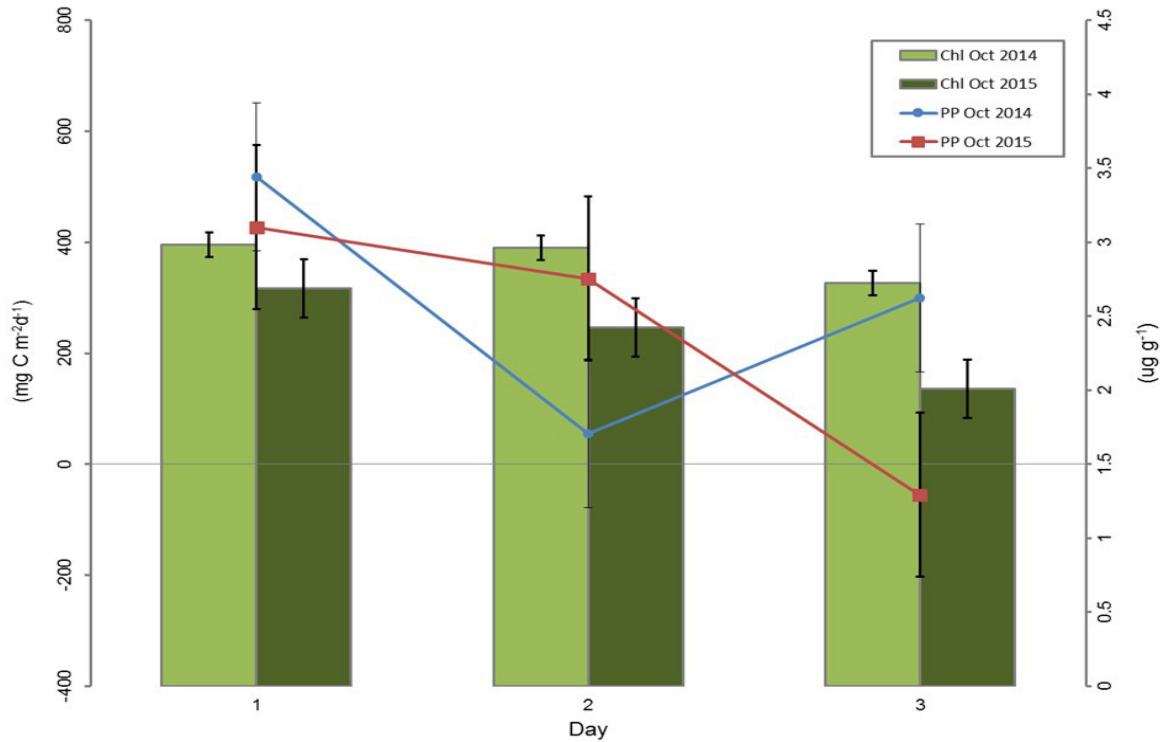


Figure 27: Net daily production ( $\text{mg C m}^{-2}\text{d}^{-1}$ ) and Chl-*a* concentrations ( $\mu\text{g g}^{-1}$ ) of sediment dwelling benthic micro-algae in October 2014 and 2015 at site Cygnet Bay South over sequential days.

### 3.6 Sub-surface sediment chemistry

Microprofiles of dissolved oxygen in illuminated sediment cores showed sub-surface maxima, approximately 1 mm below the sediment surface, with concentrations up to 3.5 times the saturation of the overlying water (Figure 28a). Such oversaturations with oxygen have often been observed in photosynthetically active sediments (Revsbech et al., 1988). In this case, the sub-surface oxygen features disappear following 10 minutes of dark exposure (Figure 28b), and conversely increased in intensity during sunlit incubation at ambient temperature and salinity (Figure 29), supporting the view that the high sub-surface oxygen concentrations were associated with photosynthetic activity. In most cases, the oxygen concentration decreased sharply below the photosynthetically active layer, penetrating only 1-2 mm into the sediment, indicating a high rate of oxygen consumption below the photic zone (Figure 28a). However, in several cases a more gradual decrease of oxygen was recorded, extending the oxygen penetration depth down to 5 mm below the sediment surface (Figure 28a).

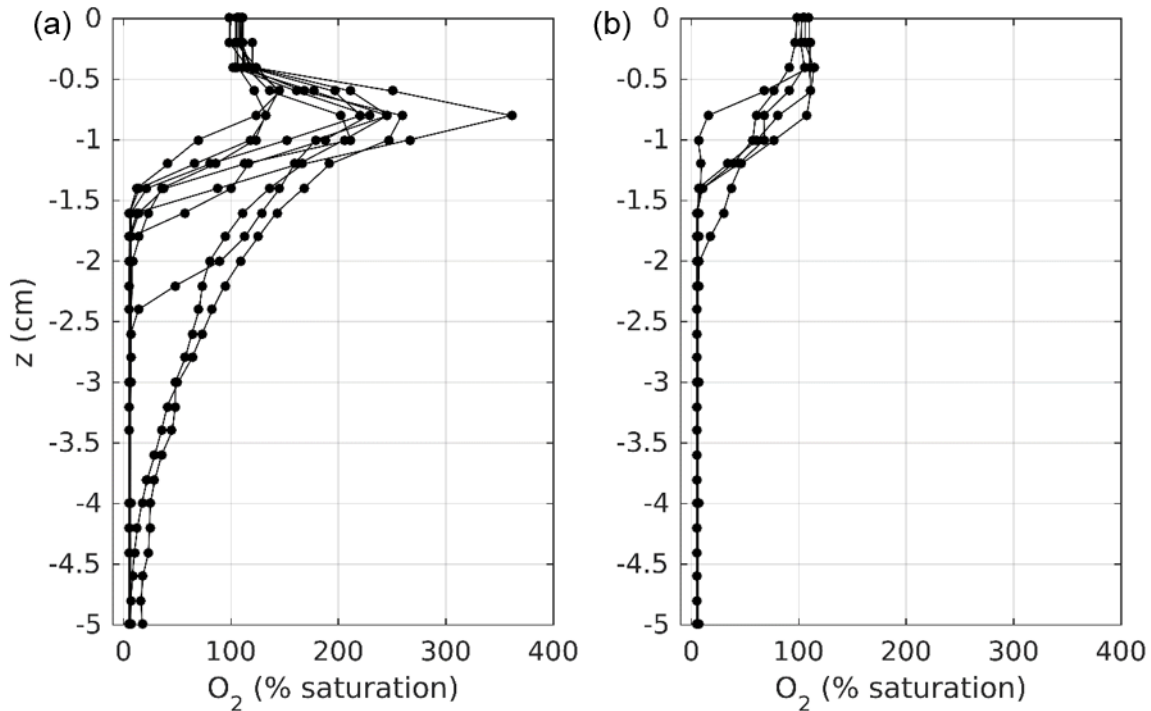


Figure 28: Vertical profiles of sediment dissolved oxygen (a) exposed to sunlight, and (b) after 10 mins in the dark. The sediment-water interface is at approximately  $z = -0.5$  cm.

Some of the samples (e.g. core #5) showed blackened layers of sediment indicating the presence of sulphide (Figure 30). This was confirmed by microprofiles of  $H_2S$  that recorded an increase in concentration with depth (Figure 31b, core #5) roughly coinciding with the appearance of the blackened layer. The presence of sulphide in marine sediments is known to result from reduction of sulphate that occurs under anoxic conditions. Microprofile results for core #5 were consistent with this, showing that the onset of  $H_2S$  was located immediately below the oxic zone at a sediment depth of  $\sim 1.7$  mm (Figure 31, core #5). In contrast, other samples (e.g. core #8) showed little visible (Figure 30) or chemical (Figure 31, core #8) evidence of sulphide in the top 5 mm of sediment; these samples were also characterised by a deeper oxic layer (Figure 31a, core #8).



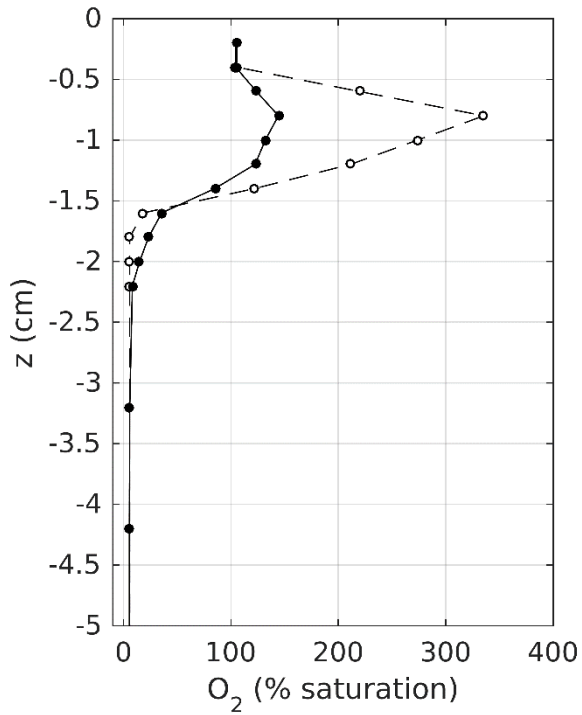


Figure 29: Development of the sub-surface dissolved oxygen ( $O_2$ ) maximum observed early in the day immediately after collection (solid line, closed symbols) and then following  $\sim 2$  hours of incubation in strong sunlight (dashed line, open symbols). The sediment-water interface is at approximately  $z = -0.5$  cm.

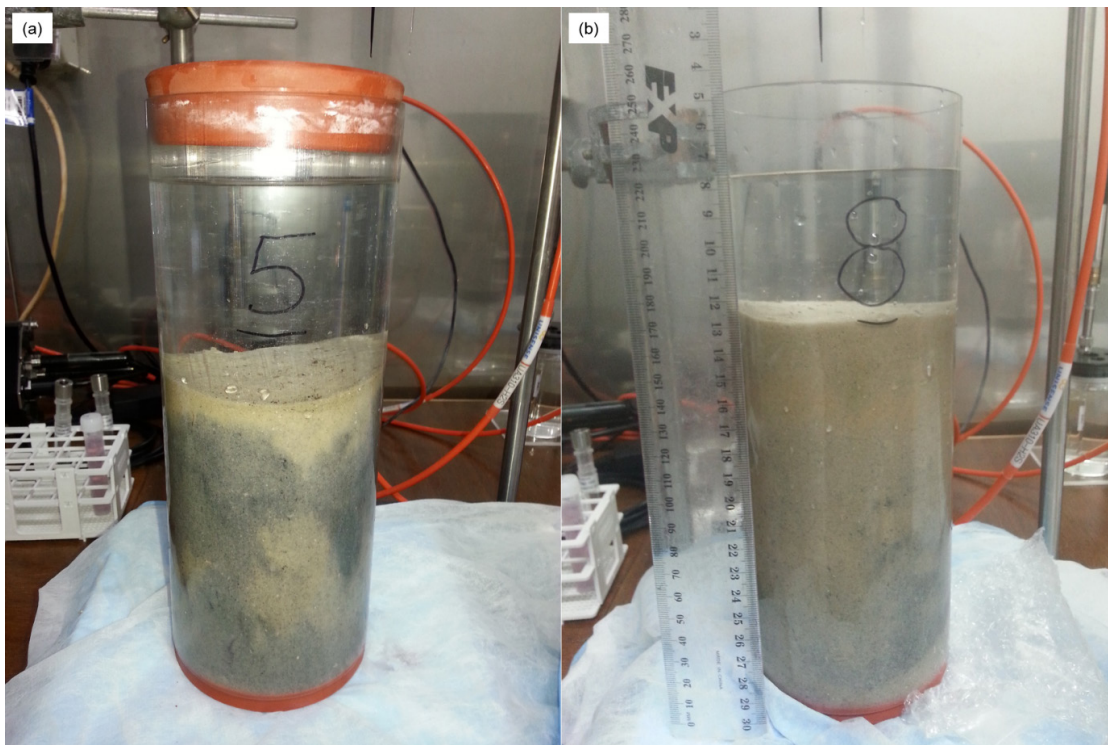


Figure 30: Contrasting appearance of two sediment cores collected in Cygnet Bay at approximately the same location, one on the ebb tide (panel 'a', core #5), and the other 3 hours later on the flood tide (panel 'b', core #8). Core #5 (ebb tide) shows extensive patches of black coloration approximately 2 cm from the sediment surface indicative of sulfide, while in core # 8 black coloration is greatly reduced and restricted to deeper layers.

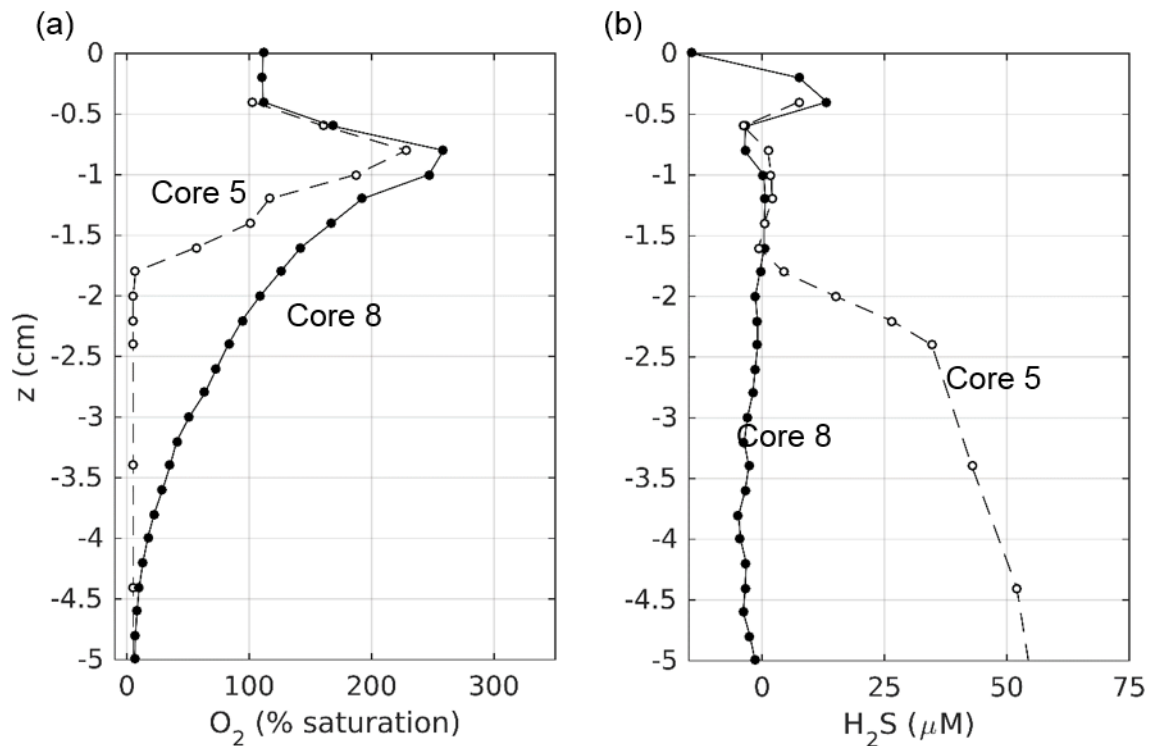


Figure 31: Vertical profile of (a) dissolved oxygen ( $O_2$ ), and (b) hydrogen sulphide ( $H_2S$ ) for core #5 (dashed line, open symbols) and core #8 (solid line, closed symbols) corresponding with the photographs shown in Figure 30. The sediment-water interface is at approximately  $z = -0.5$  cm.

### 1.7 Microbial carbon and nitrogen cycling

Concentrations of DOC and TDN, ranged between 1.8 to 25.8 and 0.3 to 3.2mg/L respectively, and were significantly different between post and pre wet season (Figure 32). Bacterial carbon production rates were high in both seasons and bare sediments had significantly higher rates pre wet season (Figure 33). Bacterial biomass were also higher pre wet season and particularly high biomass found in the mangrove sediments (Figure 34). There was no correlation between DOC, TDN and bacterial carbon production rates thus suggesting that the microbial community is not limited by either C or N in these habitats. High temperatures around 30 degrees in both benthic and pelagic habitats further indicate optimal conditions for bacterial carbon production. Bioassays using DOC sources from the three different benthic habitats and a pelagic bacterial community showed that it was the quality and chemical characteristics of the C and N pool rather than quantity that drives the growth of the pelagic microbial community (Figure 35). Further, it illustrates connectivity between benthic and pelagic habitats as the benthic DOC source is a labile carbon source that can be incorporated into new pelagic bacterial biomass.

Bacterial carbon utilisation were high and of the 31 carbon substrates tested anywhere between 21 to all substrates could be used by the microbial communities in the benthic and pelagic habitats. The most common carbon sources utilised were carbohydrates, amino acids and polymers (Figure 36). Carbon utilisation patterns were similar among the three benthic habitats (Figure 37) however there were inter annual variations in substrate utilisation rates (Figure 38) and metabolic diversity (as indicated by variations in the Shannon-Weaver index, Figure 39).

Sediment microbial community structure varied significantly between the different sampling sites (ANOSIM  $R = 0.34$ ,  $p < 0.01$ ), but not between sediment categories (mangrove, bare or seagrass sediment). Microbial communities isolated from seawater did not vary between sampling sites, but were significantly different from sediment microbial communities ( $R = 0.83$ ,  $p < 0.01$ ) (Figure 40).

There was no significant variation in the abundance of ammonia-oxidising bacteria (AOB) between different sites, whereas the abundance of ammonia-oxidising archaea (AOA) varied weakly but significantly between sites ( $R = 0.13$ ,  $p < 0.05$ ) (Figure 40). Similarly, the structure of AOB communities did not differ significantly between sampling sites, whereas there was significant variation in AOA community structure between different sites ( $R = 0.40$ ,  $p < 0.01$ ). In particular, the AOA community structure clearly changes along the two transects taken on Sunday Island (Figure 40).

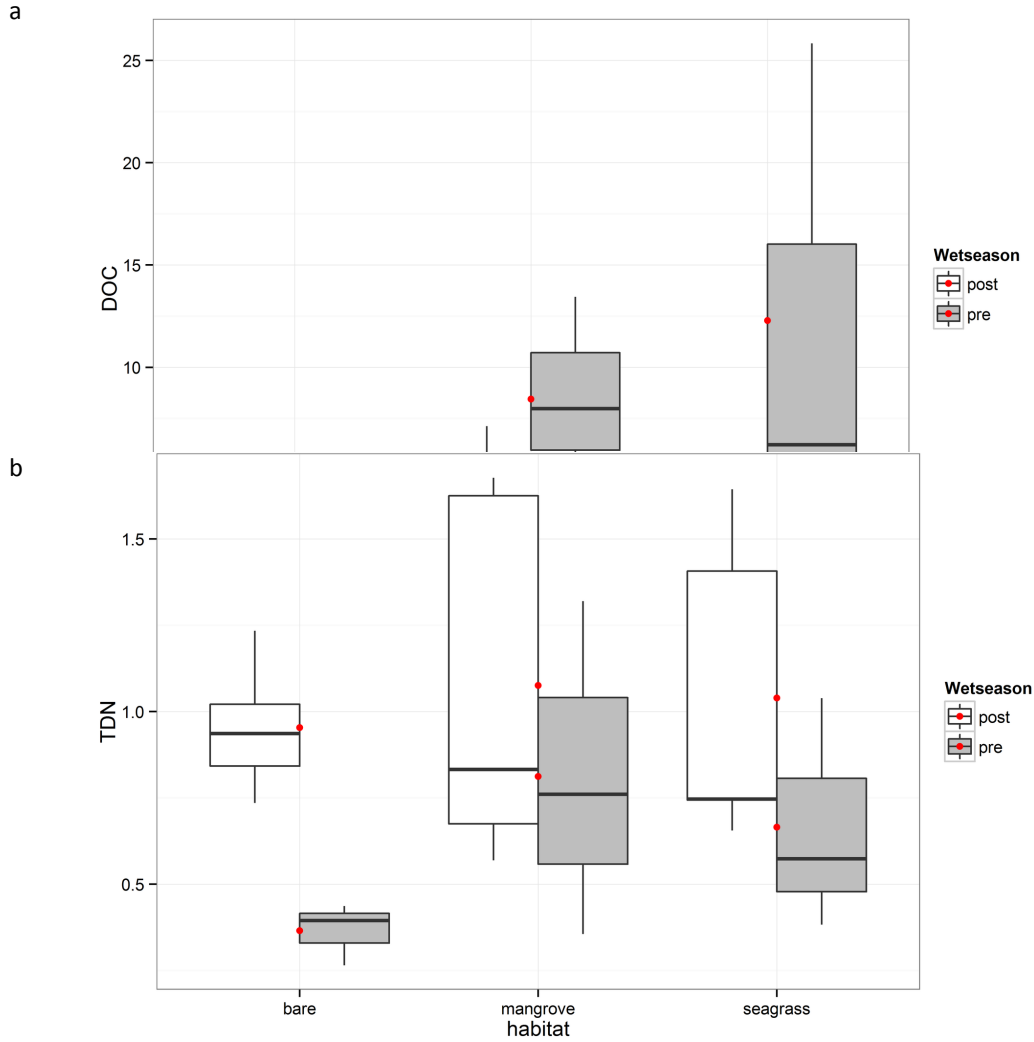


Figure 32: Boxplot of (a) dissolved organic carbon (DOC) and (b) total dissolved nitrogen (TDN) concentrations (mg/L) post- and pre-wet season, with red dot showing arithmetic mean.

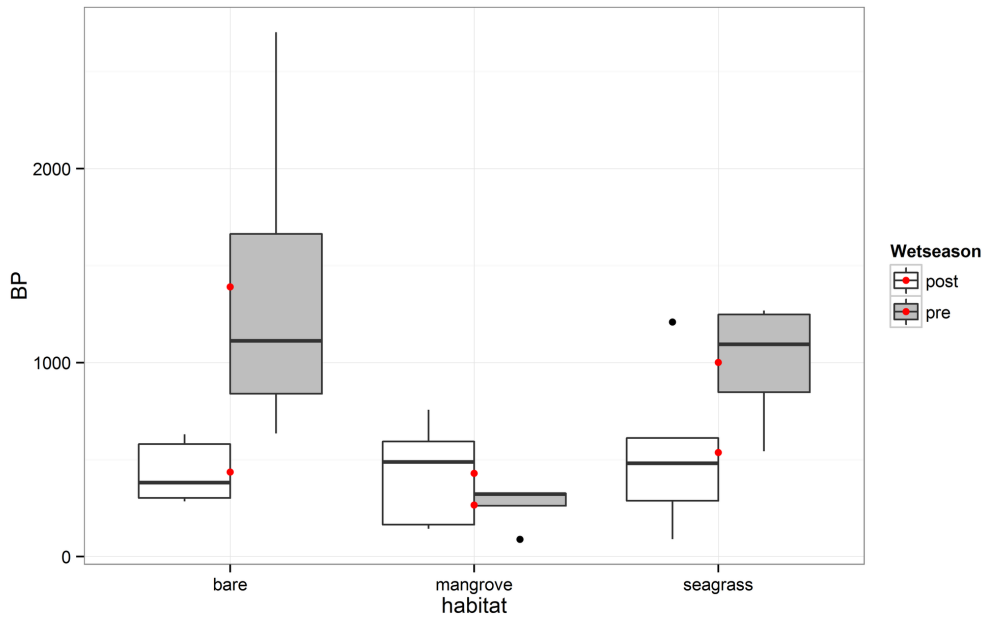


Figure 33: Boxplot of bacterial production rates ( $\text{mg C m}^{-3} \text{ day}^{-1}$ ) post- and pre-wet season, with red dot showing arithmetic mean.

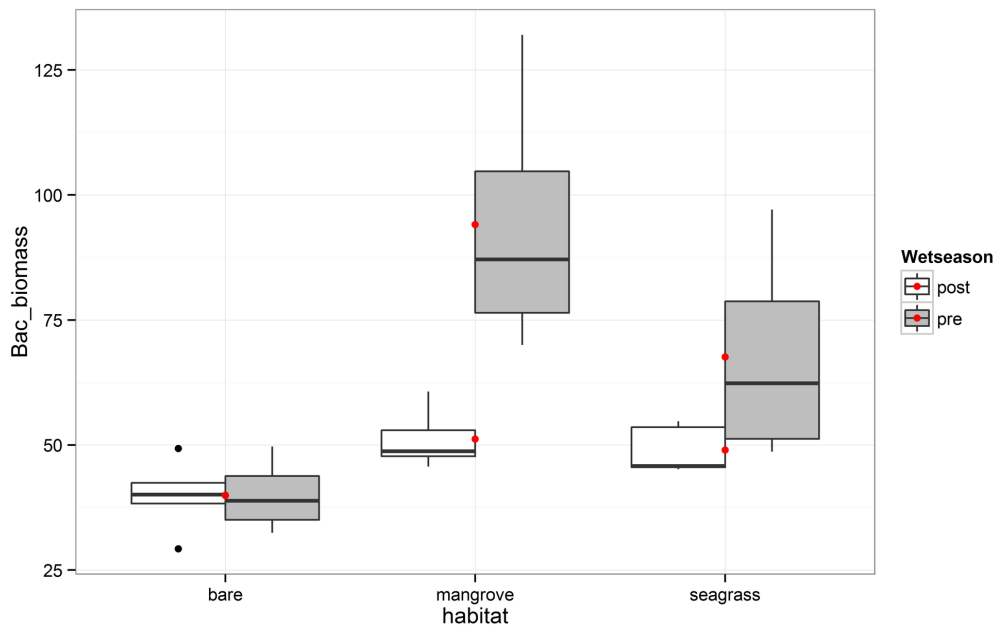


Figure 34: Boxplot of bacterial biomass ( $\text{mg C m}^{-3}$ ) post- and pre-wet season, with red dot showing arithmetic mean.

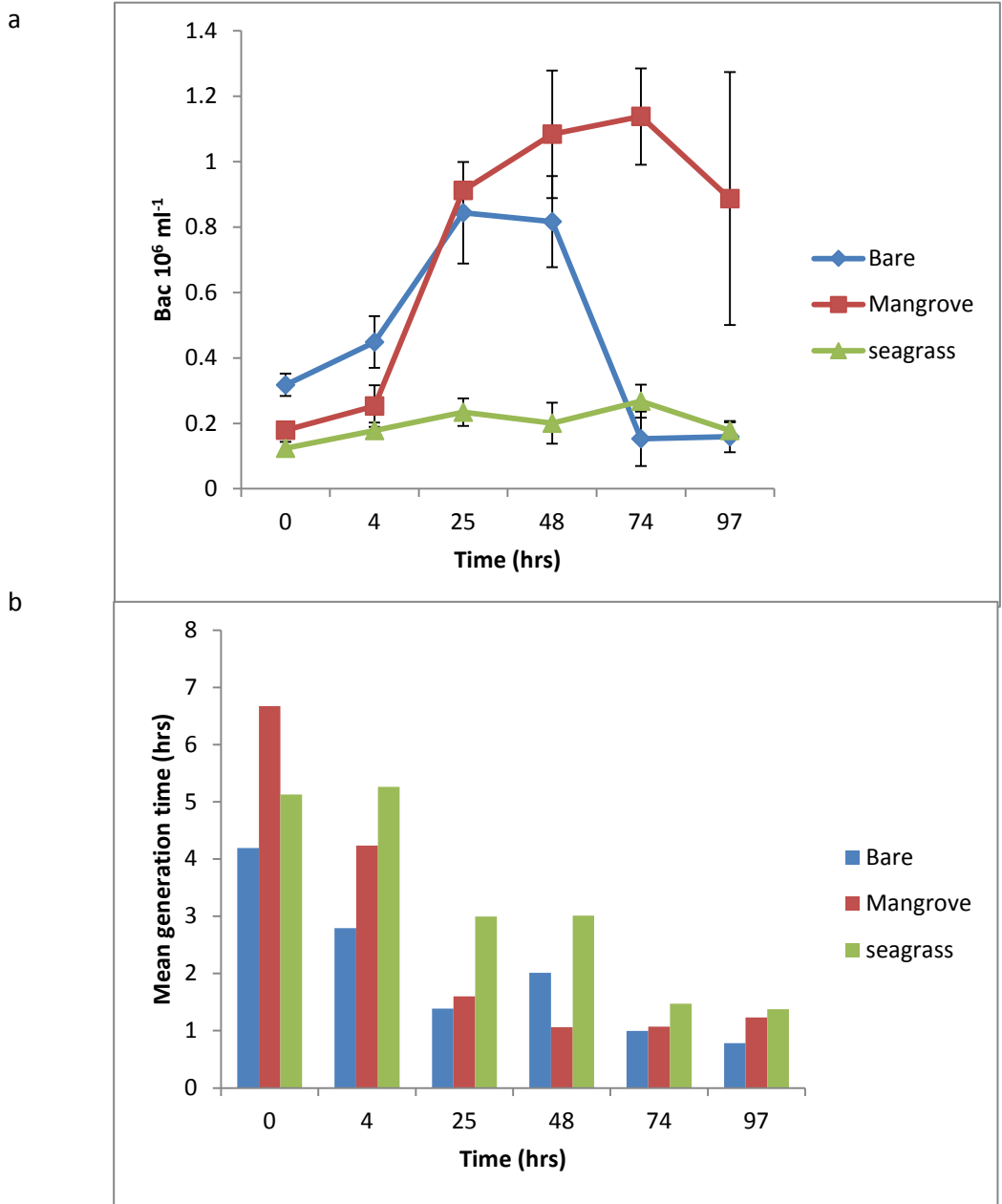


Figure 35: Mean (a) bacterial abundance and (b) generation time changes over time in a bioassay using three different DOC sources (bare sediments, mangrove sediments, seagrass sediments).

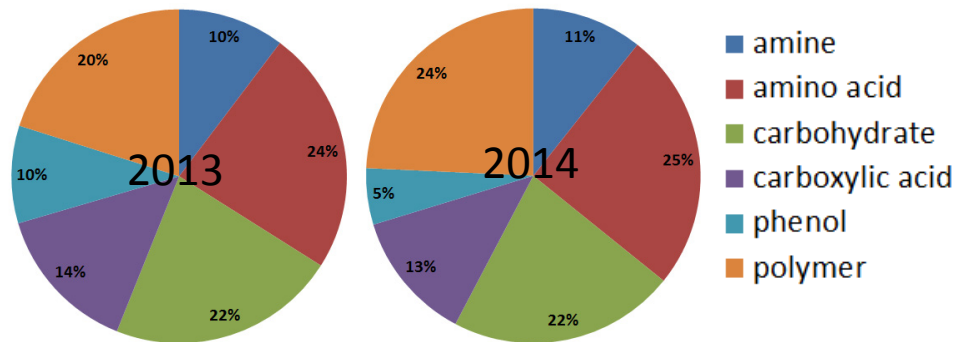


Figure 36: Proportion of each carbon substrate utilised by the benthic bacterial community in 2013 and 2014.

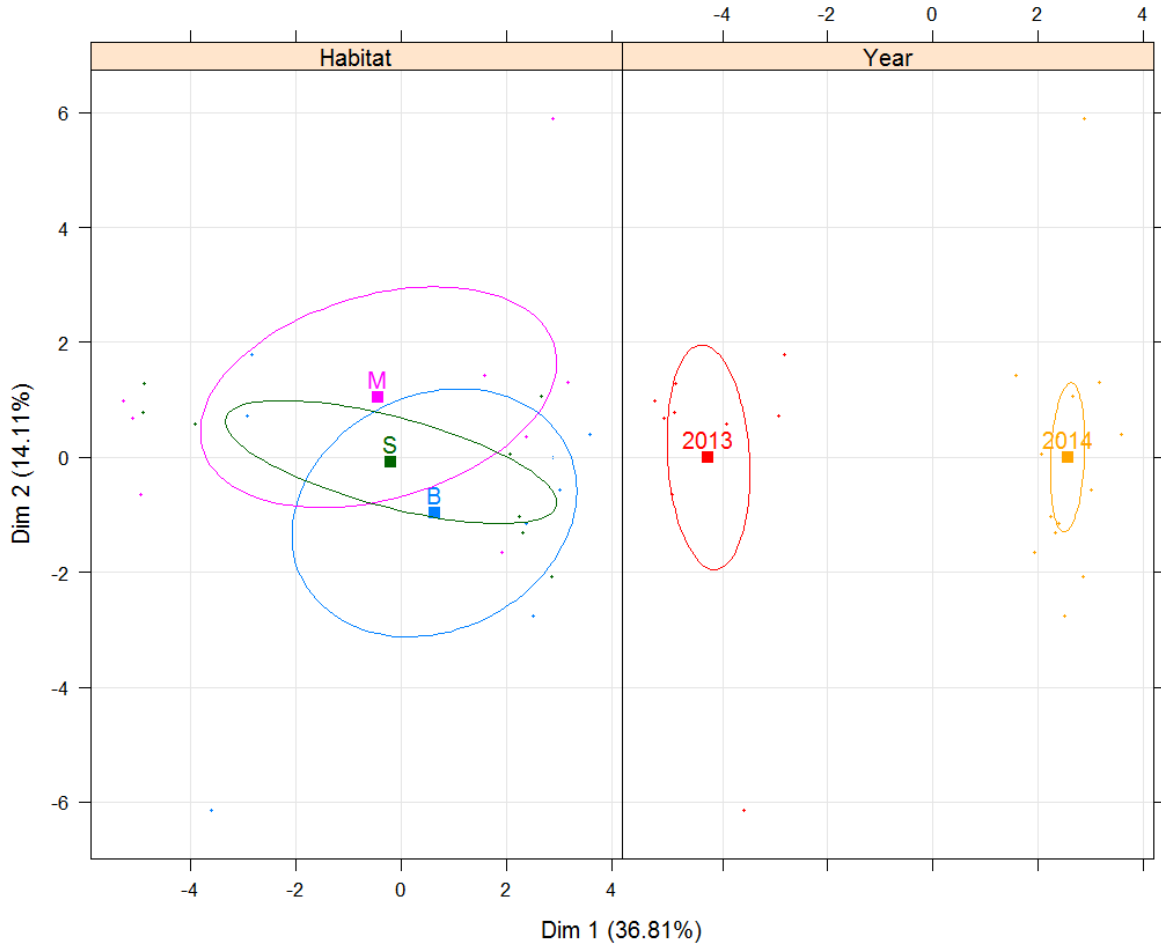


Figure 37: Principal component scores for carbon substrate utilisation pattern by habitat and year.

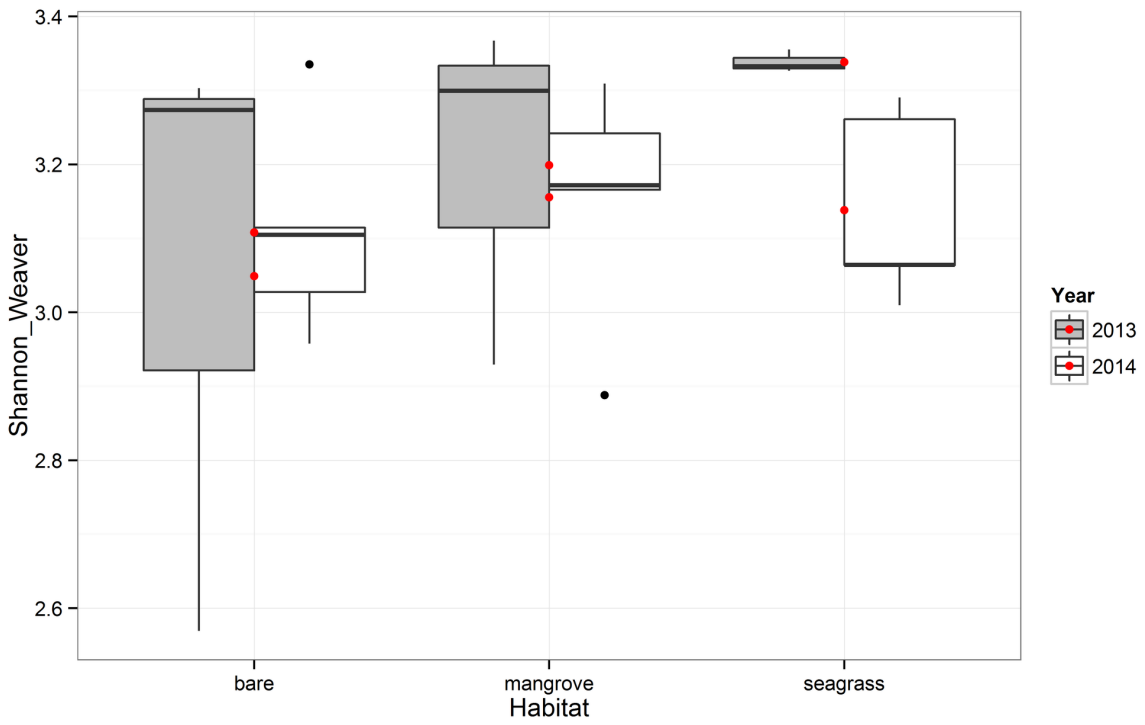


Figure 38: Boxplot of Shannon-Weaver diversity index of the microbial communities by habitat and year.

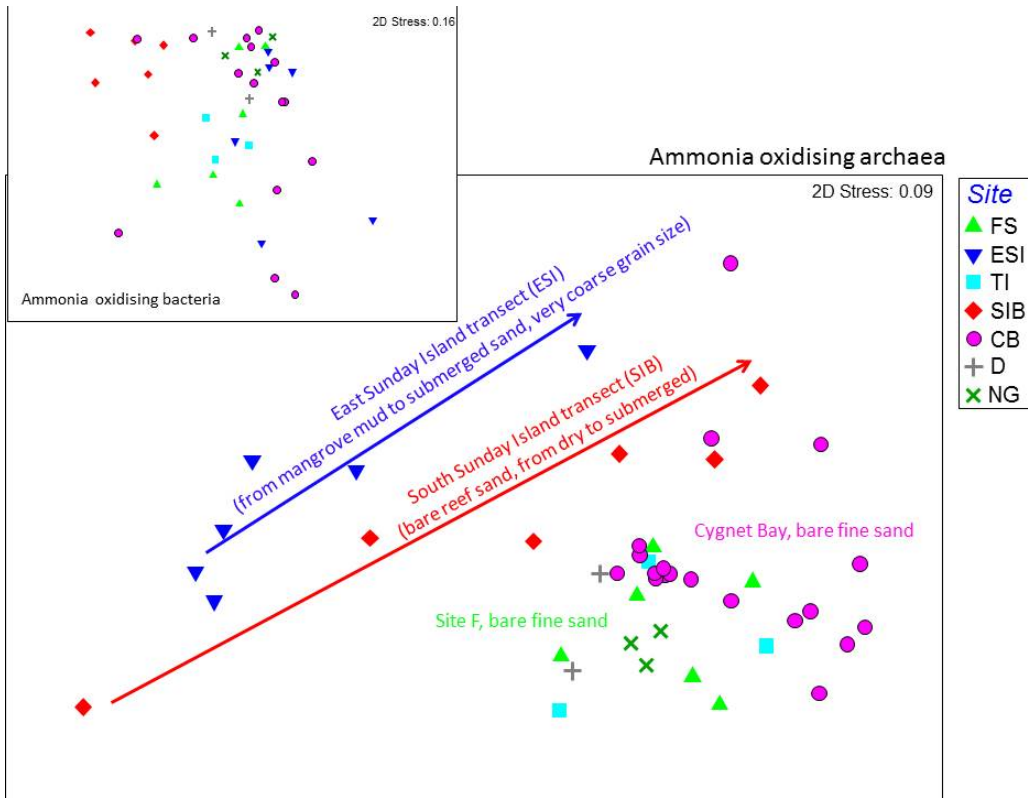


Figure 39: Non-metric multidimensional scaling plot (MDS) of the community structure of ammonia oxidising bacteria (AOB) and ammonia oxidising archaea (AOA), obtained from Bray-Curtis resemblance matrices calculated from standardised and square root-transformed microarray analyses of the *amoA* gene. Data are differentiated by sampling site. FS, Ngaloon; ESI, East Sunday Island; TI, Tallon Island; SIB, South Sunday Island; CB, Cygnet Bay; D, Galadiny; NG, Nguloon (Ngaloon).

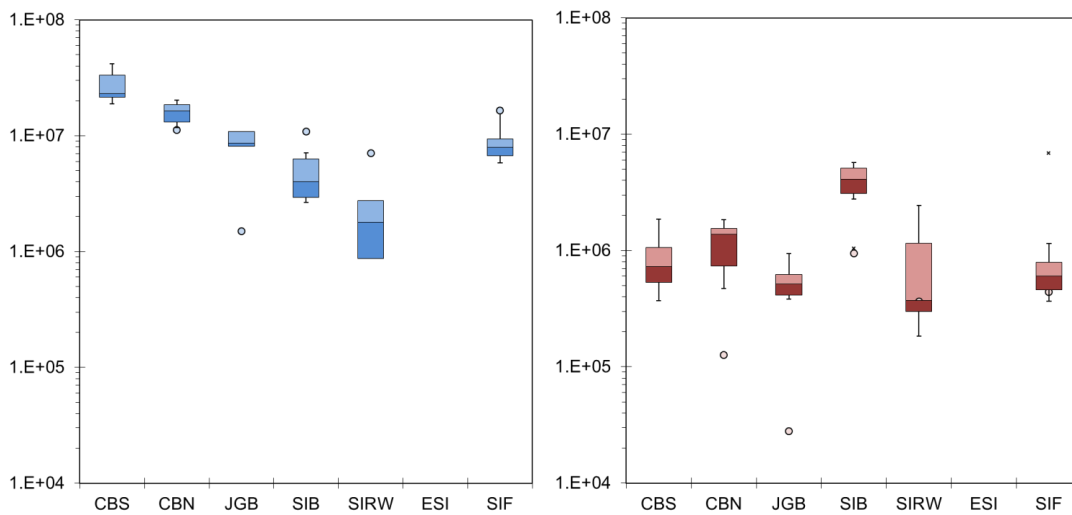


Figure 40: Abundance of ammonia oxidising bacteria (blue boxes) and Archaea (red boxes) between different sediment sites in Cygnet Bay and the Sunday Island Group. Gene abundances were measured using the quantitative polymerase chain reaction (qPCR). The gene abundances in the overlying water, where measured, are represented by open dots.

### 3.7 Light, temperature and depth

Generally, depths at high tide ranged from 2-3 m at Jalan, Laanyi and Ngaloon to more than 4 m at Galadiny and Moyorr (Figure 41). Relative patterns in depth among sites were not always maintained among deployments or even between tides: for example, at Moyorr during the last deployment depth was considerably greater relative to other sites during the second tide (Figure 41).

Patterns in water temperature were irregular and sometimes varied by more than 8°C across a single tidal cycle (e.g. October 2014). Water temperature rose rapidly during the daytime high tides. Temperatures during April 2015 were coolest — this corresponded to a period of strong winds, and appeared to have been influenced by the prevailing weather conditions.

Like water depth, relative differences among sites in light intensity were not always maintained between deployments. Differences in light were not always strongly correlated with water depth, with the highest light intensities sometimes recorded at the deepest sites.

Table 11: Summary statistics of light (PPFD), temperature and depth for each deployment at each site.

| Jalan      |       |            |             |       |       |       |       |       |          |
|------------|-------|------------|-------------|-------|-------|-------|-------|-------|----------|
| Deployment | PPFD  |            | Temperature |       |       | Depth |       |       |          |
|            | total | Solar noon | Min         | max   | mean  | mean  | max   | min   | Day mean |
| Nov2013    | 33.44 | 1373.75    | 28.18       | 35.42 | 30.56 | -1.17 | -3.14 | -0.39 | -1.05    |
| Apr2014    | 26.03 | 1279.31    | 29.49       | 35.87 | 31.86 | -0.90 | -2.68 | -0.14 | -0.93    |
| Nov2014    | 29.27 | 1270.64    | 26.54       | 34.28 | 29.49 | -0.93 | -2.05 | -0.39 | -0.86    |
| Apr2015    | 12.26 | 478.65     | 27.34       | 30.78 | 29.09 | -1.08 | -2.95 | -0.30 | -1.19    |
| Moyorr     |       |            |             |       |       |       |       |       |          |
| Deployment | PPFD  |            | Temperature |       |       | Depth |       |       |          |
|            | total | Solar noon | Min         | max   | mean  | mean  | max   | min   | Day mean |
| Nov2013    | 26.76 | 1207.02    | 28.78       | 35.04 | 30.39 | -1.84 | -4.47 | -0.40 | -1.64    |
| Apr2014    | 15.38 | 669.28     | 29.66       | 33.68 | 31.13 | -1.19 | -2.79 | -0.21 | -1.31    |
| Nov2014    | 22.30 | 835.86     | 26.69       | 32.48 | 28.12 | -1.84 | -4.53 | -0.06 | -1.73    |
| Apr2015    | 6.66  | 137.28     | 27.76       | 30.42 | 29.23 | -1.83 | -4.73 | -0.25 | -2.12    |
| Laanyi     |       |            |             |       |       |       |       |       |          |
| Deployment | PPFD  |            | Temperature |       |       | Depth |       |       |          |
|            | total | Solar noon | Min         | max   | mean  | mean  | max   | min   | Day mean |
| Nov2013    | 39.43 | 1581.93    | 28.67       | 33.82 | 29.99 | -0.79 | -2.53 | -0.16 | -0.66    |
| Apr2014    | 31.90 | 1450.02    | 30.10       | 34.88 | 31.32 | -0.72 | -2.29 | -0.10 | -0.74    |
| Nov2014    | 28.54 | 1277.20    | 26.52       | 32.22 | 27.87 | -0.77 | -2.52 | -0.15 | -0.69    |
| Apr2015    | 14.75 | 605.40     | 27.98       | 30.44 | 29.37 | -0.87 | -2.67 | -0.19 | -0.96    |
| Ngaloon    |       |            |             |       |       |       |       |       |          |
| Deployment | PPFD  |            | Temperature |       |       | Depth |       |       |          |
|            | total | Solar noon | min         | max   | mean  | mean  | max   | min   | Day mean |
| Nov2013    | 36.64 | 1589.92    | 28.52       | 34.66 | 30.19 | -1.24 | -3.27 | -0.40 | -1.10    |
| Apr2014    | NA    | NA         | 30.37       | 35.02 | 31.40 | -1.16 | -3.15 | -0.28 | -1.20    |
| Nov2014    | NA    | NA         | 26.78       | 33.06 | 28.00 | -1.11 | -3.36 | -0.22 | -1.02    |
| Apr2015    | 8.20  | 289.32     | 27.63       | 30.21 | 29.11 | -1.30 | -3.63 | -0.33 | -1.42    |
| Galadiny   |       |            |             |       |       |       |       |       |          |
| Deployment | PPFD  |            | Temperature |       |       | Depth |       |       |          |
|            | total | Solar noon | min         | max   | mean  | mean  | max   | min   | Day mean |
| Nov2013    | 33.26 | 1625.88    | 28.52       | 33.61 | 29.78 | -1.79 | -4.47 | -0.44 | -1.58    |
| Apr2014    | 28.71 | 1484.29    | 29.94       | 33.08 | 30.98 | -1.53 | -4.21 | -0.16 | -1.57    |
| Nov2014    | 13.78 | 471.33     | 26.12       | 30.73 | 27.29 | -1.50 | -4.39 | -0.19 | -1.43    |
| Apr2015    | 9.66  | 299.22     | 26.17       | 30.18 | 28.87 | -1.79 | -4.83 | -0.33 | -1.93    |



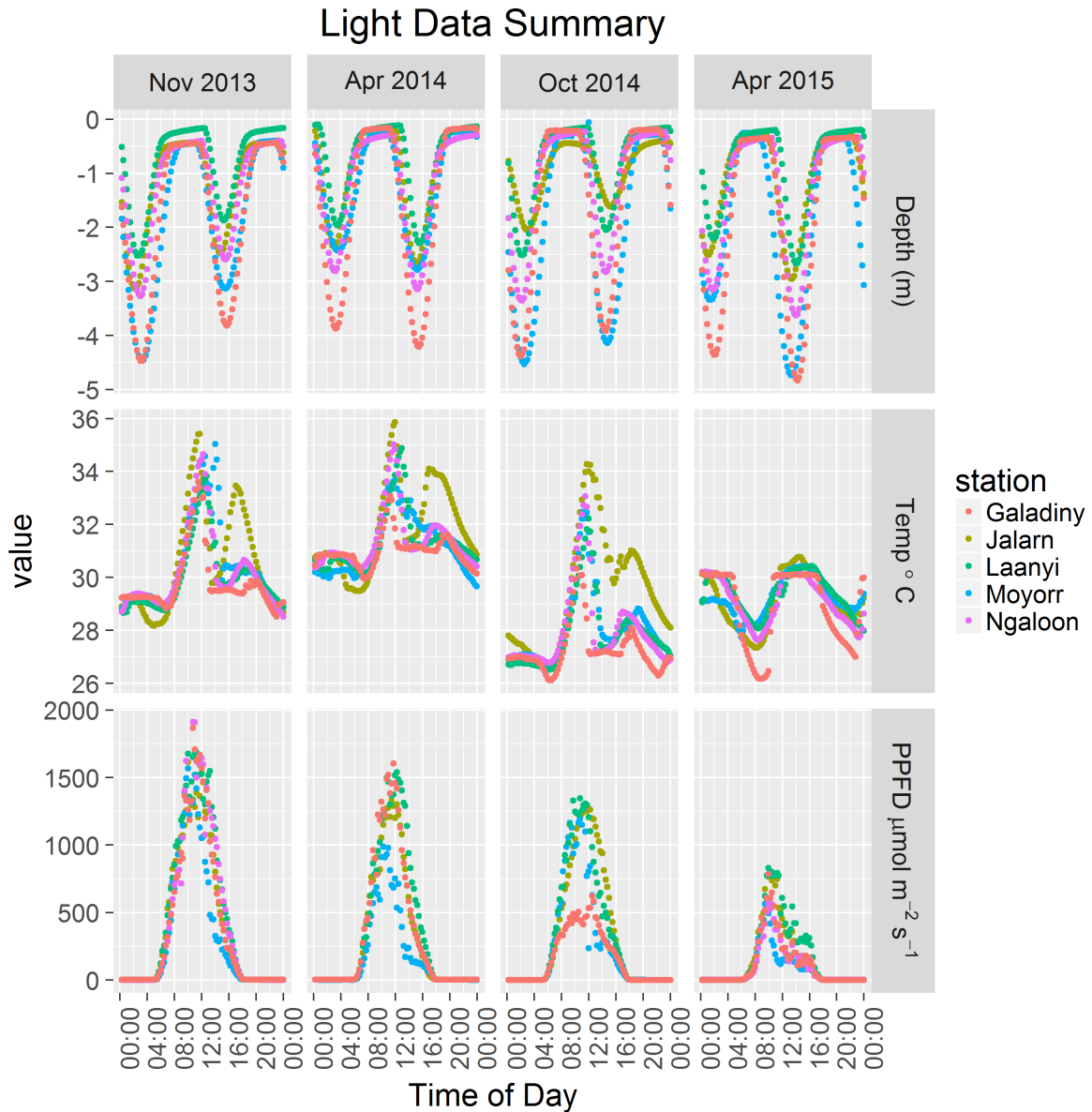


Figure 41: Temperature (Celsius), light intensity (measured as Photosynthetically Active Radiation), and depth (metres) of the mean condition experienced across the day at each Galadinyuring each deployment.

### 3.8 Planktonic microalgae

Assessments of water quality were done for all seagrass and soft sediments sites over the course of the study during fieldtrips. Salinity was determined from samples collected from the water column in proximity to the study sites. Interestingly, salinity, averaged across all sites increased over the course of the study from ~34 PSU in April 2014 to 35.5 PSU in October 2015 (Figure 42). Values measured in October 2014 and April 2015 did not differ significantly averaging ~34.7 psu across all sites (Figure 42).

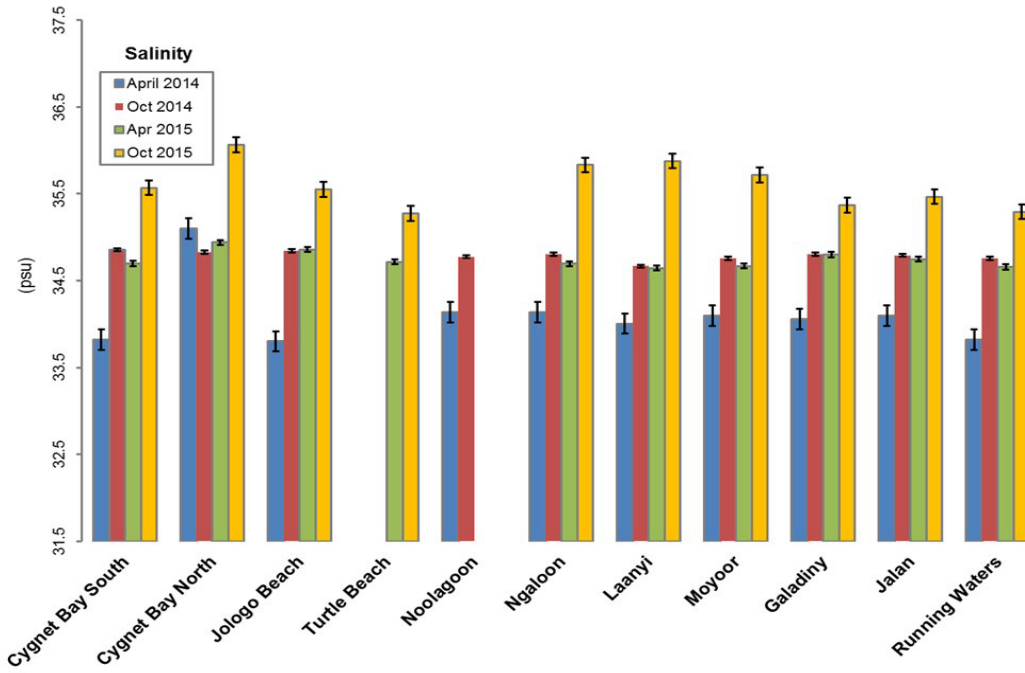


Figure 42: Water column salinity (psu) from seagrass and soft sediment study sites.

To better understand the light climate in the water column and the influence on the seagrass and soft sediment sites, samples of total suspended material (TSM) were collected. At sites located around Sunday Island there generally appeared to be reduction of TSM from ~5 mg L<sup>-1</sup> to ~3 mg L<sup>-1</sup> over the course of the study (Figure 43). A similar trend was observed at Cygnets Bay South, but it should be noted that the high values observed there and at Cygnets Bay North in April 2014 (Figure 43) are likely an artefact of sample collection during incoming tide (caused by the possible resuspension of material) as opposed to sample collection at other sites on slack high tide.

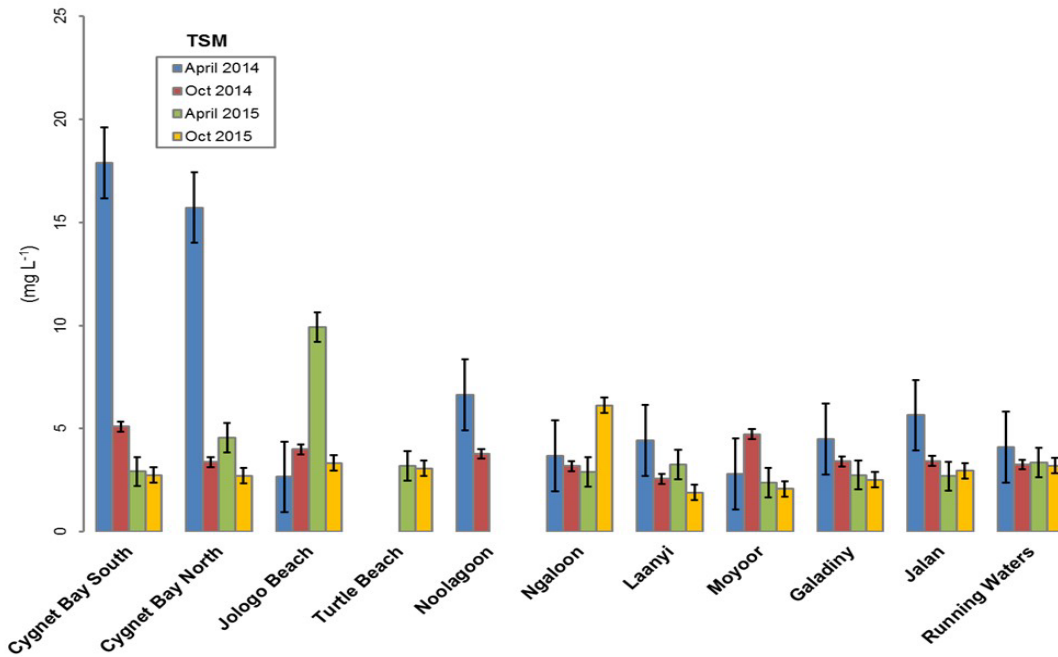
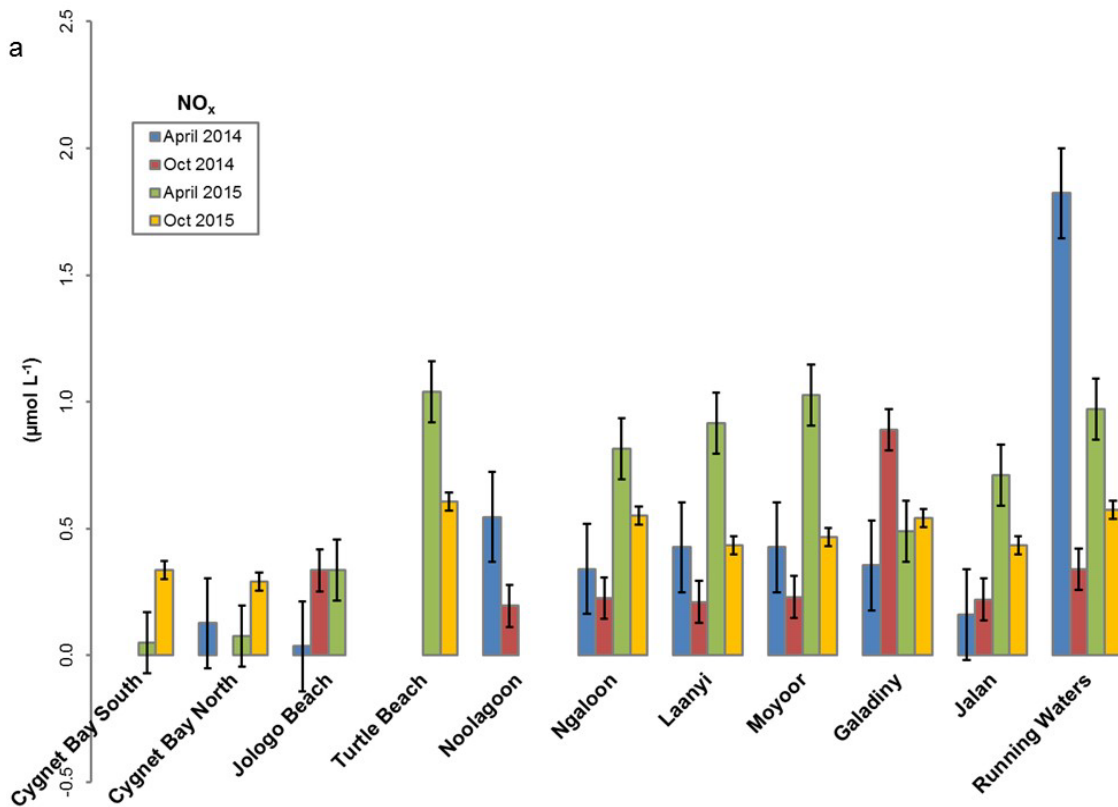


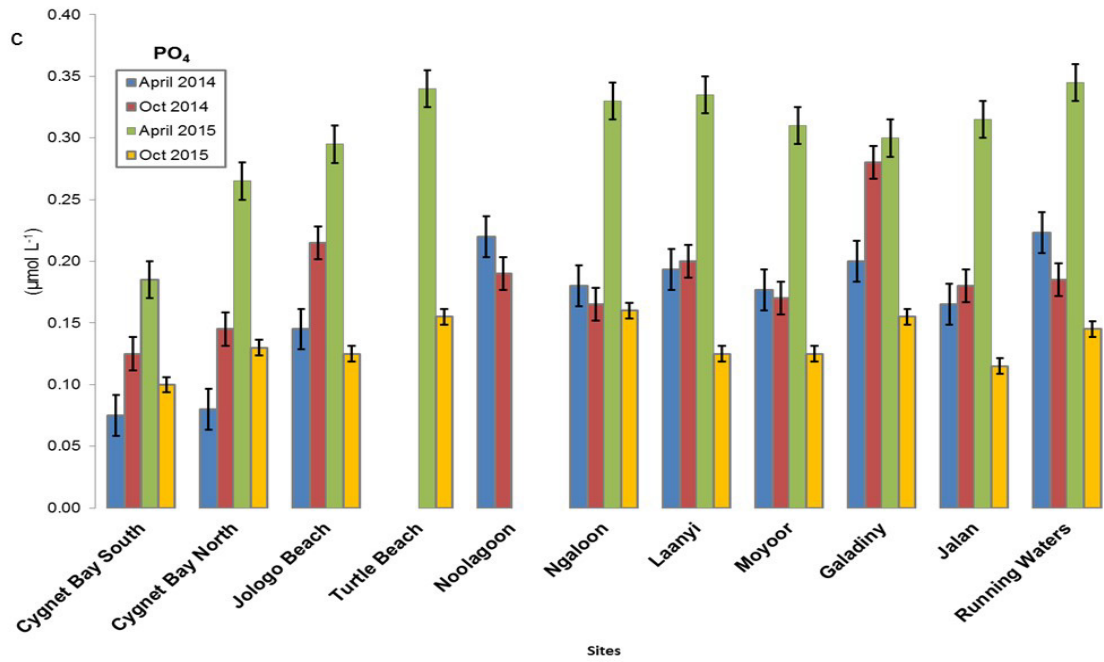
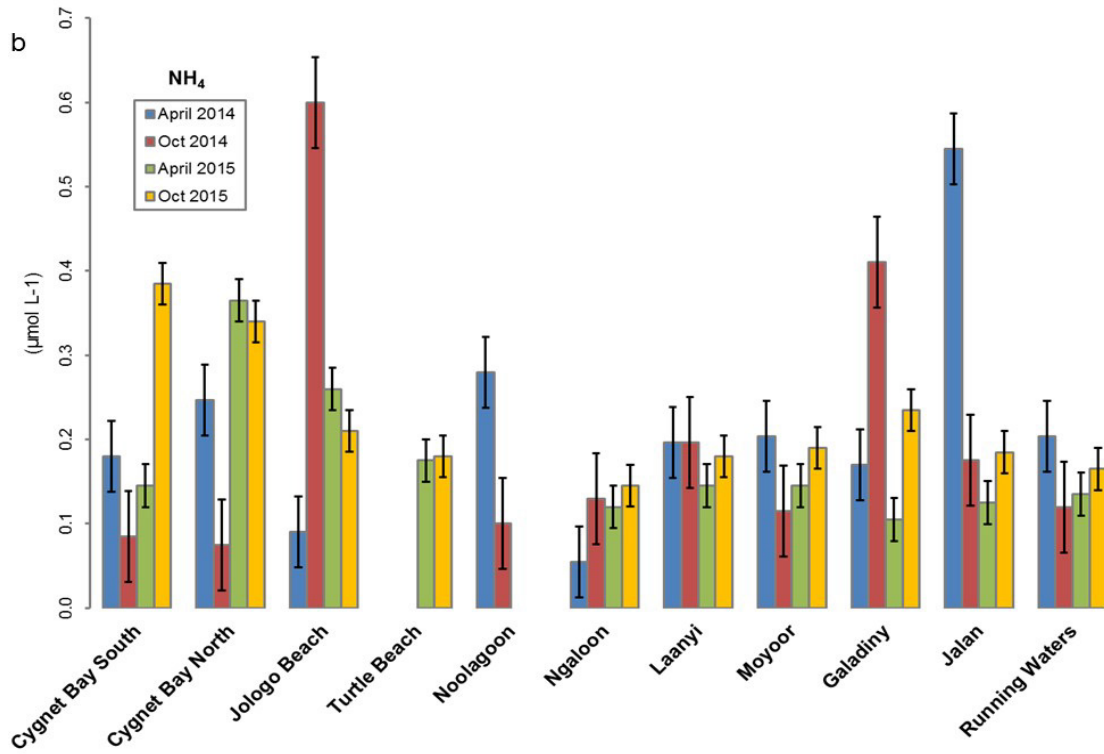
Figure 43: Total suspended material [TSM] (mg L<sup>-1</sup>) measured from water column samples in proximity to seagrass and soft sediment study sites.

Nutrient supply to the sample sites from the water column were assessed by analysing water samples for nitrate [NO<sub>x</sub>] (Fig 44a), ammonia [NH<sub>3</sub>] (Fig 44b), phosphate [PO<sub>4</sub>] (Fig 44c) and silica [Si] (Fig 44d) concentration. Nitrate and phosphate were found in lower concentrations in proximity to soft sediment sites on the mainland (Cygnet Bay and Ardyloon) and comparatively lower than that measured around Sunday Island.

Cygnet Bay South in 2014 had [NO<sub>x</sub>] below the limit of detection, but increased in 2015 from 0.05 µmol L<sup>-1</sup> in April 2015 to 0.35 µmol L<sup>-1</sup> in October 2015. [NH<sub>3</sub>] fell from 0.18 µmol L<sup>-1</sup> in April 2014 to 0.09 µmol L<sup>-1</sup> the following trip in October then increased over successive trips to a maximum of 0.4 µmol L<sup>-1</sup> in October 2015. Silica followed a similar trend as ammonia. At Cygnet Bay North, nitrate decreased from 0.1 µmol L<sup>-1</sup> in April 2014 to below detection in October 2015, but similar to Cygnet Bay South, increased during 2015. [NH<sub>3</sub>] and [Si] at Cygnet Bay North followed a similar trend to that of [NO<sub>x</sub>], however [PO<sub>4</sub>] increased to a maximum value of 0.27 µmol L<sup>-1</sup> in April 2015 before falling to less than 15 µmol L<sup>-1</sup> in October 2015. The concentration of nitrate at Jologo Beach increased from 0.04 µmol L<sup>-1</sup> in April 2014 to a steady concentration of 0.35 µmol L<sup>-1</sup> in October 2014 and April 2015, before dropping below the detection limit in October 2015. [Si] and [PO<sub>4</sub>] followed similar trends to the other mainland sites, but unlike the other nutrient species, [NH<sub>3</sub>] spiked at 0.60 µmol L<sup>-1</sup> in October 2014.

Nutrient concentrations at Sunday Island showed very similar trends comparatively between sites. [NO<sub>x</sub>] spiked in April 2015 with the exception of SI D which had a maximum value of 0.9 µmol L<sup>-1</sup> in October 2014, and Sunday Island Running Waters which had the highest recorded value of 1.8 µmol L<sup>-1</sup> in April 2014. [NH<sub>3</sub>] values were typically highest in April 2014 decreasing to a minimum in October 2014 before steadily increasing during the rest of the study period. Jalan had a spike of [NH<sub>3</sub>] in April 2014 of 0.55 µmol L<sup>-1</sup> and Galadiny having a maximum value of 0.4 µmol L<sup>-1</sup> in October 2014. Maximum values of [PO<sub>4</sub>] at all Sunday Island sites occurred in April 2015 ranging between 0.31 and 0.34 µmol L<sup>-1</sup>. [Si] spiked at Ngaloon and Sunday Island Running Waters in April 2014, and Galadiny in October 2014. For the rest of the study period concentrations remained relatively steady between sites ranging between 3.8 and 5.0 µmol L<sup>-1</sup>.





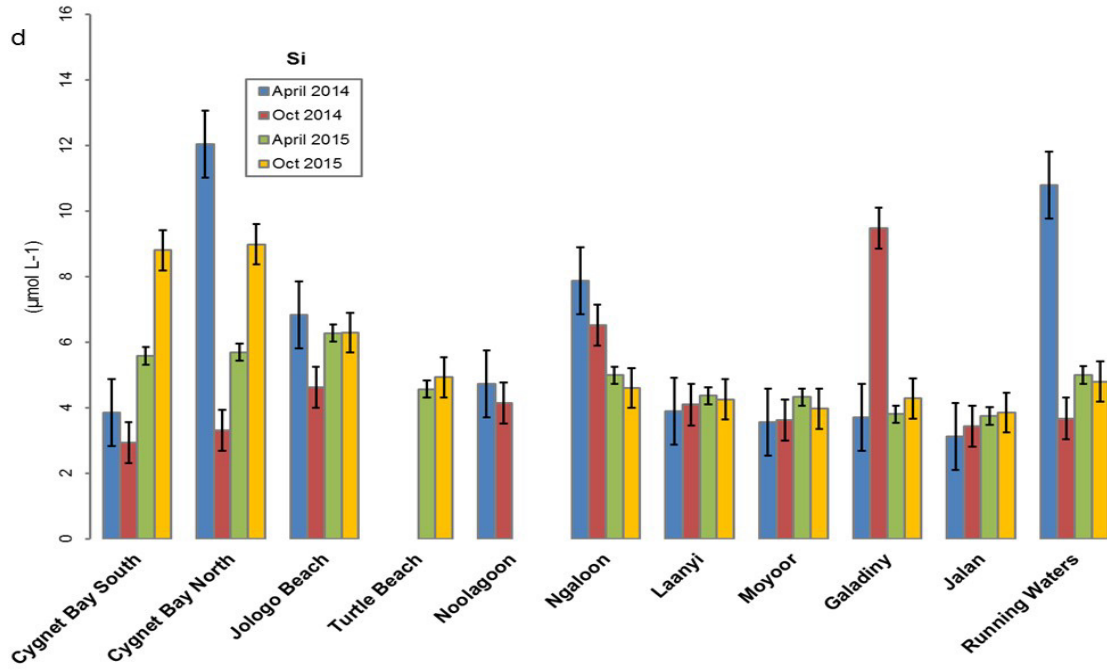


Figure 44: Concentration of nutrient species Nitrate (a), Ammonia (b), Phosphate (c) and Silica (d) analysed from water column samples collected in proximity to seagrass and soft sediment sites.

In general phytoplankton (from extracted chlorophyll) biomass was greater in the post wet (April) field samplings at most sites (Figure 45). On the mainland, Cygnet Bay South and Jologo Beach had higher water column phytoplankton biomass than Cygnet Bay North. Chlorophyll-*a* at Cygnet Bay North didn't show very much variability ranging between 0.45 and 0.58  $\mu\text{g L}^{-1}$ . Cygnet Bay North and Jologo Beach comparatively, had a broader range of phytoplankton biomass in the water column with Cygnet Bay North having at highest recorded value (1.22  $\mu\text{g L}^{-1}$ ) in April 2015 (Figure 45).

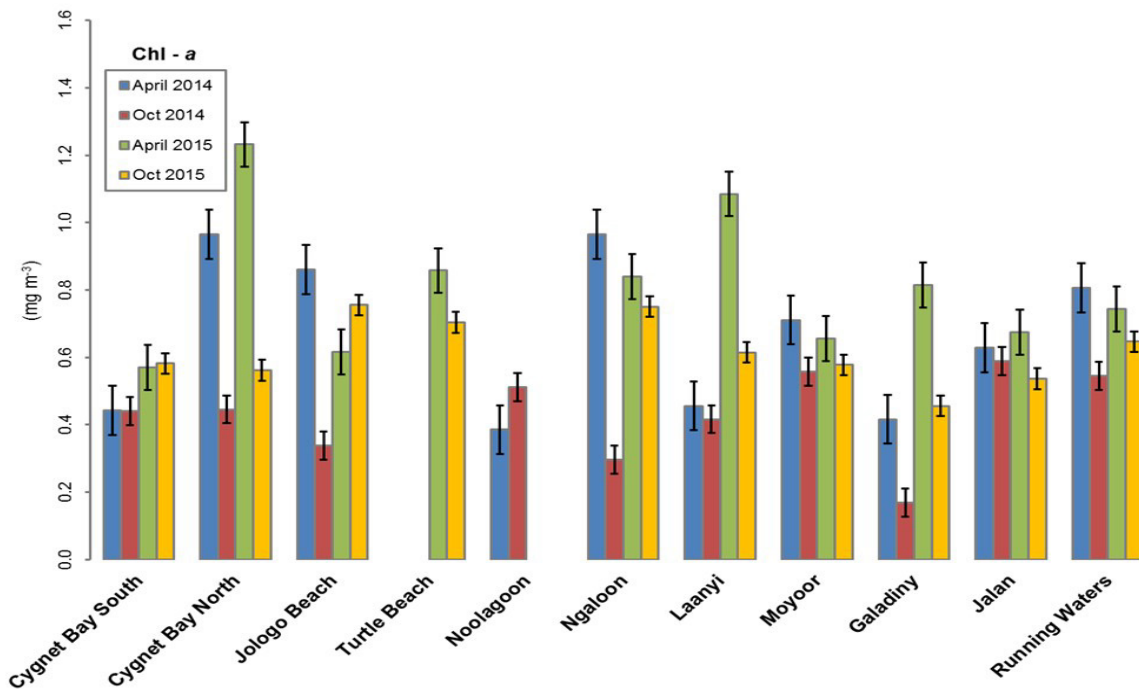


Figure 45: Water column phytoplankton biomass measured from extracted chlorophyll-*a* ( $\mu\text{g L}^{-1}$ ) collected in proximity to seagrass and soft sediment sites.

The phytoplankton community in waters around Sunday Island were dominated by diatoms at all sites in both April and October 2014 (Figures 46 and 47). However, at mainland sites Cygnet Bay South and Jologo Beach the community shifted from a predominance of prasinophytes in April 2014 to diatoms in October 2014. The most abundant taxa at Cygnet Bay North during both seasons were prasinophytes, followed by diatoms. Haptophytes and chlorophytes were the other taxa contributing significantly to the phytoplankton community composition (Figures 46 and 47).

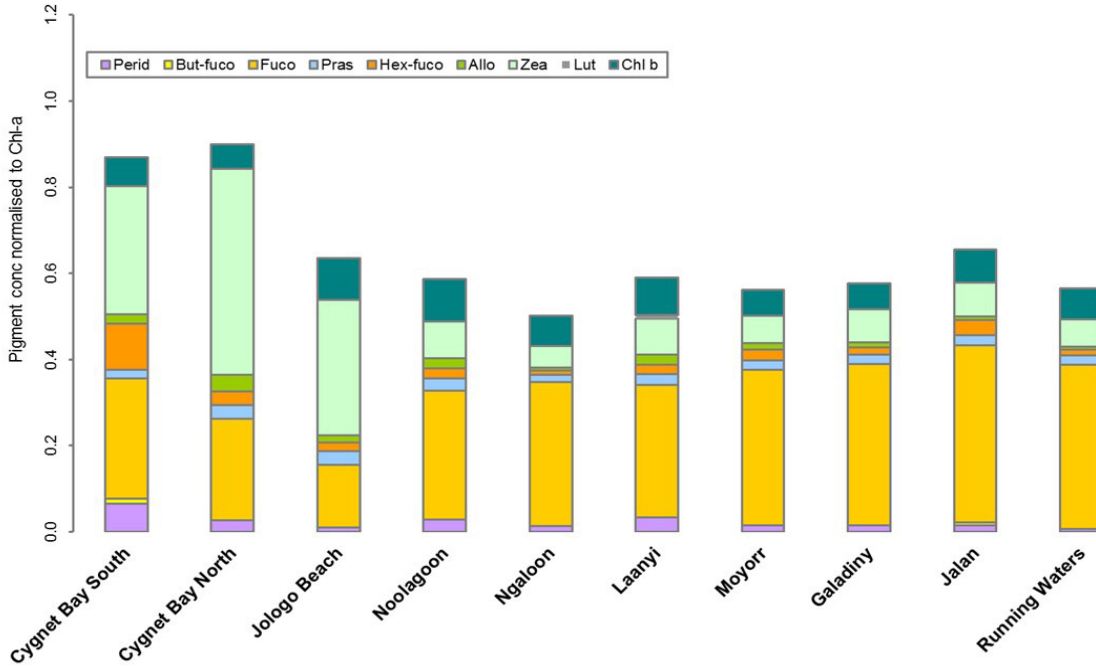


Figure 46: Phytoplankton community composition (determined from accessory pigments) in April 2014.

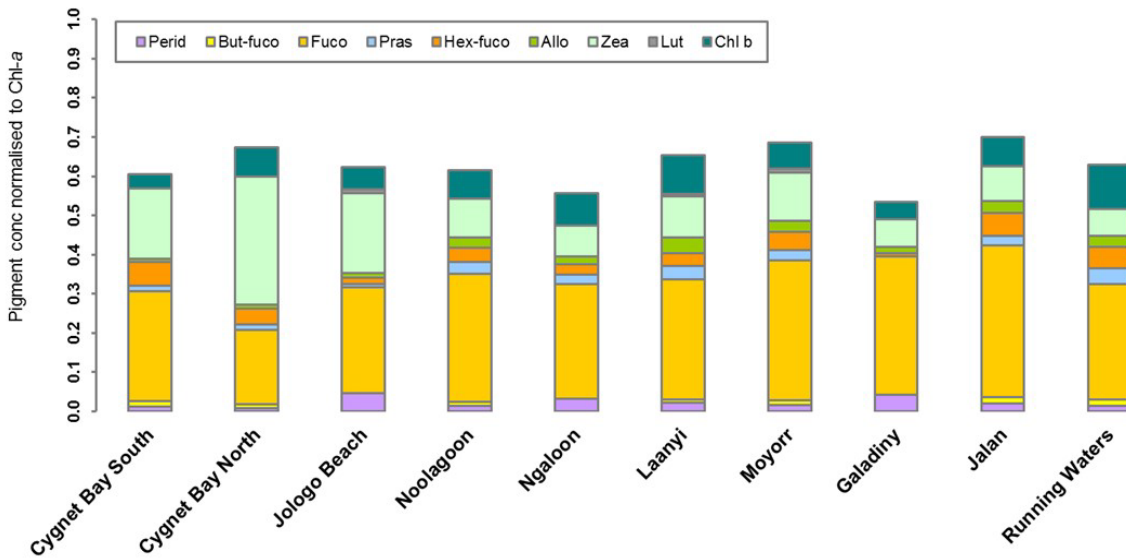


Figure 47: Phytoplankton community composition (determined from accessory pigments) in October 2014.

Particulate organic carbon (POC) (Figure 48a) and Particulate nitrogen (PN) (Figure 48b) ( $\text{mg L}^{-1}$ ) was greater at the mainland sites than those recorded around Sunday Island. At Sunday Island maximum values of both POC and PN were recorded in April 2014 with the exception of Moyorr which had a maximum value of  $0.17 \text{ mg L}^{-1}$  for POC and  $0.017 \text{ mg L}^{-1}$  PN in October 2014. On the mainland POC and PN concentrations followed similar seasonal trends at Cygnet Bay North and Jologo Beach having maximal values in April 2015. Cygnet Bay South was different from the other study sites showing a post wet season (April) increase in both POC and PN. The relationship between carbon and chlorophyll-*a* over the study period was not very strong yielding a  $R^2$  value of 0.079.

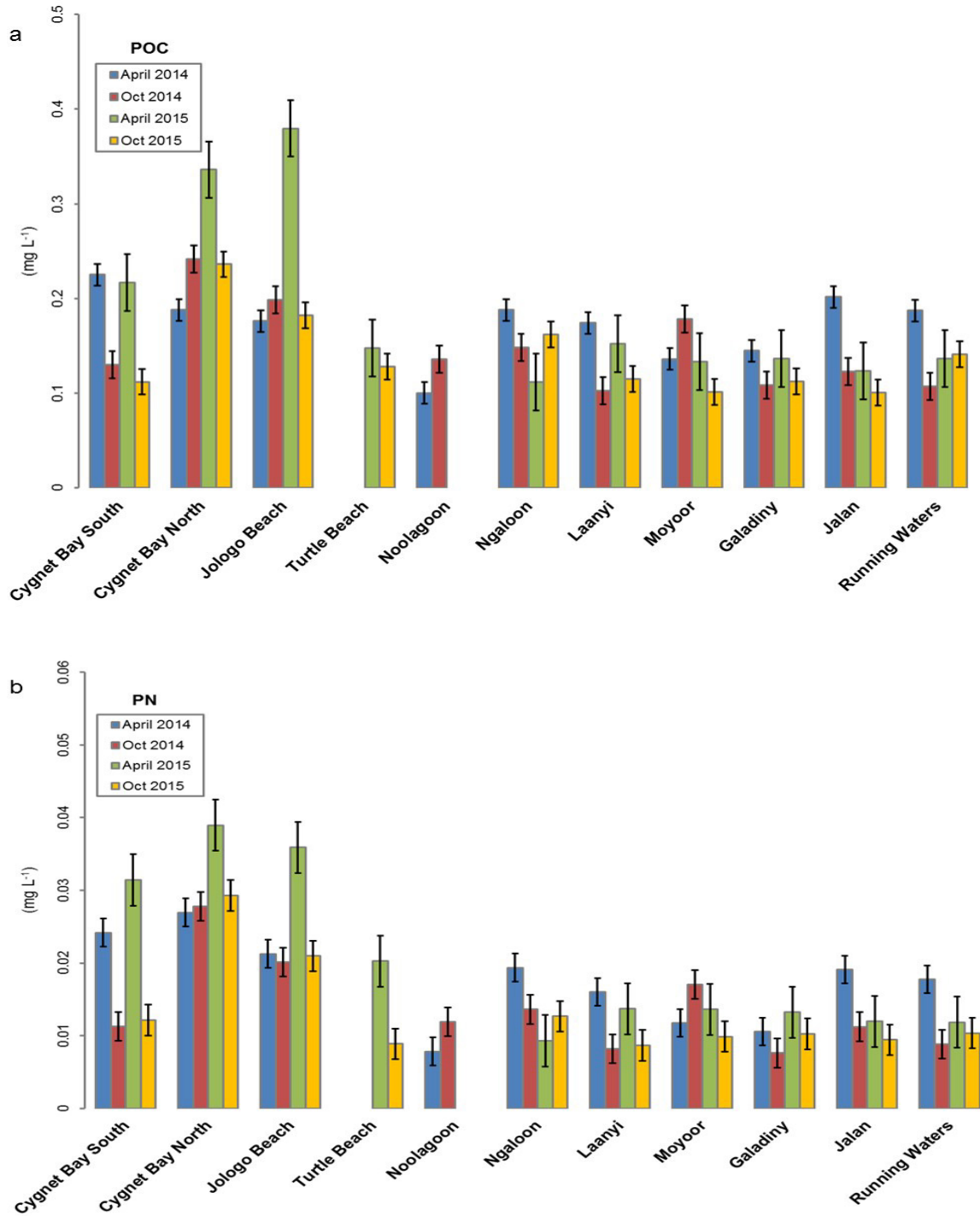


Figure 48: Water column particulate organic carbon (a) and particulate nitrogen (b) ( $\text{mg L}^{-1}$ ) collected in proximity to seagrass and soft sediment sites.

## 4 Discussion and Conclusions

As outlined in the Introduction, this project had three specific objectives:

- to understand the temporal and spatial variations in biomass and productivity of seagrasses, macroalgae and benthic microalgae;
- to investigate the rates and magnitude of microbial carbon and nitrogen cycling processes, and how they influence primary production; and
- to investigate the rates and net effect of herbivory on seagrasses, macroalgae and benthic microalgae.

### 4.1 Seagrass biomass and growth

Shoot density, biomass, and growth rates were temporally and spatially variable across our study area. Unlike with *Sargassum*, there was no strong seasonal pattern in seagrass biomass, density or growth. Monthly surveys also revealed high variability between months for *E. acoroides* and *T. hemprichii*. These surveys encompassed a single year, and monthly sampling across multiple years would show if there is regular periodicity in seagrass growth in the Kimberley, and help reveal the environmental drivers that regulate both seagrass species. Our surveys showed that biannual sampling is insufficient for seagrass monitoring in the Kimberley, monthly seagrass monitoring is needed to quantify temporal patterns and reveal the likely causes of those patterns.

Seagrass monitoring surveys often just focus on measuring shoot density as the indicator of meadow changes over time. However, in our study seagrass biomass and growth rates showed different temporal patterns, and were highly variable. Given the varying temporal patterns in shoot density, biomass, and productivity, we recommend that future seagrass monitoring programs measure all of these parameters, especially as they reveal seagrass dynamics that occur over different timescales. For example, growth rates change quickly and respond to contemporary conditions, while shoot density is a longer-term integrative measure of seagrass health. Given the high variability in shoot density, biomass and productivity of seagrasses in the Kimberley, we recommend coupling these measurements with environmental data to better explain the observed patterns in seagrass growth.

Sexual reproduction in seagrasses of the Kimberley is poorly characterised, yet is crucial for understanding population ecology. Our surveys recorded flowers only in late November for both *T. hemprichii* and *E. acoroides*. Seagrasses are particularly vulnerable to reductions in light availability during reproductive events, and so they might be particularly vulnerable to disturbances during the wet season. However, more research examining recruitment and seed ecology in Kimberley seagrasses will be required to understand current and predict future population trajectories, given the current paucity of data. We recommend that future seagrass monitoring should also include measurements of reproductive phenology, coinciding with natural seagrass reproductive cycles in November-March.

Our recommendations for future seagrass monitoring programs involve measuring a range of seagrass variables (shoot density; biomass; productivity) every month, while examining reproductive phenology frequently between November and March (Table 12). We estimate a field cost of \$1100 per Ngaloon or such surveys, plus additional costs associated with laboratory processing of seagrass tissues for biomass and productivity. If such a project was carried out across multiple years, it would provide a robust analysis of seagrass dynamics in the Kimberley that would capture monthly, seasonal, and annual trends. The Bardi Jawi Rangers collected shoot density, biomass and productivity for the monthly surveys of seagrasses in this project, providing important additional data and greatly increasing the value of the dataset. Further collaborations with community groups and traditional landowners would likely facilitate a monthly seagrass monitoring program.



Table 12: Proposed future seagrass monitoring program, with associated costs and time requirements.

| Monitoring variables       | Trends                                     | Sampling pattern                   | Field sampling | Field costs  | Laboratory processing | Laboratory costs |
|----------------------------|--|------------------------------------|----------------|--|-----------------------|------------------|
| Shoot density              | Monthly variability & Seasonal variability | Monthly (to capture variability)   | ~ 1 hr / site  | ~ \$1100/ site (incl. boat hire, fuel, + 3 people) | NA                    | NA               |
| Biomass (AG and BG)        | Monthly variability & Seasonal variability | Monthly                            | ~ 1 hrs / site |  | ~ 4 hrs /site         | ~ \$100 /site    |
| Productivity (Area and DW) | Seasonal variability                       | Monthly                            | ~ 1 hrs / site |  | ~ 4 hrs / site        | ~ \$100 / site   |
| Nutrients                  |  |                                    |                |  |                       |                  |
| Reproduction               | Yearly                                     | Weekly/ Fortnightly (Nov to March) | ~ 2 hrs / site |  | NA                    | NA               |

The information provided from this study expands our knowledge of seagrass ecology and physiology for the two dominant seagrass species (*T. hemprichii* and *E. acoroides*) in the Bardi Jawi IPA in the Kimberley. The density and biomass for *T. hemprichii* and *E. acoroides* differ greatly from *Halophila decipiens*, a small bodied seagrass that is also prevalent in the Kimberley, but with a very different life history strategy (Table 13). *H. decipiens* is an ephemeral, transient species, and aboveground biomass is only visible during the dry season when light availability is highest. *H. decipiens* flowers at the end of the dry season, producing seeds that contribute to a sedimentary seed bank that reaches highest density in the wet season, when light availability is lowest. These *H. decipiens* seeds then germinate at the beginning of the dry season, when light availability increases. The highly seasonal patterns in *H. decipiens* density, biomass, and reproduction differ greatly to those of *T. hemprichii* and *E. acoroides*, which did not show strong seasonal patterns. Such differences in life history and growth patterns in seagrasses are vital to characterise in seagrasses, because they influence monitoring and management strategies.

Despite the extreme tidal fluctuations in the Kimberley, seagrasses are still able to persist, grow and produce new leaf biomass. This highlights their ability to adapt and thrive across a wide range of environmental conditions. For example, productivity rates of *E. acoroides* are comparable to the estimates derived from other tropical environments such as those found in Indonesia, the Philippines, and Malaysia (Ooi et al. 2011). Growth and productivity rates of *T. hemprichii*, however, were lower relative to values reported in the Philippines, Indonesia and Malaysia (Ooi et al. 2011).

Relative to other observations in Asia and Africa, Kimberley seagrasses (particularly *T. hemprichii*) allocates significantly more biomass to belowground rhizomes and roots relative to aboveground shoots and leaves. The typical observations in microtidal and less-energetic (Indonesia) and typhoon-prone (the Philippines) areas are that *T. hemprichii* shoots tend to allocate more biomass to their leaves than to root-rhizome tissues (Ertfemeijer & Herman, 1994; Vermaat et al., 1995). To illustrate this difference, shoots of *T. hemprichii* in the Philippines were found to invest about 250 g DW m<sup>-2</sup> in leaves as compared to just 77 g DW m<sup>-2</sup> in their root/rhizome system (Vermaat et al., 1995) whereas in the Kimberley, particularly at Tallon Island, this species allocated about 50 g DW m<sup>-2</sup> in leaves and more than 400 g DW m<sup>-2</sup> in roots and rhizomes.

Table 13: Comparison of key characteristics from three dominant seagrasses in Kimberley

| Seagrass species  | Density & Biomass  | Productivity   | Reproduction   |
|---|--|--|--|
| <i>Thalassia hemprichii</i> /<br><i>Enhalus acoroides</i><br>(this study) | No obvious trends over time. Large temporal and spatial variability                                    | Seasonal trends with a tendency of higher rates during monsoonal season – November to April, especially for <i>Enhalus</i> | Flowering en of the Dry Season (October-November) and seed dispersal during wet season (November to April)   |
| <i>Halophila decipiens</i><br>(Hovey et al. 2015)                         | Transient species with standing stock during dry season (May to October) High inter-annual variability | Strong trends of growth and productivity in the dry season from May to October   | Flowering during dry season (July to Nov)<br>Seed bank year around (peak densities in October to January during wet season)<br>Seed germination initiated at the end of the wet season in April and continues into the dry season.<br>High interannual variability |

#### 4.2 Macroalgae biomass and growth

The lagoons at the locations we surveyed hosted numerous species of brown macroalgae, of which the genus *Sargassum* was particularly prominent. Five species of *Sargassum* were recorded, with *S. polycystum* the most abundant. *S. polycystum* also yielded the highest growth rates of any of the species. Our method, which involved measuring the longest axis, was likely reliable because there was no evidence that the longest branches grew at different rates than other branches (the longest branch grew at faster rates than average in only 1 of 11 plants in which this was tested).

Generally, *Sargassum* were larger in April than in October-November, but the only survey in which growth rates were high was November 2013. This survey was undertaken somewhat closer to the wet season than the other surveys — this observation, together with the observation that plants were largest in April in 2014 and 2015 indicates that growth rates are likely to be highest during the wet season. Surveys during the wet season would be required to confirm this.

Relatively few studies of growth of tropical *Sargassum* exist for us to compare our results to. May-Lin and Chin-Lee (2013) reported that *Sargassum* inhabiting shallow reef in Malaysia (including *S. polycystum*) exhibited a regular pattern with two growth peaks per year, in January-February and June-July, with growth rates up to 4 mm<sup>-1</sup> d<sup>-1</sup>. We recorded highest growth in November, and did not survey during the middle of the year, so we do not know what seasonal patterns *Sargassum* exhibit in the Kimberley. However, the growth rates we recorded were an order of magnitude higher – up to 21.6 mm<sup>-1</sup> d<sup>-1</sup> at Laanyi in November than May-Lin and Chin-Lee (2013).

#### 4.3 Rates of consumption

Rates of herbivory on seagrasses were highly variable, but the most notable pattern was a higher rate of consumption of *Thalassia hemprichii* than *Enhalus acoroides*. Consumption of *Thalassia* reached as high as 60% (at Ngagoon in October 2015), and was almost always higher than 5%. In contrast, consumption of *Enhalus* was almost always less than 5%, and was not detected on three site-survey combinations: high consumption of *Enhalus* was recorded only at Jalan in April 2015.

These differences in rates on consumption contrast with the relatively similar rates of productivity of the two species of seagrasses, which implies that they might play different ecological roles. It is likely that a large proportion of the production of *Thalassia* is directly consumed by herbivores — this is examined in more detail in the companion WAMSI Kimberley Node project 1.1.2, but is likely due to consumption by golden-lined rabbitfish (*Siganus lineatus*) and green turtles (*Chelonia mydas*). On the other hand, it is likely that a relatively small proportion of the production of *Enhalus* is directly consumed — based on knowledge of seagrass

ecosystems elsewhere, it is likely that the production is either sequestered in sediments or contributes to detrital food webs.

We measured consumption as percentage consumption during a 24-hour period: our results are high relative to those of other studies. Kirsch et al. (2002) in the Florida Keys found up to ~30% of the mass of *Thalassia testudinum* offered was consumed, but typically <5% was consumed; in contrast, we found up to 60% of *Thalassia hemprichii* was consumed, with an average consumption of 16%. The lower consumption of *Enhalus* that we recorded was not observed by a similar study in Indonesia (Unsworth et al 2007), which found that consumption of *Enhalus* was typically greater than that of *Thalassia*: the main herbivores in their study were parrotfish.

Our results show that *Thalassia* is an important food source for herbivores, including species that are in turn important for food and culture of the local communities.

#### 4.4 Stable isotopes

Broadly,  $\delta^{13}\text{C}$  of mangroves was different to that of seagrasses and macroalgae (mangroves -28.8, seagrass -14.4, macroalgae -16.4), but they tended to have similar  $\delta^{15}\text{N}$  (mangroves 2.1, seagrass 3.0, macroalgae 3.5). Within this overall trend, there were differences between some seagrasses and some brown algae: *Enhalus* tended to have higher  $\delta^{13}\text{C}$  than *Thalassia* and other seagrasses (e.g. *Enhalus* -10.8; *Thalassia* -17.8), and *Turbinaria* spp tended to have higher  $\delta^{13}\text{C}$  than other macroalgae (*Turbinaria* spp -10.9, other brown algae -15.8).

For the main species that were collected during each survey, spatial and temporal patterns were complex, and differences among seasons or locations did not seem to be consistent. The differences in  $\delta^{13}\text{C}$  between *Enhalus* and *Thalassia*, and between *Turbinaria* and other macroalgae, are likely to be due to use of different types of dissolved carbon: those with  $\delta^{13}\text{C}$  of higher than -10‰ are very likely to be using bicarbonate. These differences are likely to be useful for determining the main sources of primary production that sustain herbivores and other consumers in the region, and these data will be used in other studies in the KMRP.

#### 4.5 Benthic Microalgae

Benthic microalgae (BMA) are responsible for a significant proportion of estuarine and coastal primary production, especially on intertidal flats where higher plants or macroalgae are absent (Blanchard and Cariou-Le Gall 1994; Underwood and Kromkamp 1999). Photosynthesis by BMA can result in large diel oscillations in oxygen concentration, pH, and other variables near the sediment-water interface (Revsbech et al. 1988). These extreme chemical conditions impact on the sediment redox profile affecting bottom-water oxygen, nitrification-denitrification, and nutrient flux from the sediment (e.g. Sundbäck 1991; Sundbäck et al. 2006). Extrapolymetric substances produced by benthic microalgae can also have a stabilizing effect on the sediment (Cahoon 1999). Overall, benthic microalgae play a key role in neritic ecosystems. Mean global estimates of benthic microalgal production in intertidal tropical regions are reported to be ~450 mg C m<sup>-2</sup> d<sup>-1</sup> (Cahoon 1999), within the range of estimates made for Cygnet Bay South (350 - 1100 mg C m<sup>-2</sup> d<sup>-1</sup>) and Jologo Beach (200 - 600 mg C m<sup>-2</sup> d<sup>-1</sup>). Even so, rates exceeding 1000 mg C m<sup>-2</sup> d<sup>-1</sup> have also been reported for tropical regions (Cahoon 1999), so the highest rates measured at Cygnet Bay during Sep 2013 (1100 mg C m<sup>-2</sup> d<sup>-1</sup>) are also not unusual.

The large variations (up to 10 times) in micro-algal production observed over the course of three consecutive days at Cygnet Bay South, suggest that fine-scale temporal variability dominates over seasonal variability which is characterized by variations of a factor of 3 or less. Variations in chlorophyll over the same period were small, suggesting that the variations in production are sufficiently short-lived to prevent a noticeable biomass response. This kind of short-term variability means that care is needed in design of chamber-based production studies to ensure that estimates are robust and reliable, and not overly influenced by short-term variation. The results also suggest that chlorophyll-*a* biomass is not a good proxy for BMA production in this region.

Results of the sediment micro-profiles suggests that sub-surface oxygen production by BMA depends strongly on sunlight exposure, suggesting that changes in the timing of daily measurements may account for some of the observed variability in oxygen flux. Equally, the depth of oxygen penetration in sediments varies with tidal

exposure, being deeper following periods of drying, and shallower during periods of wetting. Visual evidence of widespread bio-irrigation on exposed tidal flats (Figure 49) during low tide, is consistent with increased oxygen penetration into the sediment observed in the oxygen micro-profile results. We suspect therefore that tidal dynamics may also account for some of the observed daily variations in production.



Figure 49: Bio-irrigation of sediments at Cygnet Bay South (a) resulting from burrowing and digging activities of many species (gastropods, rays, crustaceans, etc.) including Soldier crabs (*Mictyris longicarpus*) (b).

Negative rates of oxygen flux measured at Cygnet Bay North during Sep 2013 and Apr 2014 indicate that despite the presence of micro-algae, periods of heterotrophy can occur where bacterial respiration of organic matter exceeds micro-algal production. It is not clear what caused a shift from net oxygen consumption to net production at Cygnet Bay North between April and October 2014, but these results further highlight the large temporal variability in oxygen dynamics that can occur in this region.

Finally, marine sediments are important sites of denitrification (Middleburg et al. 1996) accounting for up to 13% of the pelagic nitrogen demand in some coastal waters (Seitzinger & Giblin, 1996). Although denitrification was not measured directly during this study there is evidence from the pore-water nutrient content that nitrate was reduced compared to phosphate at Cygnet Bay South, Cygnet Bay North, Jologo Beach and Ngaloan. We suspect that the relative loss of nitrate is due to sedimentary denitrification. In the sedimentary redox profile denitrification occurs before sulphate reduction, and the presence of sulphide observed close to the sediment surface at many sites (especially at Cygnet Bay South) indicates that the necessary chemical conditions needed for denitrification are widespread.

#### 4.6 Microbial carbon and nitrogen cycling

Our results revealed extremely high and variable bacterial carbon production rates, ranging from 0.9  $\mu\text{g}$  to 3.6  $\text{mg C L}^{-1} \text{ day}^{-1}$ , with the highest bacterial biomass and dissolved organic carbon measured during October-November surveys. Our rates were within or above the range previously reported from tropical coastal ecosystems (Lee et al., 2009; Wallberg et al., 1999). Measurements also revealed high bacterial carbon utilisation rates, particularly of carbohydrates, amino acids and polymers. There is likely to be a high connectivity between

benthic and pelagic habitats via the flow of DOC, with pelagic bacterial communities able to use a benthic dissolved organic carbon source.

A very active and productive (fast growing) bacterial community exists in the benthic and pelagic habitats of the region, indicating an important role of microbial cycling of both dissolved nutrients in these systems.

#### 4.7 Water quality

Measures of water quality were made at soft sediment and seagrass sites during the study to evaluate potential physical drivers and constraints of BMA and seagrass biomass and production in areas subjected to extreme tidal ranges. Overall, seasonal trends were not abundantly clear from these snapshots of data collected. From some of the BMA production data collected it appears that the dynamics of the system are such that changes happen at very short temporal scales in these study areas. TSM seems to be dictated by the influences of tides and tidal range with quick moving water re-suspending benthic sediments into the water column that eventually re-settle. The timing and location of collection seems to influence the amount of TSM at any given time. We suspect that low tide exposure has more of an impact on BMA and seagrasses photosynthesis, with photo inhibition occurring during these periods. Water column nutrients are also likely influenced by tidal movements with encroaching water and sediment dynamics causing the release of nutrients from trapped interstitial pore water and burial of organics. Phytoplankton biomass did not appear to have any overall seasonal trends with the community dominated by diatoms at most sites. Unfortunately our analyses cannot differentiate between benthic and pelagic species so it is quite possible that motile epipsammon and epipelon were re-suspended into the water column adding a bias to the biomass of the pelagic communities during sampling. The correlations between chlorophyll-*a* and particulate organic carbon was not very strong. There appeared to be numerous potential carbon inputs and sources (such as mangrove leaves, freshwater springs, anthropogenic sources, etc.) in these areas which could explain the lack of a direct relationship between phytoplankton chl-*a* and POC. Interestingly, the measurements of water column salinity increased over time. Liu et al., 2016 noted a decadal increase in rainfall in the Cygnet Bay area from 2000 to 2011. However anecdotal information from the Bardi Jawi Rangers indicated that the wet season in 2015/16 was much drier than normal so we speculate that this increase in salinity is a result of lower rainfall in this area, where evaporation is already very high (Liu et al., 2016).

## 5 Summary

*Objective 1: To understand the temporal and spatial variations in biomass and productivity of seagrasses, macroalgae and benthic microalgae.*

We recorded rates of productivity of seagrass and macroalgae that are high relative to other studies, and rates of productivity of benthic microalgae that are in the range of measurements previously recorded from tropical ecosystems. Seagrass productivity did not show any strong patterns associated with season or geography. Productivity of *Sargassum* was highest during the survey that was closest to the wet season, suggesting that rates of productivity of macroalgae (or at least of *Sargassum*) are highest during the wet season.

*Objective 2: To investigate the rates and magnitude of microbial carbon and nitrogen cycling processes, and how they influence primary production.*

Rates of bacterial carbon production were among the highest recorded, with higher production recorded for benthic habitats than pelagic habitats. Bioassays revealed connectivity between benthic and pelagic habitats as the pelagic bacterial community readily used dissolved organic carbon originating from both seagrass and mangrove benthic habitats. The high rates of microbial activities facilitate C and N production in these systems, particularly in the benthos, which may in turn influence the growth and standing stock of primary producers (seagrass and mangroves).

*Objective 3: To investigate the rates and net effect of herbivory on seagrasses, macroalgae and benthic microalgae.*

The focus of measurements of herbivory was on seagrass. Rates of herbivory were among the highest recorded, with higher consumption recorded for *Thalassia* than *Enhalus*. It is likely that a large proportion of the production of *Thalassia* is directly consumed by herbivores.

## 6 Recommendations

We make the following recommendations:

### ***For seagrasses***

We recommend monthly seagrass monitoring to quantify temporal patterns and reveal the likely causes of those patterns.

We recommend that future seagrass monitoring programs measure seagrass shoot density, biomass and growth rates. We also recommend coupling these measurements with environmental data to better explain the observed patterns in seagrass growth.

We recommend that future seagrass monitoring also include measurements of reproductive phenology

### ***For macroalgae***

We recommend detailed sampling throughout the wet season, and a monthly sampling program

We recommend extending the measurements from *Sargassum* linear extension to density, biomass and change in biomass (growth)

We also recommend extending the initial sampling on *Sargassum* to other macroalgal species, like *Turbinaria*, *Lobophora* and *Gracilaria*.

### ***For microbial processes***

We recommend a more detailed study of microbial nutrient cycling among the major habitats to test if these systems are not phosphorus limited at certain times of the year.

For grazing rates on seagrasses and macroalgae:

We recommend more tethering experiments monthly or bimonthly across the seasons combined with visual surveys of fish community structure

We also recommend continued satellite tagging of turtle and that this be extended to dugongs where possible.

## 7 References

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## **8 Communication**

### **Students supported**

Lisa DeWever (M. Sc., European Institute for Marine Studies, France), Lucie Chovrelat (M. Sc., European Institute for Marine Studies, France), Emy Guilbault (M. Sc., Montpellier SupaGro, France).

### **Journal publications**

Pedersen O, Colmer TD, Borum J, Zavala-Perez A, Kendrick GA (2016) Heat stress of two tropical seagrass species during low tides – impact on underwater net photosynthesis, dark respiration and diel in situ internal aeration. *New Phytologist* 210:1207–1218, 10.1111/nph.13900

### **Proceedings/Technical Reports**

Kendrick GA, Fraser MW, Cayabyab N, Vanderklift M (submitted) Seagrasses of the Kimberley. *Natural World of the Kimberley Proceedings*. Kimberley Society Seminar 15th October 2016, The University of Western Australia, Crawley

### **Submitted manuscripts**

As above

### **Presentations**

Pedersen O, Kendrick GA, Borum J, Zavala-Perez A, Colmer T (2015) Heat stress of two tropical seagrass species during low tides–net photosynthesis, dark respiration and diel in situ internal aeration. The 52nd Australian Marine Science Association Annual Conference - Lecture Theatre D2.211

Kendrick GA (2015) Living on the edge: seagrasses adapted to extreme environments in the Kimberley. Kimberley teachers Training Workshop at UWA (SPICE), Kendrick gave the Dinner Lecture on seagrasses

Kendrick G A (2016) Seagrasses of the Kimberley, *The Natural World of the Kimberley: A Kimberley Society Seminar*, Saturday 15 October 2016 The University Club The University of Western Australia

Vanderklift M (2016) The ecology of green turtles in Bardi Jawi sea country. 3rd Australian Sea Turtle Symposium, Darwin, 22-24th August 2016.

Vanderklift M (2016) Presentation to Kimberley Marine Research Station. April 2014.

Regular presentations of project results to Bardi Jawi rangers during each survey.

### **Other communications achievements**

Class and field activities with One Arm Point Remote Community School.

### **Knock on opportunities created as a result of this project**

University of Copenhagen – University of Western Australia collaborative research program: “Seagrass Ecophysiology of the intertidal platforms of the Sunday Islands”

### **Key methods for uptake (ie advisory committee, working group, website compendium of best practice.)**

KISSP Presentation mid 2016.

Lunch and Learn presentation at Parks and Wildlife.

Meeting with Node Leader and KMRP Advisory Group to discuss management needs and application

### **Other**

WAMSI Article (November 2015) Field trip finds turtle and fish food abundant in Bardi Jawi country

<http://www.wamsi.org.au/news/field-trip-finds-turtle-and-fish-food-abundant-bardi-jawi-country>

CSIRO ECOS Blog Article (December 2015) A field trip to Bardi Jawi country: turtles and fish and seaweed, oh my! <https://blog.csiro.au/a-field-trip-bardi-jawi-country-turtles-fish-food-and-fun/>

DPaW Kimberley Tide Article (December 2015) Field trip to Bardi Jawi country

KSN 2.2.4 Summary (April) – Benthic primary productivity: production and herbivory of seagrasses, macroalgae and microalgae (released April 2016) <https://indd.adobe.com/view/0239eb73-cbba-4ccb-93ca-c2e6d5cc6547>

DPaW Lunch and Learn Seminar (April) [Seagrasses of the Kimberley presented by Professor Gary Kendrick \(14 April 2016\)](#)

New Phyt blog (May 2016) Behind the cover <https://www.newphytologist.org/blog/behind-the-cover-210-4/>

Coastlines article (released 7<sup>th</sup> July 2016) The Kimberley – understanding the growth of seagrass and macroalgae [https://www.planning.wa.gov.au/dop\\_pub\\_pdf/Coastlines\\_Winter\\_2016.pdf](https://www.planning.wa.gov.au/dop_pub_pdf/Coastlines_Winter_2016.pdf)

Science in Public (July 2016) Saving seagrass sanctuaries <http://stories.scienceinpublic.com.au/2016/seagrass/>