



Key Ecological Processes in Kimberley Benthic Communities: Herbivory

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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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Front cover images (L-R)

Image 1: Satellite image of the Kimberley coastline (Image: Landgate)

Image 2: Bite marks on seagrass from the herbivorous golden-lined rabbitfish *Siganus lineatus* (Image: Matt Vanderklift)

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

Image 4: Bardi Jawi Ranger measuring seagrass growth (Image: Mat Vanderklift)

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Executive Summary

The main aim of this research was to understand the relative importance of direct consumption of seagrass as a proportion of total seagrass production in the Kimberley, to identify the main species of herbivores, and to understand the relative importance of different primary producers to the diet of selected key species of herbivores. Although primary producers occupy a wide variety of habitats, the primary focus of this study was the seagrass meadows of Tallon Island (Jalan) and Sunday Island (Iwany) located in the Bardi Jawi Indigenous Protected Area. The research used data collected, and extended research conducted, as part of WAMSI Kimberley Marine Research Program (KMRP) Project 2.2.4 (Benthic primary productivity).

We measured higher rates of grazing on seagrass than anywhere else in the world — in some places during some surveys the rates of consumption were more than ten times the rates of growth. This was particularly pronounced for the seagrass *Thalassia hemprichii* (otherwise known as turtlegrass), for which average consumption across the study was higher than growth. *Thalassia* is one of the most abundant seagrasses in the terraced lagoons that are characteristic of the Kimberley, and the apparent contradiction of high abundance and high consumption is probably reconciled by a combination of fast growth rates and patchy grazing; indeed rates of consumption of *Thalassia* varied by two orders of magnitude among sites and surveys.

In contrast, consumption of the seagrass *Enhalus acoroides* was on average lower than growth. An inference from this finding is that much of its production is probably not consumed by herbivores. We did not set out to study the fate of seagrass production, but it is likely that much leaf biomass is ultimately exported from the meadows as detritus.

There were several species of herbivores that were abundant in the seagrass meadows, but the golden-lined rabbitfish *Siganus lineatus* was ubiquitous and abundant in all Remote Underwater Video (RUV) deployments. Stable isotope and gut-content analyses confirmed that the diet of *S. lineatus* is primarily comprised of seagrass, especially *Thalassia*. *S. lineatus* is a highly valued food source for the Bardi Jawi people, who call them *barrbal*.

Another potentially significant herbivore is the green turtle *Chelonia mydas*. Green turtles were seen during RUV deployments, but were not abundant. However, boat-based observations during the rising tide found that they were abundant in some areas. Stable isotope and gut-content analyses showed that *C. mydas* consumed a variety of plants, but brown algae and the seagrass *Thalassia* were particularly prominent in their diet. There was some, albeit equivocal, evidence that different individuals might have preference for either brown algae or seagrass. Satellite tags showed that they frequently tended to spend their time in places with abundant seagrass.



1 Introduction

Herbivory is a key ecological process that sustains and underpins food webs, and can regulate the biomass of primary producers in an ecosystem. It has long been hypothesized that rates of herbivory are greatest in the tropics, although strong evidence to support this is limited. Nevertheless, one of the ecosystems in which rates of herbivory are typically high is tropical corals reefs (Poore et al. 2012; Hyndes et al. 2016). Tropical seagrasses might also once have hosted particularly high rates of herbivory, but in many parts of the world populations of large herbivores have been reduced, and so herbivory on tropical seagrasses may be lower than it once was (Heck and Valentine 2006). Contemporary rates of herbivory on seagrasses are not typically high (Poore et al. 2012).

Parts of the Kimberley host extensive stands of seagrasses and macroalgae, and research has recently revealed that their rates of productivity are exceptionally high (Kendrick et al. 2017). In addition, compared to many other tropical regions, the Kimberley has experienced relatively low rates of harvest of marine fauna, raising the possibility that rates of herbivory might be higher than those found elsewhere. Indeed, initial research within the WAMSI Kimberley Marine Research Program (KMRP) indicated that consumption of seagrass, although patchy, was generally quite high, especially on the seagrass *Thalassia hemprichii* (Kendrick et al. 2017). However, the identity of the main herbivores, and the importance of seagrasses, macroalgae and other potential food sources to their diet were not resolved by that study.

A key initial step in understanding herbivory is to identify the main species of herbivores, and characterise their diet. This study aimed to provide initial information addressing these knowledge gaps. Because resources were limited, most effort was focused on addressing the knowledge gaps for the seagrass-dominated ecosystems within the region.

2 Materials and Methods

The research on herbivory was focused on the islands and coast of the Bardi Jawi Indigenous Protected Area (IPA), encompassing Jalan (Tallon Island) and Iwany (Sunday Island), where there are two sampling locations (Laanyi and Ngaloon) in the West Kimberley of Western Australia (16.4°S, 123.2°E). We conducted four surveys from October 2014 to April 2016 (Figure 1).

At these locations the following measurements or collections were made (not all measurements were made during each survey):

1. Remote underwater video to identify the species of herbivores present, with particular focus on the species present in seagrass habitats.
2. Rates of herbivory on seagrass. These data are presented in the report for WAMSI KMRP Project 2.2.4, here the focus is on assessing rates of herbivory as a proportion of primary production;
3. Collections of golden-lined rabbitfish (*Siganus lineatus*) for stomach content and stable isotope analyses;
4. Blood samples from green turtles (*Chelonia mydas*) for stable isotope analyses; and
5. Satellite telemetry of green turtles to test whether individuals spent a large proportion of time in seagrass habitat.

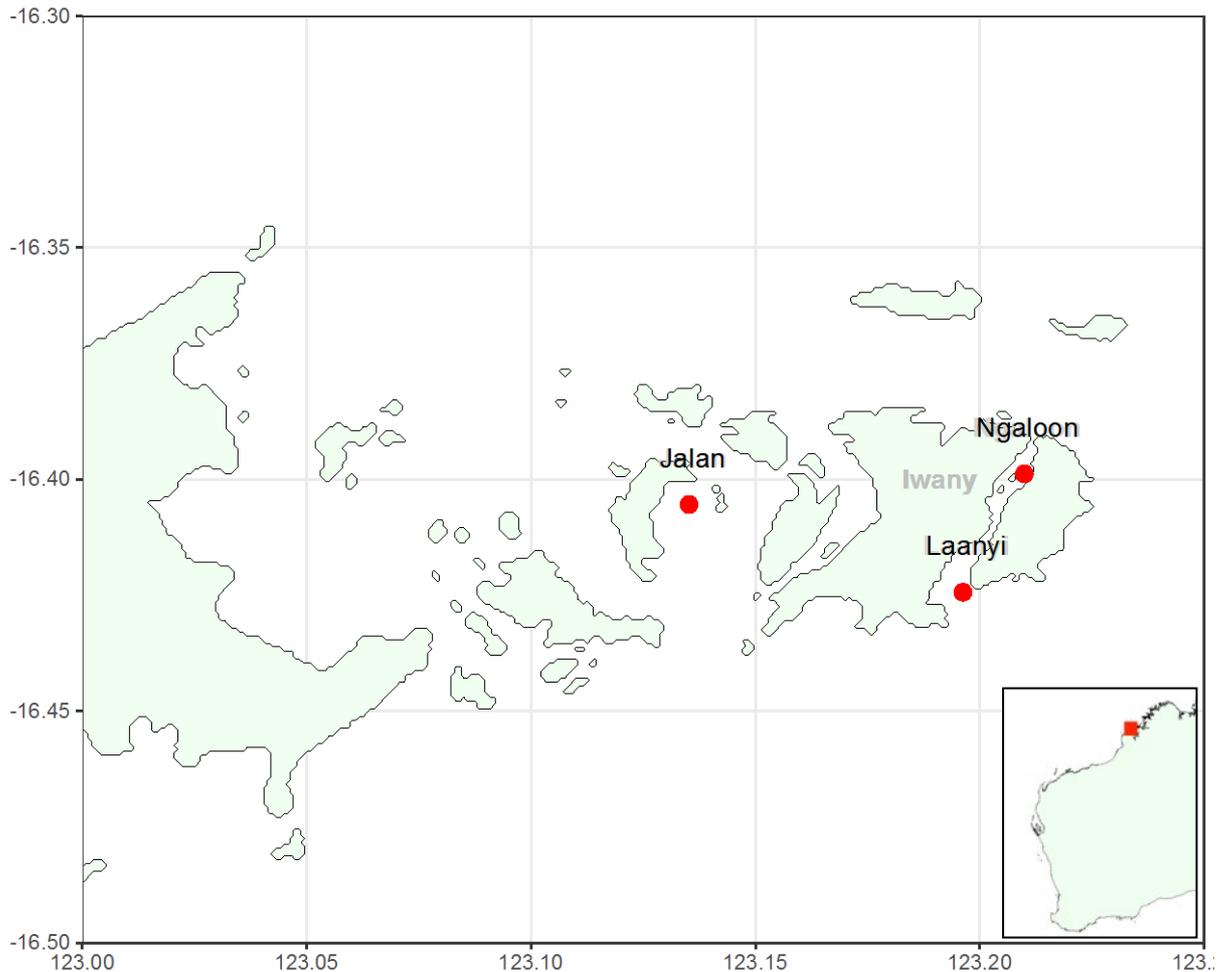


Figure 1: Locations where herbivory measurements and rabbitfish collections were made during this study. The locations Ngaloan and Laanyi are on Sunday Island (iwany, noted in grey font).

2.1 Remote Underwater Video (RUV)

Data from stereo-RUV deployments described earlier in Section 2.2 (Sampling design and methods) were used to identify the main consumers of seagrass or macroalgae present in each of the five main Kimberley habitats (macroalgal beds, coral reefs, mangrove, intertidal rockpools and seagrass meadows). Briefly, five stereo-RUV units (comprising two GoPro Hero 3+ video cameras in waterproof housings mounted on a custom-made aluminium base bar) were deployed in each habitat during daylight hours. Each unit was separated by a distance of 50 m and left to record for 20 minutes. Note that while data used in section 2 was for juvenile fishes only, data presented here includes all fishes recorded by stereo-RUVs regardless of their life stage (i.e. juveniles and adults).

Species were identified by three experienced observers using expert knowledge aided by published fish guides wherever necessary. The relative abundance was then calculated as the MaxN of these species in each habitat (i.e. the maximum number of individuals per species seen in a single video frame) and averaged across all deployments. Herbivorous pomacentrids (damselfishes) were not included because they do not typically consume large erect algae or seagrass.

Additional RUV deployments were done in seagrass meadows at Jalan and Ngaloan during April 2015 (two of the sites included in measurements of rates of herbivory) to quantify variation in the composition and relative abundance of potential herbivores, as well as quantify bite rates by fish. These deployments used different systems than those described above for estimating abundance of herbivorous fishes, and comprised single GoPro Hero 4 Silver cameras in waterproof housings. On each

of three days, ten units were deployed in meadows of each of the two main species of seagrass, *Thalassia hemprichii* and *Enhalus acoroides*. Each camera filmed for 3-4 hours during each deployment. Cameras were placed on steel camera frames; each held two cameras facing in opposite directions. Individual frames were separated by at least 25 m. In the laboratory, 34 minutes from each camera during each deployment were analysed using EventMeasure software (SeaGIS Pty Ltd). The observer recorded the MaxN for each fish species, as well as the total number of bites on the seagrass canopy made by each species of fish. The mean MaxN for each species was calculated for each camera.

2.2 Rates of herbivory

Net rates of herbivory (as a percentage of growth) were calculated from data collected during the companion WAMSI KMRP Project 2.2.4 (Kendrick et al. 2017). Rates of growth of the seagrasses *Thalassia hemprichii* and *Enhalus acoroides* were calculated as mm² per shoot per day from surveys in which growth was measured using a standard hole-punch method described in Kendrick et al. 2017. Rates of consumption were calculated as mm² per shoot per day from tethering experiments. Rates of consumption of *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: 16.405°S, 123.135°E), Laanyi (16.424°S, 123.196°E) and Ngaloan (16.398°S, 123.209°E) (both on Sunday Island). Fifteen shoots of each species were deployed on each day (n = 270 shoots per species).

Net herbivory was calculated as consumption/growth × 100. Standard errors were calculated from the appropriate methods for error propagation for multiplication.

2.3 Rabbitfish collections

Golden-lined rabbitfish (*S. lineatus*) were collected by spear in October 2014 and April 2015. Ten individuals were collected from Jalan, Laanyi and Ngaloan in each survey (n=60). Individuals were weighed (wet weight, in grams) and measured (total length, in mm), and a small piece of dorsal muscle excised by scalpel for stable isotope analysis. The stomach was removed from individuals taken in October 2014 (n=30). Samples were frozen (-20°C) and transported to the CSIRO Floreat laboratories (Perth, Western Australia).

2.4 Green turtles

Green turtles (*C. mydas*) were captured during two surveys: April 2015 (n=32) and April 2016 (n=30). Turtles were captured using the “rodeo” method, in which individuals are captured in the water by an experienced person jumping from a boat. After capture, each individual turtle was weighed and measured (curved carapace length, in mm). Blood was extracted from a vein in the neck using a 22G x 1.5 inch needle, and immediately frozen (-20°C) and transported to the CSIRO Floreat laboratories (Perth, Western Australia) for stable isotope analyses (described below).

Stomachs of five individual green turtles were donated by Bardi Jawi hunters in early 2016 for stomach content analyses.

2.5 Stomach content analyses

After thawing, the stomachs of rabbitfish (*S. lineatus*) were separated from the rest of the digestive tracts and rinsed with distilled water. The entire stomach was used. For green turtles (*C. mydas*) a randomly-selected subsample of approximately 50 ml was taken from each stomach, because the total amount of material was too great. For both rabbitfish and turtles, the stomach contents were spread in a 13 cm diameter glass dish with filtered water set over a sheet with 60 randomly-positioned dots. Stomach contents were viewed through a magnifying lamp and food items covering each dot recorded to the highest taxonomic level.

Permutational multivariate analysis of variance (PERMANOVA) was used to test whether there were differences in the composition of stomach contents of *S. lineatus* among sites. The stomach content data contained numerous zeros, so tests were based on Bray-Curtis dissimilarities calculated using untransformed data. Analyses were conducted using the vegan package in R.

2.6 Stable isotope analyses

Data for potential diet sources (seagrasses, macroalgae, mangroves) were collected as part of a companion study (WAMSI KMRP Project 2.2.4), and the methods for collection of those data are described in Kendrick et al. 2017. Briefly, seagrass leaves, macroalgae thalli and mangrove leaves were collected by hand, frozen (-20°C) and transported to the CSIRO Floreat laboratories, where they were later thawed, cleaned, dried in an oven at 60°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 and are expressed in ‰ using conventional delta (δ) notation δX (‰) = $[(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$; where X is ^{13}C or ^{15}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 N_2 for nitrogen).

Rabbitfish muscle tissue was thawed, cleaned, dried in an oven at 60°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. Stable nitrogen and carbon isotope compositions are reported in the standard δ -notation (e.g. Skrzypek 2013) after multi-point normalization of raw isotope data to isotope international reference scale (VPDB for carbon and atmospheric N_2 for nitrogen) using international standards provided by International Atomic Energy Agency ($\delta^{13}\text{C}$ - NBS22, USGS24, NBS19, LSVEC; $\delta^{15}\text{N}$ - N1, N2, USGS32) and laboratory standards (Skrzypek 2013). The uncertainty associated with stable isotope analyses (one standard deviation) was not more than 0.10‰.

Mixed-effects ANOVA was used to test if patterns in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *S. lineatus* muscle varied among sites (three levels, random) or surveys (two levels, fixed). ANOVA was also used to test whether $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *C. mydas* blood varied among years.

Overall patterns of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among species were visualized through biplots.

Further analyses were performed using a Bayesian Isotope Mixing Model with prior information on the dietary proportions gained from the gut content analyses. Analyses were done using the SIAR (Stable Isotope Analysis with R) package (Parnell et al. 2010). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of seagrass and macroalgae were taken using the data collected in the companion study (WAMSI KMRP Project 2.2.4), and the isotopic signatures for diazotrophic cyanobacteria were taken from the literature (Capper et al. 2006). Mixing models were run with carbon and nitrogen enrichment factors of 0.7 ± 0.42 ‰ and 3.35 ± 2.33 ‰ respectively.

For turtles, the main seagrass observed in stomachs was *Thalassia hemprichii*, so this was the only seagrass species retained in models. A variety of macroalgae were observed, but most had very similar

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and so a single group of macroalgae was modeled. *Turbinaria* typically had lower $\delta^{13}\text{C}$, but were not included in models because they were very infrequent in turtle stomachs (<1%). There was evidence of a bimodal distribution in turtle $\delta^{13}\text{C}$, so separate models were run for turtles that yielded red blood cell $\delta^{13}\text{C}$ greater and less than -14‰.

2.7 Movement of green turtles

Ten green turtles were tagged with satellite tags: four in April 2015, and six in April 2016. SPLASH10-F-296A and SPLASH10-F-296C Wildlife Computer Argos transmitter with Fastloc[®] GPS, temperature and depth recorders were used. Tags were programmed to transmit 254 times per day with position estimates having priority over depth and temperature.

Satellite tags were attached to the first two vertebral scutes immediately posterior to the nuchal scute using a two-part epoxy resin (Sika AnchorFix[®]-3+, Sika Australia Pty Ltd). Prior to attachment, a paint scraper was used to remove any flaking scute material. This was followed by gently sanding the area with wet and dry sandpaper. The area was then wiped with 100% ethanol and allowed to dry before attaching the tag. Once the epoxy resin had set, the tag was coated with antifoul paint (International Ultra high strength hard antifouling paint) and allowed to dry overnight. Tagged animals were released close to their capture site either on the same day, or the day after, capture.

The satellite fixes were plotted to enable visual estimation of long distance movements and home range estimates (50 and 95% kernel utilization distribution: KUD) were calculated using the *adhabitateHR* package in R.

KUDs were calculated for all satellite-tagged turtles using raw (unfiltered) GPS data (Fastloc). These data were downloaded from the Wildlife Computers Portal. To reduce the influence of position accuracy on KUD estimates, only Fastloc data were used in the analysis. Argos locations typically have an accuracy of several hundred metres to several kilometres (Hays et al. 2001; Teo et al. 2004; Witt et al. 2010). The accuracy of Fastloc-GPS locations is significantly better with positions calculated using 4 satellites within 724 m of true position and when 6 or more satellites detect the tag, accuracy is within 70 m of the true location in 95 % of calculations (Dujon et al. 2014).

The KUD is a probability density function that quantifies an individual's relative use of space (Kernohan et al. 2001). It depicts the probability of an animal occurring at a location within its home range as a function of relocation points (data obtained from satellite tag detections) (White and Garrot 1990).

The 50 and 95% KUD's were plotted on maps of modelled seagrass distribution produced from spectral classification of Landsat imagery taken in September 2014 as part of a companion project (WAMSI KMRP Project 1.2.5). Seagrass coverage was modelled using a Bayesian likelihood model using spectral classification of Landsat imagery taken in 2014 (see Bayliss and Wilcox 2016). This seagrass map has a significant uncertain spectral class of "possible seagrass" throughout that requires extensive field validation; hence our ability to classify the importance of seagrass is preliminary. Field-based observations of seagrass suggest that while the modelled seagrass distribution accurately reflects large seagrass beds, the ability to incorporate sparse seagrass and seagrass in deep water is limited. Furthermore, green turtle diet is not restricted to seagrass with animals also feeding on a variety of benthic algae.

3 Results

3.1 Remote Underwater Video (RUV)

The main species of herbivorous fish (Appendix 2) varied among habitats (Figure 2). In coral- and algae-dominated habitats, the highest MaxN were yielded by the surgeonfish *Acanthurus grammoptilus*, while in seagrass meadows the highest MaxN were yielded by the golden-lined rabbitfish *Siganus lineatus*. MaxN of all herbivorous species tended to be low in mangrove and rockpool habitats.

The results from the comparisons among habitats were broadly reflected in the comparison of two of the seagrass-dominated sites used for the measurements of herbivory during April 2015 (Figure 3, note that the numbers differ from Figure 2 because the locations were different). The golden-lined rabbitfish *S. lineatus* was abundant at both sites; the surgeonfish *A. grammoptilus* was abundant only at Ngaloon. Observations of potential bite rates recorded from the same set of videos revealed idiosyncratic patterns that varied between the two sites, and between meadows of the two most dominant species of seagrasses (*T. hemprichii* and *E. acoroides*) (Figure 4). *A. grammoptilus* was recorded frequently biting at *Thalassia* at Ngaloon, while *S. lineatus* was recorded most frequently biting at *Enhalus* at Jalan. The damselfish *Dischistodus darwiniensis* was frequently recorded biting at *Thalassia* at Jalan. Note that observations of bites do not necessarily allow inference of herbivory on seagrass, because individuals could be selectively biting at epiphytic algae growing on the seagrass blades.

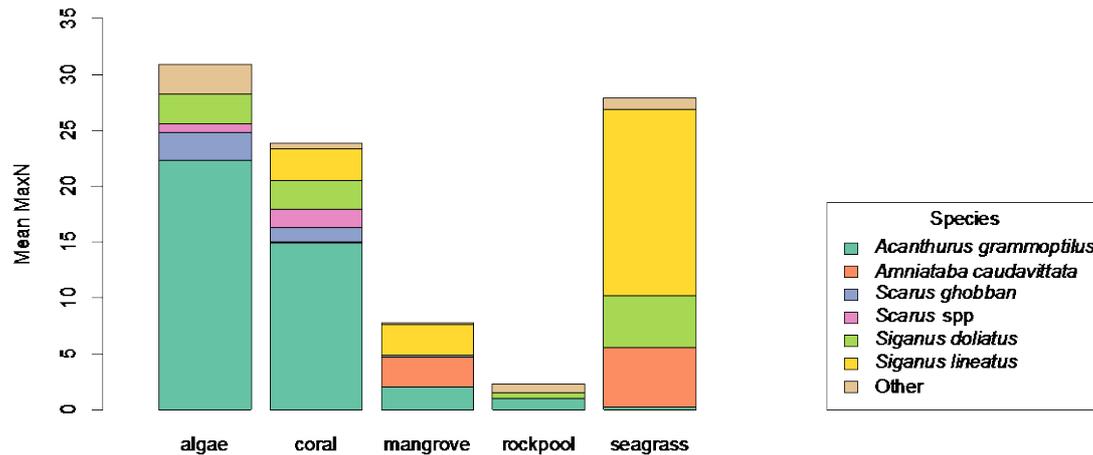


Figure 2: Mean MaxN of the most abundant species of herbivorous fish observed in five distinct habitats in the Bardi Jawi IPA. The “Other” category includes the pooled means of all other observed species of herbivores: pooling MaxN in this way does not have any ecological meaning, but is shown simply to illustrate patterns.

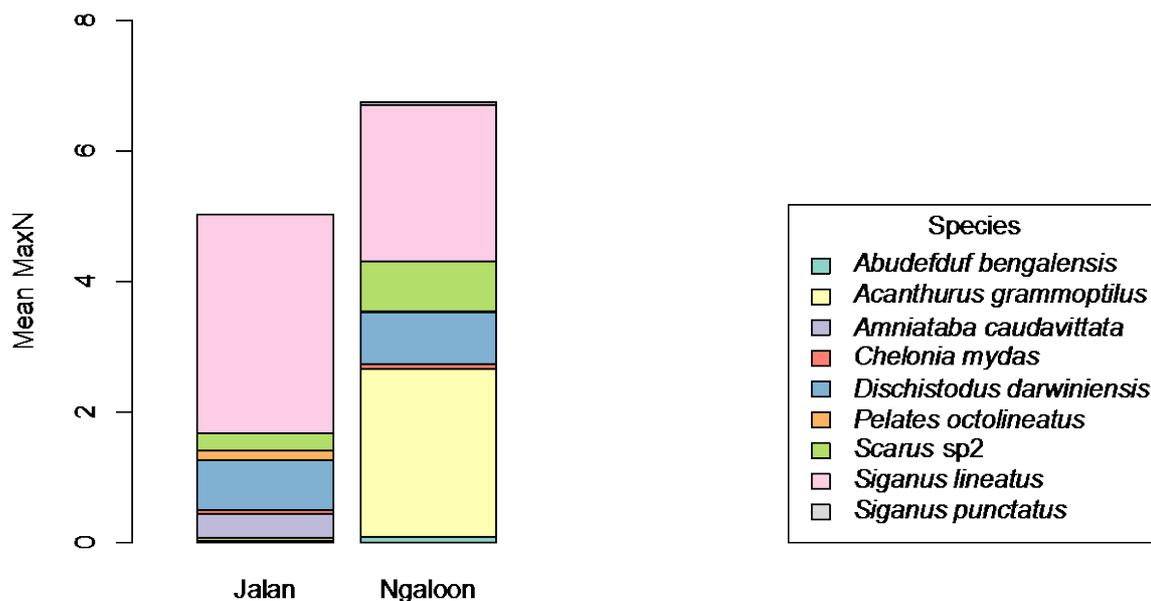


Figure 3: Mean MaxN of the most abundant species of herbivorous fish (plus the green sea turtle *Chelonia mydas*) observed in two of the seagrass meadows in the Bardi Jawi IPA. Data were obtained from RUV deployments during April 2015.

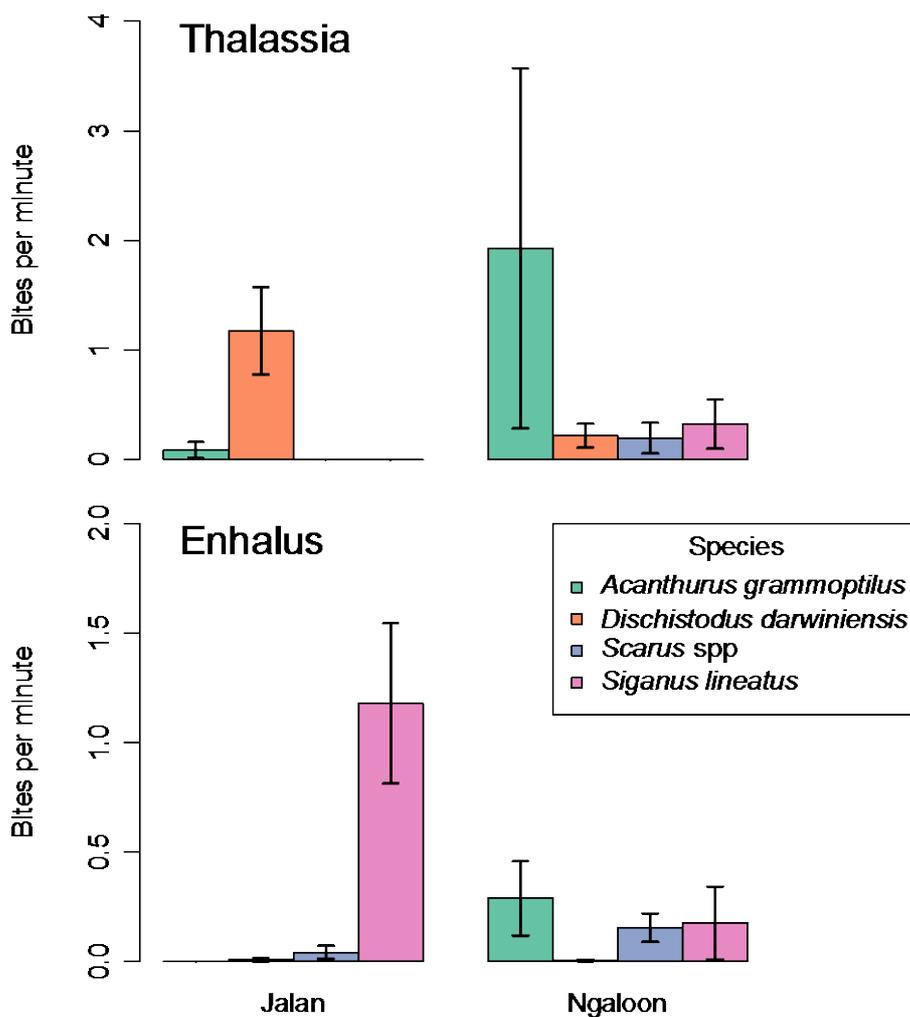


Figure 4: Mean bites per minute (±SE) of herbivorous fish recorded from RUV deployments at two sites (Jalan, Ngaloon) in April 2015 (n=24 at Jalan, n=32 at Ngaloon).

3.2 Rates of herbivory

Net rates of herbivory (as a proportion of daily production) were highly variable, ranging from 38-1433% for *Thalassia* and 0-572% for *Enhalus* (Figure 5). The mean net consumption of *Thalassia* was 401%, and the mean net consumption of *Enhalus* was 166%, indicating that on average rates of consumption exceeded growth.

Thalassia was consumed during each deployment at each location, and on five deployments the rates of consumption exceeded the rates of growth (55% of deployments). Rates of consumption were an order of magnitude higher than rates of growth (>1000%) at Ngaloon during two deployments. *Enhalus* was not consumed at all during four deployments, and was consumed at rates exceeding those of growth on four deployments.

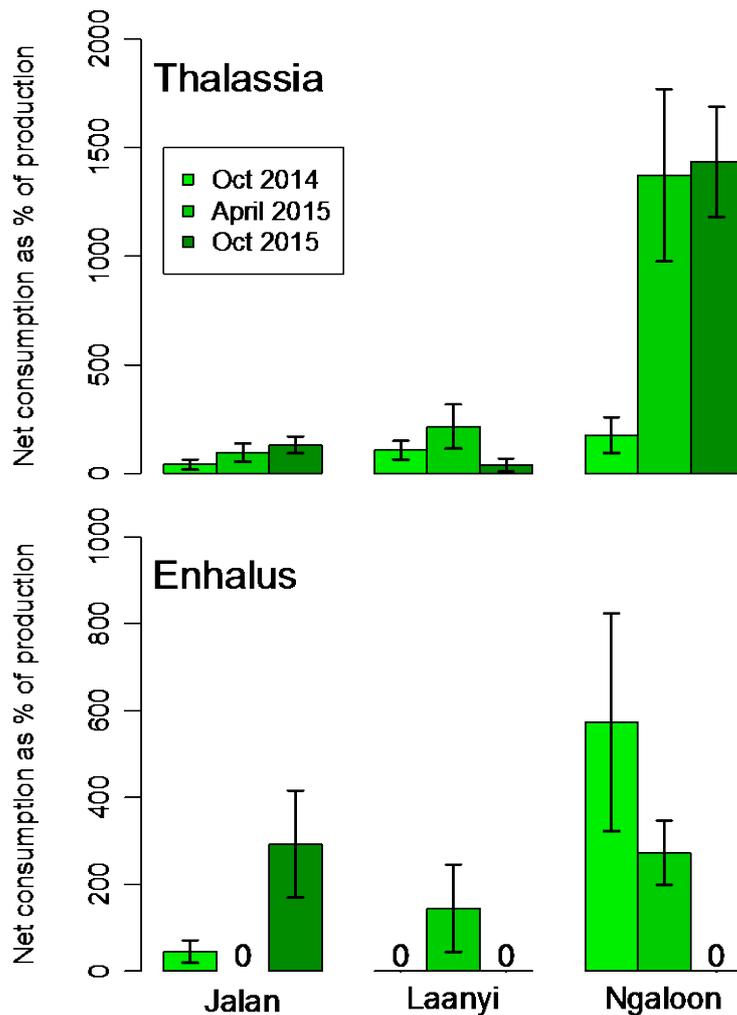


Figure 5: Net rates of herbivory (\pm SE) as a percentage of daily growth for *Thalassia* and *Enhalus* at three sites during three surveys. 0 indicates that there was no consumption of seagrass recorded on tethered seagrass during that deployment.

3.3 Diet of green turtles

Of the five individual green turtles (*C. mydas*) for which stomach contents were quantified, three were dominated by the seagrass *T. hemprichii* (80-100%; Figure 6). The stomach of the other two individuals contained exclusively macroalgae of various kinds. No animal matter was recorded in the stomach of any of the five individuals.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *C. mydas* blood did not differ between 2015 and 2016 ($P > 0.2$ in each case), so data for

all subsequent analyses were pooled. $\delta^{13}\text{C}$ spanned a wide range (-20.61‰ to -7.97‰), but the range in $\delta^{15}\text{N}$ was smaller (4.24‰ to 8.93‰) (Figure 7). $\delta^{13}\text{C}$ exhibited a bimodal distribution, with a breakpoint around -14‰. Separate mixing models were performed for two groups of turtles: those with blood $\delta^{13}\text{C}$ greater than -14‰, and those with blood $\delta^{13}\text{C}$ less than -14‰. Results from the two analyses were slightly different, but seagrass was indicated to be likely the main diet source for both groups. 95% confidence intervals for macroalgae were 0-56% for individuals with $\delta^{13}\text{C}$ less than -14‰, and 1-40% for individuals with $\delta^{13}\text{C}$ greater than -14‰. 95% confidence intervals for seagrass were 44-100% for individuals with $\delta^{13}\text{C}$ less than -14‰, and 60-99% for individuals with $\delta^{13}\text{C}$ greater than -14‰ (Figure 8).

Stomach contents of *Chelonia mydas*

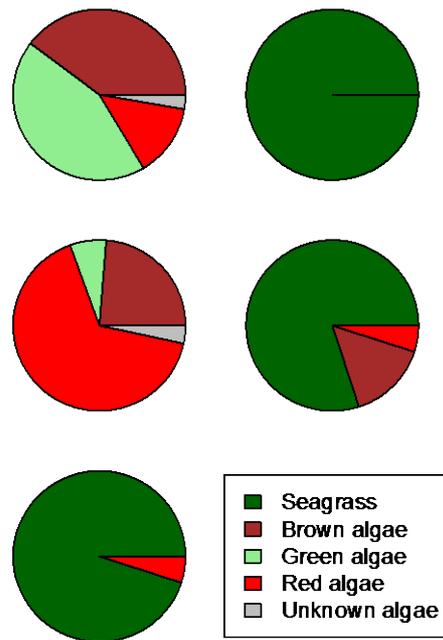


Figure 6: Stomach contents of five individual *C. mydas* captured by Bardi Jawi hunters. Each pie chart shows the stomach contents of a single individual.

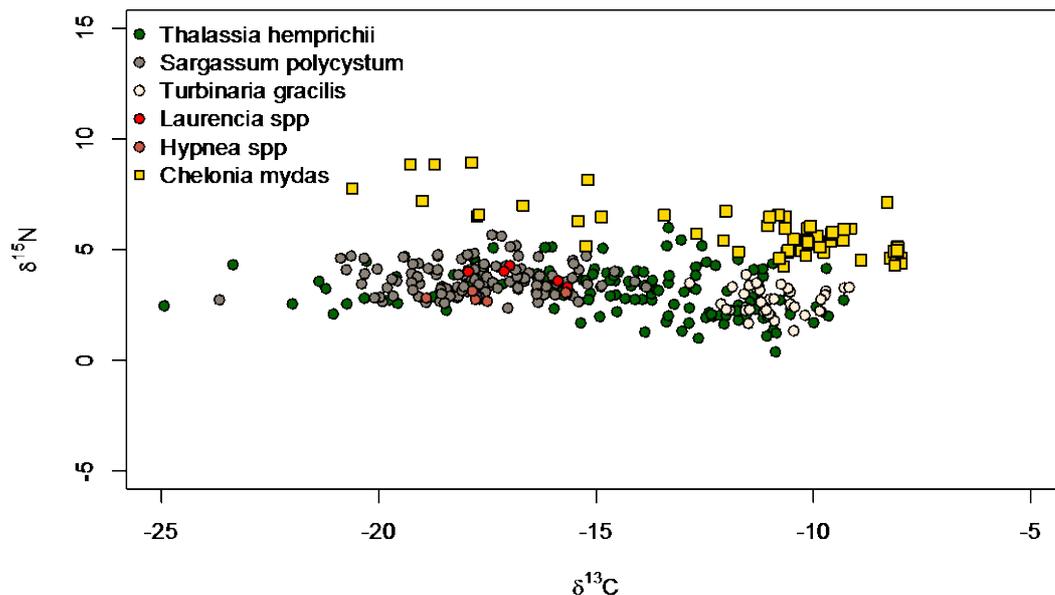


Figure 7: Individual measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *C. mydas* blood and benthic primary producers likely to be consumed by *C. mydas*. All data were collected from within the Bardi Jawi IPA.

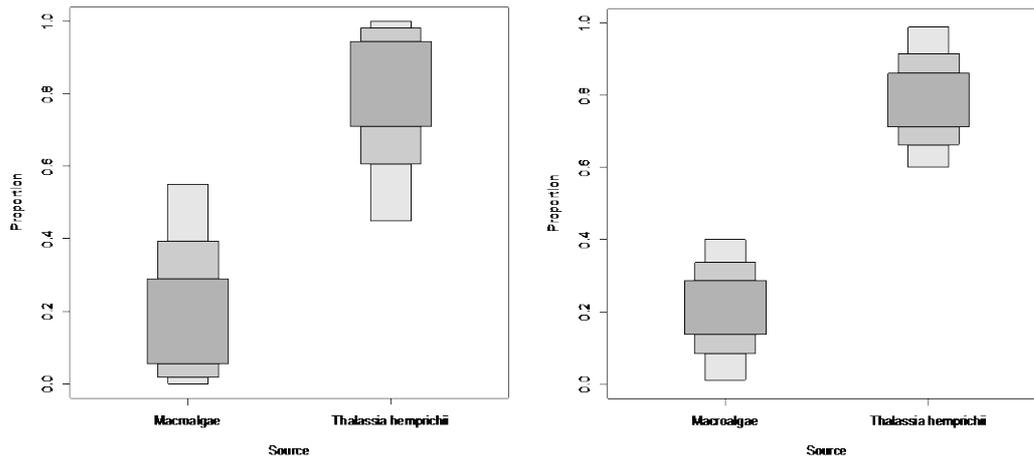


Figure 8: Boxplots showing likely proportions of macroalgae and seagrass (*T. hemprichii*) consumed by *C. mydas*. Individuals were separated into two groups based on $\delta^{13}\text{C}$ of blood, those with $\delta^{13}\text{C}$ below -14‰ (left, $n=42$) and above -14‰ (right, $n=12$) as described in the text. Plots show the 50%, 75%, and 95% probabilities for each potential food source.

3.4 Diet of the golden-lined rabbitfish

The stomach contents of golden-lined rabbitfish *S. lineatus* varied significantly among sites ($F = 3.07$, $p = 0.026$). At all sites seagrass (primarily *T. hemprichii*) comprised the bulk of the stomach contents (Table 1, Figure 9). At Jalan a large proportion of bluegreen algae was also found in the stomachs, while at Laanyi and Ngaloon proportionally more red algae was observed.

The $\delta^{15}\text{N}$, but not $\delta^{13}\text{C}$, of *S. lineatus* muscle varied significantly among sites (Table 2). $\delta^{15}\text{N}$ was lower in April 2015 ($7.15\text{‰} \pm 0.19$) than October 2014 ($8.24\text{‰} \pm 0.13$), but the difference was not statistically significant (Table 2). Subsequent analyses considered *S. lineatus* collected at different sites separately. $\delta^{13}\text{C}$ of *S. lineatus* spanned a narrower range than that of *C. mydas* (-18.89‰ to -9.22‰), and the range in $\delta^{15}\text{N}$ was relatively low (5.41‰ to 9.20‰) (Figure 10).

Mixing models indicated that the diet of *S. lineatus* at all sites was likely dominated by seagrass (Figure 11), and the ranges of plausible contributions at all sites were similar (5-95% percentiles: 60-89% at Jalan, 55-90% at Ngaloon, 58-90% at Laanyi). Macroalgae was the likely next most consumed at all sites, while the likely contributions of cyanobacteria were relatively low.

Table 1: The relative abundance (as %) of foods observed in the stomachs of *Siganus lineatus*. Data are mean relative abundance (out of a maximum possible value of 60 dots), \pm standard errors, $n=10$ in each case.

Site	Seagrass	Mangrove root	Red algae	Brown algae	Green algae	Bluegreen algae	Other
Jalan	39.6 \pm 6.4	0.3 \pm 0.2	3.2 \pm 2.6	0.2 \pm 0.2	0.8 \pm 6.8	15.4 \pm 6.8	0.5 \pm 0.5
Laanyi	39.9 \pm 4.2	0.0	14.1 \pm 3.5	0.2 \pm 0.2	0.0	5.8 \pm 3.9	0.0
Ngaloon	48.5 \pm 2.1	0.0	10.1 \pm 2.3	0.2 \pm 0.2	0.0	0.0	1.2 \pm 1.0

Stomach contents of *Siganus lineatus*

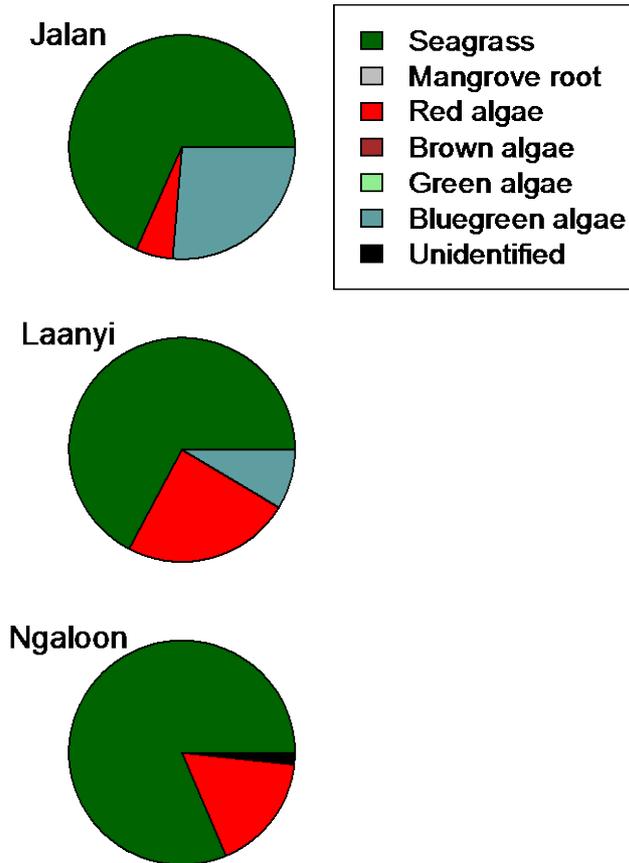


Figure 9: Stomach contents of *S. lineatus*. Each pie chart shows the mean values for each site (10 individuals per site).

Table 2: Results of analyses of variances testing for patterns in the stable isotope compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of dorsal muscle of the rabbitfish *S. lineatus*.

Source	$\delta^{13}\text{C}$ [‰ VPDB]					$\delta^{15}\text{N}$ [‰ AIR]				
	df	SS	MS	F	p	df	SS	MS	F	p
Location [L]	2	4.55	2.27	0.71	0.493	2	6.06	3.03	4.77	0.012
Survey year/season?? [S]	1	1.70	1.70	5.15	0.162	1	17.00	16.99	13.33	0.070
L × S	2	0.33	0.16	0.05	0.949	2	2.55	1.27	2.01	0.143
Residual	53	168.13	3.17			53	33.65	0.63		

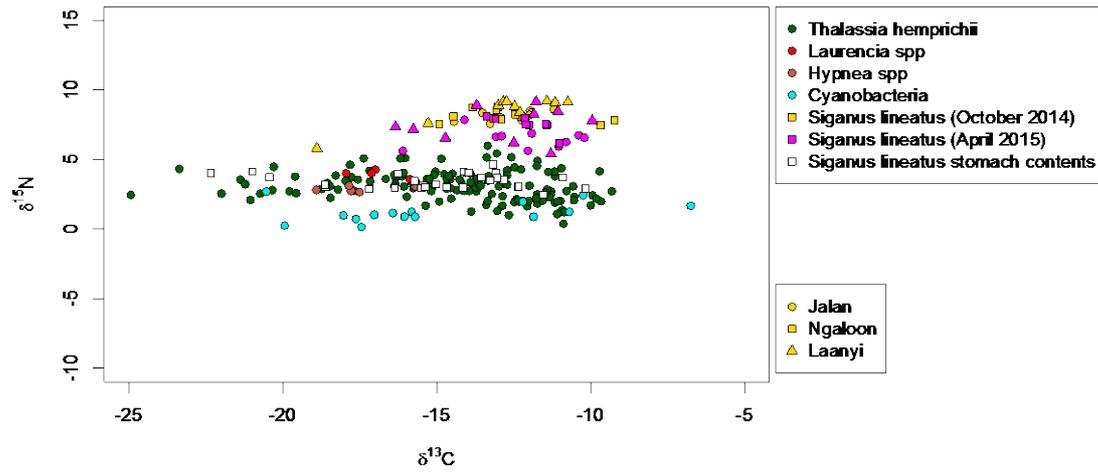


Figure 10: Individual measurements of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of *S. lineatus* muscle tissue and benthic primary producers (shown as different colours) likely to be consumed by *S. lineatus*. *S. lineatus* collected from different sites are denoted by different symbols. All data were collected from within the Bardi Jawi IPA.

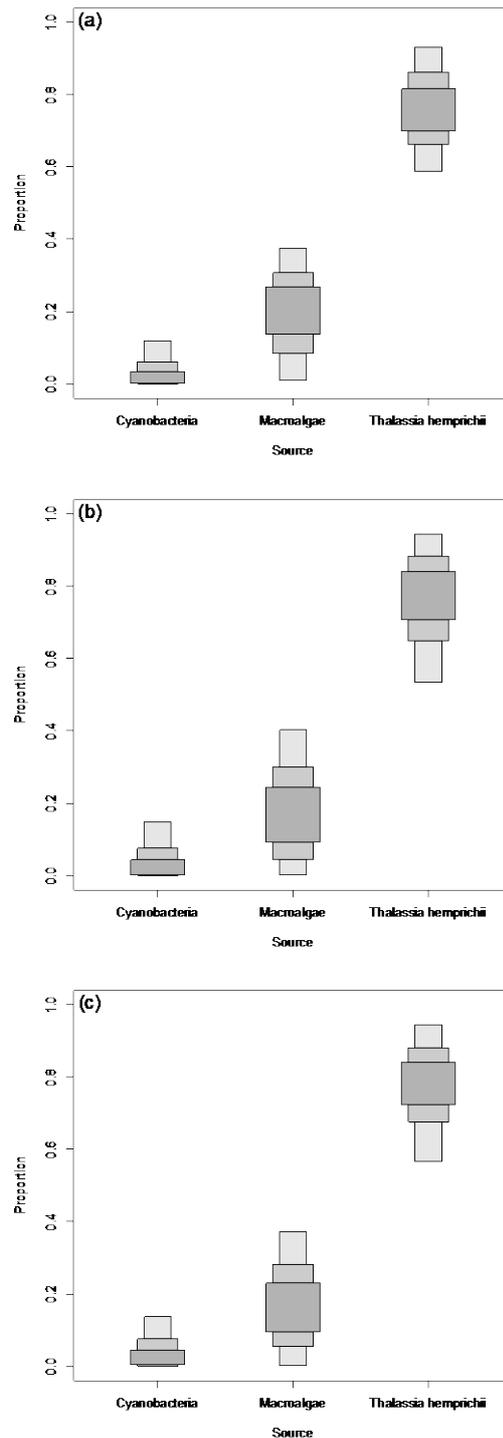


Figure 11: Likely proportions of cyanobacteria, macroalgae and seagrass (*Thalassia hemprichii*) in the diet of *Siganus lineatus* collected from (top) Jalan, (middle) Ngaloon, and (bottom) Laanyi. Plots show the 50%, 75%, and 95% probabilities for each potential food source.

3.5 Movement of satellite-tagged green turtles *Chelonia mydas*

Satellite tags were attached to 10 green turtles of varying size (62 – 92 cm curved carapace length), sex and maturity (Table 3). There was no obvious pattern in home range size related to size or sex. Core home range estimates (50% KUD) ranged from as little as 1.95 km² to 5,780 km². Large home range estimates of animals that moved long distances along the shore either west or east are less informative and likely to be an overestimate of total area used.

Table 3: Details of 10 individual green turtles *C. mydas* tagged with Argos transmitters. CCL = curved carapace length (cm); CW = curved carapace width (cm); A = adult, SA = sub adults, J = juvenile

Date tagged	Tag ID	Duration of tag detections (days)	CCL (cm)	Mass (kg)	Sex	Age class	Name	50 % KUD (km ²)	95 % KUD (km ²)	Total Fastloc detections
20/04/2016	53245	130	62.7	26.4	I	J	Brianna	122.35	1427.24	90
21/04/2016	53283	113	70.9	38	F	SA	Princess	91.92	423.16	36
21/04/2016	53284	176	74.0	45.8	F	SA	Willamena	5780.78	57728.14	566
21/04/2016	53285	164	88.6	71	M	A	Monsta	425.53	2089.49	425
14/04/2015	131863	151	62.9	27.7	I	SA	Ambol	1.95	8.48	664
22/04/2016	131864	187	92.4	84.8	F	A	Kimberly	61.01	279.61	533
16/04/2015	131867	186	77.3	103	I	SA	Savannah	2.79	18.67	291
15/04/2015	131870	86	79.7	101	F	A	Iwanj	270.31	2558.65	221
15/04/2015	139289	163	84.3	91	F	A	Jarmina	2371.85	14349.04	170
22/04/2015	153515	198	86.0	67.1	F	A	Phillomena	6.00	40.88	47

The movements of 10 satellite-tagged green turtles spanned more than 600 km (Figure 12 [top]). Three individuals left the region shortly after tagging: one moved into Talbot Bay, one to the vicinity of James Price Point, and the third moved into the Pilbara near Port Hedland. The remaining 7 individuals spent most of their time around One Arm Point and nearby islands and shoals (Figure 12 [bottom]). For animals that undertook large-scale movements, of those monitored for more than two months, all animals had at least one month where core home range (50 % KUD) was less than 5 km² (Table 4).

Table 4: Monthly 50% KUD (km²) for ten green turtles tagged with satellite tags.

Tag_ID	Year	April	May	June	July	August	September	October
53246	2016	36.53	5.79	967.49	2.46			
53283	2016	40.30	121.90					
53284	2016	6146.69	9492.99	0.00	1.48	11.80	4.43	1378062.78
53286	2016	107.72	1.94	1.72	33.42	1.37	1.05	
131863	2015	0.44	0.35	9.09	1.39	1.10	0.49	
131864	2016	26.27	282.15	6.78	3.39	1.69	2.54	2.54
131867	2015	17.06	0.99	1.25	1.96	0.85	2.41	0.99
131870	2015	2712.21	3.51	0.79	1.23			
139289	2015	3.42	2502.09	4.53	2.10	2.65	2.87	
153515	2015	16.64	2.70					

Of the seven individuals that remained close to where they were tagged (Figure 13), some — but not all — showed evidence of overlap with areas where seagrass was present (or was likely to be present) based on our own observations of seagrass beds as well Landsat imagery. The proximity of large areas of high benthic algae cover to seagrass beds combined with a lack of detailed habitat maps to delineate between the two food resources (seagrass and algae) makes interpreting turtle movement in relation to habitat type difficult. For the majority of turtles that were resident within the Bardi Jawi IPA (six of seven) there was a high degree of overlap between satellite locations (Tag ID 131867, 131863, 153515, 53283, 53285 and 13864) and seagrass presence suggesting that for these individuals, seagrass might be an important part of the diet. For the individuals where satellite locations and KUD estimates didn't overlap with seagrass, it is likely that either estimates of seagrass distribution are inaccurate, animals were feeding predominantly feeding on algae or that GPS locations did not accurately reflect the animals foraging area.

Of the turtles that moved away from where they were captured, only Tag ID 131870 moved into an area where we have data on seagrass presence. Fastloc detections from this animal did not overlap with seagrass distribution in this area of Talbot Bay, however dugong (*Dugong dugon*) were observed feeding on *Halophila* spp. by one of the authors (Richard Pillans) in the areas with the highest density of Fastloc detections.

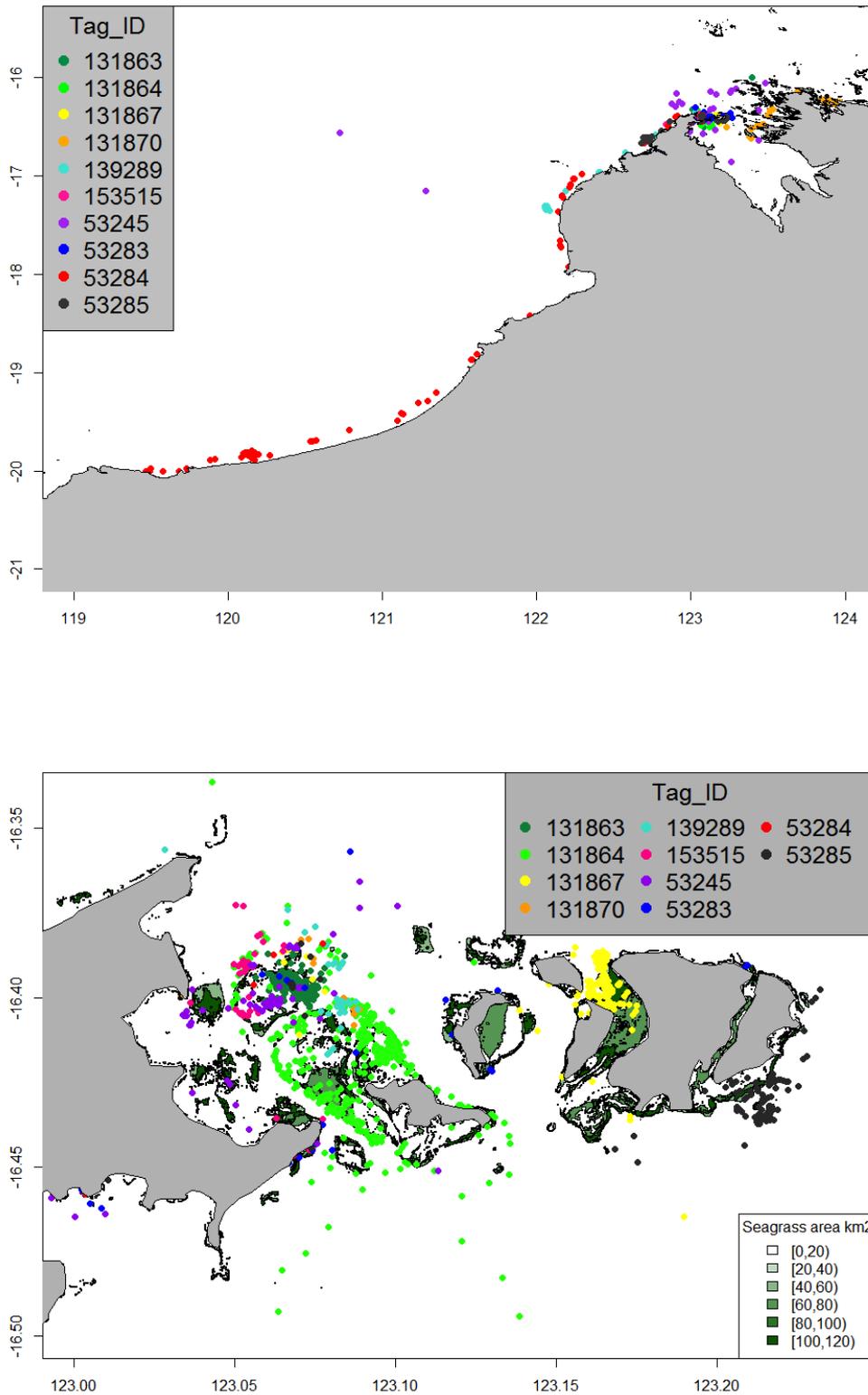


Figure 12: Fastloc GPS position estimates for each of the 10 green turtles, showing: (top) the entire geographical extent encompassed by movements, and (bottom) Fastloc GPS positions within the Bardi Jawi IPA. The green shading reflects the total area of seagrass polygons with darker shading representing larger polygons (areas of seagrass).

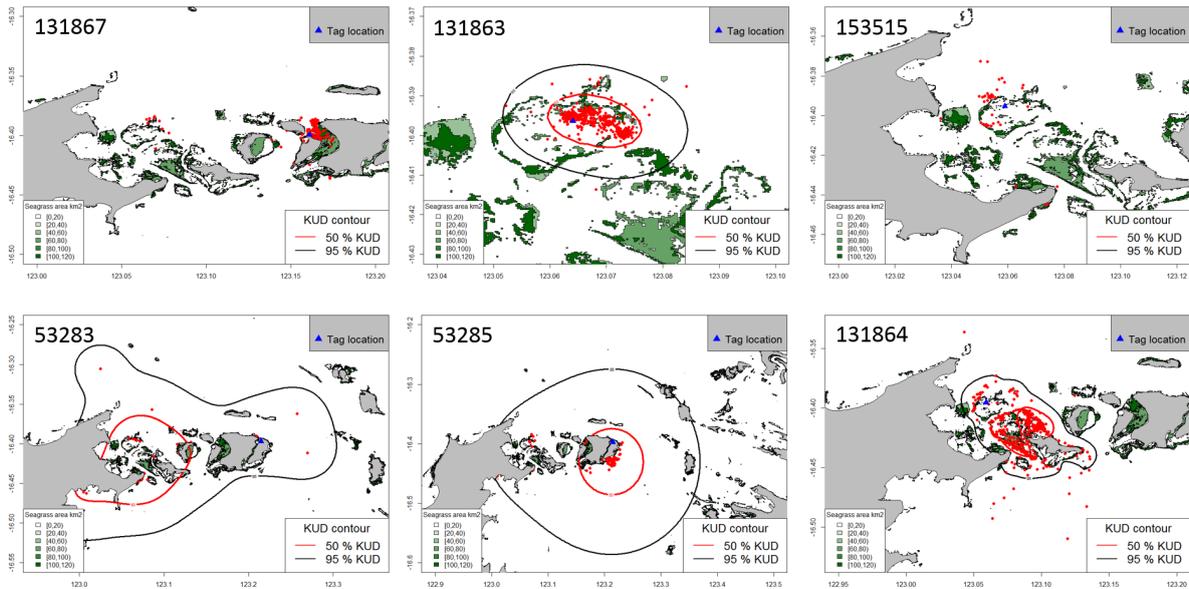


Figure 13: Fastloc GPS position and 50 and 95 % KUD estimates for 6 individual green turtles that remained in the area around One Arm Point and adjacent islands. The tag location is represented with a blue triangle and the satellite detection locations are represented by red circles. The green shading reflects the total area of seagrass polygons with darker shading representing larger polygons (areas of seagrass).

4 Discussion and Conclusions

4.1 Identity and composition of herbivores

The composition and relative abundance of species of nominally herbivorous fish varied among habitats. In habitats dominated by large brown algae or coral, the most abundant herbivorous fish was the surgeonfish *Acanthurus grammoptilus*, while in seagrass-dominated habitats the golden-lined rabbitfish *Siganus lineatus* was the most abundant species. Parrotfish (*Scarus ghobban* and *Scarus JHC* sp.3) were also present in algae- and coral-dominated habitats, and the barred rabbitfish *Siganus doliatus* was also present, but these species were less abundant.

Within these broad trends, some variation was evident between the seagrass meadows we focused on for detailed studies of herbivory. *S. lineatus* was abundant at Jalan and Ngaloan, but *A. grammoptilus* was also abundant at Ngaloan. Four species of herbivorous fishes were observed making biting movements in seagrass meadows at these sites, but patterns were inconsistent, with the damselfish *Dischistodus darwiniensis* yielding high bite rates in *Thalassia* meadows in Jalan, *A. grammoptilus* in *Thalassia* meadows in Ngaloan, and *S. lineatus* in *Enhalus* meadows at Jalan. Note that these observations do not necessarily reflect herbivory, because individuals could be biting at epiphytes on the seagrass, or even fauna inhabiting the meadows.

Green turtles *Chelonia mydas* were observed on RUV at both sites, but were not observed grazing.

The patterns observed are broadly consistent with the composition of fish faunas observed in other tropical ecosystems, particularly Indo-Pacific ecosystems dominated by *Thalassia* and *Enhalus*. Siganids (rabbitfish) are typically among the most common herbivores, and can be among the most abundant of all fish (Blaber et al. 1992; Gullstrom et al. 2002). Scarids (parrotfish) can also be abundant (Gullstrom et al. 2008), particularly in Caribbean seagrass meadows (Valentine et al. 2007). Few studies have found that acanthurids (surgeonfish) are abundant in seagrass meadows. Our observations of *A. grammoptilus* at Ngaloan might be due to the close proximity of algae-dominated habitat nearby.

4.2 Rates of herbivory

The rates of consumption of seagrass we measured were among the highest recorded anywhere in the world (Heck and Valentine 2006). Using simple tethering experiments, we estimate that consumption rates frequently exceed growth rates, indicating that most seagrass production likely enters grazing pathways. Rates were patchy, but in *Thalassia* meadows were on average 401% (median 131%) of daily production, and were sometimes up to 1433%. In *Enhalus* meadows, the rates of consumption were on average 166% (median 76%) of daily production, and up to 572%. Unsworth et al. (2007) recorded similar rates of grazing in Sulawesi, but the pattern was reversed — they recorded higher rates of grazing on *Enhalus* (average 787% of daily production) than on *Thalassia* (average 64% of daily production). In the study by Unsworth et al. (2007) scarids were identified as the likely major herbivore. Kirsch et al. (2002), in a study conducted in the Caribbean, also found that rates of consumption at times exceeded rates of production, and again identified scarids as the most likely herbivores.

The observations of rates of grazing that exceed rates of production appear incongruent with the existing dense seagrass meadows. However, we observed that grazing rates were not uniformly high, and even in *Thalassia* meadows there were times and places for which production exceeded consumption. It is likely that the patchiness in activities of herbivores compensates for the episodic high grazing.

4.3 Diet of key herbivores

Given the bite rates observed on RUV in our study, it is unlikely that scarids are significant herbivores in the Kimberley seagrass meadows we studied, unlike the findings of other studies (Kirsch et al. 2002, Unsworth et al. 2007). Based on the observations of the Bardi Jawi rangers, we focused on the golden-lined rabbitfish *S. lineatus* as a likely herbivore — this was subsequently supported by the RUV observations. In addition, given the observed high abundances of green turtles *C. mydas* at our sites during the incoming tide, we also focused on their diet.

Two lines of evidence support inferences about diet: direct observations of stomach contents, and stable isotope mixing models. For *S. lineatus*, both lines of evidence yielded very similar results. Stomachs of individuals tended to have large proportions of seagrass, and this was consistent at all three sites and during both surveys. On average, more than two-thirds of the stomach contents (by volume) was comprised of seagrass — mostly this appeared to be *Thalassia*. Stable isotope mixing models supported this for all sites, with the 95% probability intervals for the proportion of seagrass consumed being 60-92% at Jalan, 53-94% at Ngaloan, and 56-94% at Laanyi.

The diet of *S. lineatus* on the Great Barrier Reef is more typically comprised of macroalgae, with little seagrass recorded (Fox et al. 2009, Hoey et al. 2013). However, this might simply be due to the habitats in which these studies were conducted — there do not appear to be published studies of the diet of *S. lineatus* in seagrass-dominated ecosystems. Other siganids are known to consume seagrass.

Results for green turtles were more complex. The number of stomachs obtained was low (n=5), because of the ethical restrictions involved in sacrificing turtles for diet analysis and the consequent need to rely on samples donated by hunters. Of the five stomachs examined, three were dominated by seagrass (*Thalassia*); one of these contained only seagrass while two had small amounts of macroalgae. The other two stomachs contained a mixture of different macroalgae.

Patterns in stable isotopes also indicated the possibility that diet varied among individuals, because there was a wide range in the $\delta^{13}\text{C}$ of blood. Separate mixing models were performed for two groups of turtles: those with blood $\delta^{13}\text{C}$ greater than -14‰ , and those with blood $\delta^{13}\text{C}$ less than -14‰ : seagrass was likely the main diet source for both groups with 95% confidence intervals of the contribution of seagrass to diet being 45-100% for individuals with $\delta^{13}\text{C}$ less than -14‰ , and 60-99% for individuals with $\delta^{13}\text{C}$ greater than -14‰ .

The findings for the diet of green turtles are broadly consistent with those of other studies, which have found that they are generally herbivorous and can consume a range of seagrasses and macroalgae (Brand-Gardner et al. 1999; Andre et al. 2006). It is possible that within this population-level generality, there is some individual-level specialization, with at least some individuals consuming very specific diets over a long period (Vander

Zanden et al. 2013). Our stable isotope data is consistent with this hypothesis, but because stable isotope composition of blood reflects relatively short-term diet (days to weeks), it is not conclusive.

4.4 Movement of green turtles

Satellite tagging of green turtles revealed that, while some individuals remained close to where they were captured, others undertook large-scale movements both to the east and west of One Arm Point. Since tagging occurred outside nesting season, these movements are likely to be associated with movements to alternative foraging grounds. Movements of non-nesting turtles up to several hundred kilometers have been documented on the east coast of Australia (Babcock et al. 2015) where animals moved north and south of Gladstone Harbour and established relatively confined home ranges between long distance movements. A similar pattern was observed in the turtles that moved away from One Arm Point with animals moving up to 670 km away before establishing a 50% KUD of less than 12 km² that persisted for months. For all turtles, the average 50% KUD in months where they didn't undertake linear movements > 30 km was 3.1 ± 3.5 km² which is comparable to other studies on green turtles around the world where 50% KUDs have been found to be between 0.18–4.04 km² (Mendonca 1983; Brill et al. 1996; Renaud et al. 1994; Whiting and Miller 1998; Seminoff et al. 2002; Makowski et al. 2006; MacDonald et al. 2012).

Such long-range movements away from a foraging area by animals that are not partaking in courtship or breeding activities are uncommon (Balazs 1980; Limpus et al. 1994; C Limpus pers. comm. March 2015). While it is common for animals to move tens of kilometres between foraging areas (Whiting and Miller 1998) and even between reefs (Gredzens et al. 2014), the scale of movement demonstrated by three of the satellite tagged turtles at One Arm Point has not been previously documented for green turtles on the west coast of Australia. Despite Babcock et al. (2015) demonstrating long distance movement of three satellite tagged non-nesting adult turtles, overall, long-range movements in Queensland are also uncommon with recapture data from Queensland turtle tagging program (tens of thousands of individuals) as well as satellite tracks from more than 60 green turtles tagged along the Queensland coast, only demonstrated one similar case of large-scale movement where a resident adult female turtle, tagged in Moreton Bay, moved to Mon Repos (~320 km by water) and then between Mon Repos and Platypus Bay (~70 km by water) (C Limpus pers. comm.). Gredzens et al. (2014) reported the movement of a “transient” adult female turtle in Torres Strait, however, this individual moved at a much smaller linear scale (approximately 40 km between reefs) than the turtles in the current study.

Given the large tidal range in the Kimberley (up to 11 m) there is likely to be a considerable tidal influence on movement of green turtles. Tidally influenced movement patterns have been found in green turtles tagged with acoustic tags in Gladstone Harbour (Babcock et al. 2015). Data from Gladstone revealed that turtles moved into shallow intertidal seagrass beds with the flood tide and then back into the subtidal channels as water depth over the seagrass became too low. Babcock et al (2015) also demonstrated that while acoustic tags revealed tidal movement, in animals tagged with both acoustic and satellite tags, satellite detections (which only provide far fewer detections per day) did not provide enough detections to adequately demonstrate tidal movement patterns. For green turtles tagged in the current project, the average number of Fastloc detections per day was 7.3 ± 4.9 (\pm standard deviation), which was similar to the average number of daily detections of satellite tagged turtles in Gladstone Harbour (6.1 ± 4.7) suggesting that our ability to interpret tidal movement will be limited by the amount of available data.

Almost all the resident green turtles displayed a high degree of spatial overlap with predicted seagrass presence which is consistent with dietary analysis of turtles in this study. For all animals there were more satellite detections on the periphery of modelled seagrass beds. The ability of carapace mounted satellite tags to obtain Fastloc GPS position estimates is influenced by a range of factors including animal behaviour (e.g. surfacing angle, surface time, level of disturbance), wind strength and direction as well as swell and atmospheric conditions. Babcock et al. (2015) demonstrated that in green turtles tagged with both satellite and acoustic tags, satellite detections resulted in KUDs on the edge of seagrass beds with more overlap of the subtidal channel and bare sand. Acoustic detections from the same individuals revealed repeated use of shallow intertidal seagrass beds

with KUDs centered on seagrass beds. Therefore, the relatively few detections of tagged turtles directly over seagrass beds is potentially due to behavioural differences while animals are feeding on seagrass, incorrect seagrass distribution maps, or animals feeding on a variety of benthic algal resources. The evidence of high contribution of seagrass to green turtle from both stomach content and stable isotope analysis suggests that the most plausible reason is a combination of fewer detections while animals were feeding over seagrass beds and an inability of the seagrass distribution model to incorporate all seagrass. Visual observations of seagrass suggest the hyperspectral imagery and associated model align with areas of high seagrass density, however in deeper areas or areas with sparse coverage of species such as *Halophila* spp. the model is not a good reflection of likely seagrass presence.

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