Sargassum blooms in the Caribbean alter the trophic structure of the sea urchin *Diadema antillarum*

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Abstract

The recent arrival of large masses of drifting *Sargassum* has caused changes in the natural dynamics of Caribbean coastal ecosystems. Atypical and massive mats of *S. fluitans* and *S. natans* with exceptional accumulations ashore were observed in the summer of 2015. This study ~~provides a trophic sketch using~~uses stable isotopes to assess ~~for~~ the impact ~~of generated by~~ *Sargassum* blooms on the ~~natural flow of the trophic structure in~~trophic dynamics of the *Diadema antillarum* urchin, a keystone herbivore ~~one of the main~~on many Caribbean reefs~~sea urchin species~~. Bayesian models were used to estimate the variations in the relative proportions of carbon and nitrogen of assimilated algal resources. At three lagoon reef sites, the niche breadth of *D. antillarum* was analysed and compared under massive influx of drifting *Sargassum* spp. *vs* no influx of *Sargassum* blooms. The effects of the leachates generated by the decomposition of *Sargassum* led to hypoxic conditions on these reefs and reduced the taxonomic diversity of macroalgal food sources available to Diadema ~~modified the organic matter in the environment, with negative consequences in the benthic trophic structure~~. Our trophic data support the hypothesis that the processes of assimilation of carbon and nitrogen were modified limiting the

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natural herbivory of *D. antillarum*. The Stable Isotopes Analysis in R (SIAR) indicated that under the influence of *Sargassum* blooms certain assimilated algal resources (*Dictyota*, *Halimeda* and *Udotea*) were higher because of the limiting available resources. The Stable Isotope Bayesian Ellipses in R (SIBER) analysis suggested a reduction in trophic niche particularly in a protected reef lagoon.

Keywords: Echinoids, pelagic macroalgae, stable isotopes, trophic ecology, coral reefs; Niche breadth, Mexican Caribbean.

Introduction

The arrival of massive amounts of pelagic *Sargassum* spp. has caused changes in the natural benthic dynamics of Caribbean coastal ecosystems for the last eight years (Gower, Young & King, 2013; Schell, Goodwin & Siuda, 2015). Pelagic *Sargassum* is a complex of two species, namely *S. fluitans* and *S. natans* (Oyesiku & Egunyomi, 2014). The Mexican Caribbean shores ~~have~~ faced atypical massive mats of pelagic *Sargassum* in the summer of 2015 (van Tussenbroek et al., 2017; Cuevas, Uribe-Martínez & Liceaga-Correa, 2018) and almost all of 2018. Several studies revealed that these atypical massive mats of *Sargassum* have a new possible distribution source different to the historic North Atlantic Recirculation Region (NARR) known as "The Sargasso Sea" (Schell, Goodwin & Siuda, 2015). The massive influx on the Caribbean shores has~~ve~~ its most likely explanation of new origin in the North Equatorial Recirculation Region (NERR) (Johnson et al., 2013; Schell, Goodwin & Siuda, 2015).

High oceanic temperatures and nutrient inputs (Franks, Johnson & Ko, 2016; Wang et al., 2018), among other oceanographic coupled patterns like changes ~~in patterns~~ of surface currents are the probable cause of a new region of *Sargassum* flourishment (Johnson et al., 2013; Gower, Young & King, 2013; Sissini et al., 2017).

Since 2011, extensive masses of *Sargassum* appeared in unusual ways in oceanic waters off northern Brazil (De Széchy et al., 2012; Sissini et al., 2017), along the West Indies and Caribbean coasts (Gower, Young & King, 2013) from Trinidad to the Dominican Republic (Rodríguez-

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Martínez, van Tussenbroek & Jordán-Dahlgren, 2016; van Tussenbroek et al., 2017), and along the west African coast from Sierra Leone to Ghana (Smetacek & Zingone, 2013).

During 2015 the accumulation reached up to 2.4 m^3 per linear meter of beach (Rodríguez-Martínez, van Tussenbroek & Jordán-Dahlgren, 2016). Changes in habitat structure ~~of the original habitat~~ can directly influence~~s directly on~~ trophic dynamics (Hunter & Price, 1992; Sweatman, Layman & Fourqurean, 2017), have been shown to cause~~with~~ synergistic effects on coral reefs (Smetacek & Zingone, 2013). ~~such as the~~ For example, ~~Harmful~~ harmful macroalgae blooms ~~that~~ have been recognized as drivers of degradation in coral reef habitats (Lapointe et al., 2005) and have effects on the diversity of reef biota (Bauman et al., 2010; Louime, Fortune & Gervais, 2017), like variations in the sea urchin populations (Lapointe et al., 2010). The decomposition of the *Sargassum* biomass that reached the coast is a disturbance agent that can modify the physical, physiological and ecological processes in near-shore coral reef communities. The modified flow of carbon and nitrogen by this disturbance could have adverse ~~negative~~ effects at different scales. *Sargassum* disturbance, coupled with the pre-existing threat on coral reefs, add to the drivers of Anthropocene reef~~s~~ degradation (Alvarez-Filip et al., 2011; Cramer et al., 2012). The massive decomposition of *Sargassum* is a disturbance that can alter the ecological processes in near-shore coral reef communities (Arellano-Verdejo, Lazcano-Hernandez & Cabanillas-Terán, 2019). The main detrimental effect would be on the trophic chain of the benthic communities, but the negative effects would ~~be~~ also act on tourism and local fisheries (Ferreira et al., 2009; Solarin et al., 2014; Louime, Fortune & Gervais, 2017; Cuevas, Uribe-Martínez & Liceaga-Correa, 2018). The effect of *Sargassum* and their leachates on the diet of D. antillarum can improve our understanding on the impact on trophic ecology of one of the most important sea urchins of the Mexican Caribbean.

Evaluating consumers and resources through a trophic approach by tracking the relationships between consumers and prey provides relevant information on the trophic structure and dynamics of a benthic community (Minagawa & Wada, 1984; Vanderklift, Kendrick & Smit, 2006; Behmer & Joern, 2008). Stable isotopes of Carbon ($\delta^{13}C$) and Nitrogen ($\delta^{15}N$) have been used in marine ecosystems to determine the feeding habits of species (Peterson & Fry, 1987), nutrient migrations within food webs, the trophic position of organisms and their contribution at all trophic levels (Vander Zanden & Rasmussen, 1996). It is also possible to trace the origin and transformation of

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the ingested organic matter and also to detect changes in the trophic positions of organisms that coexist in the same habitat (Hobson, 1999; Vanderklift, Kendrick & Smit, 2006; Rodríguez-Barreras et al., 2016).

Stable carbon and nitrogen isotope ratios provide time-integrated information regarding feeding relationships and energy flow through food webs (DeNiro & Epstein, 1981; Peterson & Fry, 1987; Vander Zanden & Rasmussen, 2001). Moreover, stable isotopes can be used to study the trophic niche breadth(?) of a species (Bearhop et al., 2004; Parnell et al., 2010; Phillips et al., 2014) which is directly influenced by consumers and resource input, providing quantitative information, so it can be treated as a niche for isotopic ecology as defined by Newsome et al. (2007) and Boecklen et al. (2011). Stable isotope analyses are useful for assessing the health of ecosystems because it is possible to associate consumers ~~-~~ trophodynamics and niche width with habitat disturbances (Layman et al., 2007b; Hamaoka et al., 2010) ~~and to study the trophic ecology of species with foraging habits like sea urchins (Tomas et al., 2006; Vanderklift, Kendrick & Smit, 2006; Prado, Alcoverro & Romero, 2010; Rodríguez-Barreras et al., 2016)~~. It is also possible to detect changes in the trophic spectrum in the event of anthropogenic impacts or unusual conditions that cause a shift in the ecosystem (Wing et al., 2008; Prado, Alcoverro & Romero, 2010; Tomas, Box & Terrados, 2011; Cabanillas-Terán et al., 2016). Under this view of the massive arrival of pelagic macroalgae, sea urchins are a good model to understand the variability in the benthic trophic chain, as they are considered generalist consumers with a plastic feeding habit (Lawrence, 1975; Vanderklift, Kendrick & Smit, 2006). Echinoids have the capability to modify the community structure through foraging behavior (Carpenter, 1986; Hay & Fenical, 1988; Sala et al., 1998; Eklöf et al., 2008). The main reason to focus this study on *D. antillarum* is that this species is and was the major shallow-hard-bottom grazer in our study sites. (Jorgensen, Espinoza-Ávalos & Bahena-Basave, 2008; Jordán-Garza et al., 2008). The relative position of $\delta^{13}C$ vs $\delta^{15}N$ echinoids displayed in a bi-plot can give insights about organism responses to niche shifts, diet variability and habitat modification (Layman et al., 2007a,b, 2012; Sweatman, Layman & Fourqurean, 2017).

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~~Zanden & Rasmussen, 1996). It is also possible to trace the origin and transformation of the ingested organic matter and also to detect changes in the trophic positions of organisms that coexist in the same habitat (Hobson, 1999; Vanderklift, Kendrick & Smit, 2006; Rodríguez-Barreras et al., 2016).~~

~~Stable carbon and nitrogen isotope ratios provide time integrated information regarding feeding relationships and energy flow through food webs (DeNiro & Epstein, 1981; Peterson & Fry, 1987; Vander Zanden & Rasmussen, 2001). Stable isotopes moreover can be used to study the trophic niche of a species (Bearhop et al., 2004; Parnell et al., 2010; Phillips et al., 2014) which is directly influenced by consumers and resource input, providing quantitative information, so it can be treated as a niche for isotopic ecology as defined by Newsome et al. (2007) and Boecklen et al. (2011).~~

The overarching aim of this study was to determine the variations in the relative proportions of carbon and nitrogen of assimilated algal resources and the niche breadth of *D. antillarum* under massive influx of drifting *Sargassum* spp. vs no influx of *Sargassum* blooms at back reefs. We also aimed to determine whether pelagic *Sargassum* was a substantial source of energy for *D. antillarum*.

The approach used was to compare the $\delta^{15}N$ and $\delta^{13}C$ values before and after the influx of Sargassum ~~and~~ to track changes in the ~~depict the~~ trophic ecology of *D. antillarum* (diet and trophic position) ~~based on the evidence that $\delta^{15}N$ and $\delta^{13}C$ are strongly influenced by their food resources (Phillips et al., 2014), and the relative position in δ13C vs δ15N bi-plot from consumers displays information about food web structure (Layman et al., 2012), and provides providing consumer´s responses to niche shifts and source variations (Layman et al., 2007b).~~ Hence, our hypotheses were that a significant change in the available algal sources and a shift on the trophic structure were expected as a result of the *Sargassum* subsidy.

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Material & Methods

Study sites

We determined the stable isotopes of carbon and nitrogen of *D. antillarum* at three reef lagoons with different distances from the beach to the reef crest and strategies for managing Sargassum influx (figure 1).

Mahahual (18°42'16.96"N 87° 42.619'W) is located in the northern part of the Mesoamerican Barrier Reef System in the state of Quintana Roo (MBRS). Mahahual is a former fishing village but during the last two decades has undergone reef degradation due to anthropogenic impact (Martínez-Rendis et al., 2016). It has a narrow reef lagoon (230-450 m).~~with restrictive circulation~~ *Sargassum* management in this locality was active through removing it out of beach and its *ex situ* disposition.

Xahuayxol (18°30'21.78"N; 87°45'24.84"W) has a larger reef lagoon than Mahahual, 300 to 500 m from the beach to the reef crest, ~~active circulation and higher algal masses by the coastal dynamics that apparently accumulated them gradually. However,~~ *Sargassum* was not removed from the beach (at least not in a systematic way) and remained accumulated on the shore. Xahuayxol is located south of Mahahual.This reef is the northern limit of the Marine Protected area Parque Nacional Arrecifes de Xcalak (PNAX) and human activities are less important than in Mahahual (Schmitter-Soto et al., 2017).

Xcalak (18°14'7.68"N; 87°50'1.46"W), at the southern limit of the Mexican Caribbean, is part of PNAX since 2000. It is also part of the Mesoamerican Barrier Reef System, MBRS (Hoffman, 2009). It has a wide reef lagoon (950-1200 m) ~~with active circulation~~, and *Sargassum* was accumulated in large amounts. There was an active but less intense and localized *Sargassum* management and its final disposal was *in situ* (on the highest part of beach).

The main strategy implemented by local authorities at some beaches with massive arrival of macroalgae, included the removal and its disposal in the highest part of the beach or in places destined *ex profeso*, but the *Sargassum* removal was not quantified and the information about that included here is only preliminary.

At all sampled sites, reef lagoon circulation from wave action ~~because of wave breaking~~ is the dominant forcing mechanism within many wave-exposed reef systems (Mariño-Tapia et al., 2011). ~~and d~~During the period from June to August in our study area, the wave orbital velocity is

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over the threshold of motion (Maldonado-Sánchez et al. 2019), indicating active circulation in the reef lagoons.

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Collecting and processing data

This study covers two periods: Under *Sargassum* effect (USE) during the months of July-August 2015 and without *Sargassum* effect (WSE) in July-August 2016. USE sampling for stable isotope analysis included drifting *Sargassum* (mixture of S. *fluitans* and S. *natans*), turf associated to pelagic *Sargassum*, benthic macroalgae, local turf and 19 individuals of *D. antillarum*. WSE Sampling included benthic macroalgae, local turf and 15 individuals of *D. antillarum* (see sampling details ST1). Samples sizes –were– based –on –previous– studies– (Rodríguez, 2003; Tomas et al., 2006; Wing et al., 2008; Rodríguez-Barreras et al., 2016). The sampling sites were at coastal lagoons in the back reef zone (Section c, Fig. 2), zone with no visible presence of *Sargassum* leachates (van Tussenbroek, et al. 2017) and where *D. antillarum* is distributed (Steneck & Lang, 2003; Jorgensen, Espinoza-Ávalos & Bahena-Basave, 2008; Jordán-Garza et al., 2008; Maldonado-Sánchez, 2018).

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USE measurements

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USE included measurements of dissolved oxygen (mg l^{-1}) recorded with a calibrated Multi-parameter water quality checker HORIBA 50 at Mahahual, Xahuayxol and Xcalak. Measurements of dissolved oxygen were made at points distributed in three sections from areas with decomposing *Sargassum* spp. (section a), leachates (section b -dark brown water-) and reef lagoon areas without *Sargassum* leachates (section c) (figure 2).

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Pelagic *Sargassum* spp., turf (benthic turf and the associated turf to pelagic *Sargassum*) and macroalgae samples were collected in coral reef patches of section c (back reef zone) for each sampling site.

USE and WSE measurements

We collected algal samples to obtain biomass, and for stable isotope analysis using nine quadrats (50 x 50 cm) per site. Pelagic *Sargassum* biomass was calculated based on sunken thalli and

overlaid on reef substrates inside the quadrats. The quadrats were located randomly within the sea urchin habitat (radius of 15 m from collected echinoids). The substrate inside each quadrat was scrapped, carefully removed, collected in bags, and frozen for later analysis.

Macroalgae were identified according to Littler and Littler (2000). Analysis were performed to genus level. For biomass estimates samples were dried for 48 h in an oven at 60ºC. Samples were weighed with a digital balance (standard error =0.0001 g). To determine *D. antillarum* differential algae assimilation considering USE and WSE, algae samples were pooled per site. The sampled echinoids and algal species for this study are not threatened. The collection permit was obtained from the CONAPESCA (PPF/DGOPA-002/17).

The collected individuals of *D. antillarum* were at the same depth range (1.5-2.5 m) and only individuals greater than 5.0 cm in test diameter were collected to avoid any ontogenic effect. Samples were frozen shortly after collection and processed later at the laboratory. The muscles of Aristotle's lanterns were carefully removed and washed from the stomach contents to estimate algal assimilation by *D. antillarum* because this tissue offers a time-integrated measure of carbon and nitrogen assimilated sources (Polunin et al., 2001; Ben-David & Schell, 2001; Phillips & Koch, 2002).

Macroalgae and local turf, pelagic *Sargassum* species (*S. fluitans* and *S. natans*), turf associated to pelagic *Sargassum*, and echinoids muscle samples were rinsed with filtered water, dried at 50º C during 48 h, grounded to a fine powder and placed in glass vial for isotope analyses. To remove carbonates from some algal species (eg. *Halimeda* spp. *Penicillus* spp. etc), the samples were washed with diluted HCl at 1 N prior to drying to avoid disturbance in the mass spectrometer reading.

A subsample of each algae and muscle (1mg) was taken to evaluate the $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios using a Delta V Plus Mass Spectrometer. Catalyzers silvered cobaltous/cobaltic oxide and chromium oxide were used. Carbon and nitrogen samples were analysed in a dual isotope mode at the Centro Interdisciplinario de Ciencias Marinas from Instituto Politécnico Nacional. Isotope samples were loaded into tin-capsules and placed in a 50-position automated Zero Blank sample carousel on a COSTECH 4020 elemental analyzer. The carbon and nitrogen isotopic results were

expressed in standard delta notation relative to Vienna Pee Dee Belemnite (VPDB) and to atmospheric air.

$$\delta 13_C = \left[\left(\frac{\left(\frac{13_C}{12_C}\right) Sample}{\left(\frac{13_C}{12_C}\right) Standard} \right) - 1 \right] \times 1000\ (‰)$$

and

$$\delta 15_N = \left[\left(\frac{\left(\frac{15_N}{14_N}\right) Sample}{\left(\frac{15_N}{14_N}\right) Standard} \right) - 1 \right] \times 1000\ (‰)$$

The standard deviations of $\delta^{13}C$ and $\delta^{15}N$ replicate analyses were estimated; the precision values were 0.2‰ for carbon and nitrogen isotope measurements. In addition, we calculated the trophic level (TL) according to Hobson and Welch (1992) for every individual of *D. antillarum* in each site, expressed as:

$$\mathrm{TL} = \frac{1 + (\mathrm{Nm} - \mathrm{Nb})}{\mathrm{TEF}}$$

Where Nm is the mean $\delta^{15}N$ ratio of each sea urchin, Nb is average basis $\delta^{15}N$ value of the algal community, and TEF is the given value for the trophic enrichment factor (TEF). We assumed a TEF of 2.4 following Moore and Semmens (2008).

Data analysis

The relative contribution of algae to the diet of the sea urchins *D. antillarum* was estimated with a Bayesian isotopic mixing model (SIAR, Parnell & Jackson, 2013), which included the isotopic signatures, fractionation and variability to estimate the probability distribution of the contribution of the food source to a mixture. This procedure supplied accurate information about the contribution of algal species to the sea urchin tissues, as it provided the proportion for every source and recognized the main sources as important components of the diet under different circumstances (Peterson, 1999; Fry, 2006; Wing et al., 2008). To run the model, the isotopic discrimination factor values used were 2.4±1.6 ‰ (mean ± SD) for $\delta^{15}N$, and 0.4±1.3 ‰ (mean ±

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SD) for $\delta^{13}C$ (Minagawa & Wada, 1984; Fry & Sherr, 1989; Moore & Semmens, 2008; Cabanillas-Terán et al., 2016).

The following algal taxa/groups were ~~pooled~~ considered for the mixing models analysis, *Caulerpa*, *Codium*, *Dictyota*, *Halimeda*, *Laurencia*, *Lobophora*, *Padina*, *Penicillus*, *Sargassum polyceratum*, *Stypopodium*, turf, and *Udotea* ~~with the exception of the morpho-functional group turf~~. The sources for the model were selected following the theoretical geometric assumptions of the mixing model according to Phillips et al. (2014) and Rodríguez-Barreras et al. (2015) to ensure reliable resources. Samples of *D. antillarum* did not require lipid extraction since C:N ratios of Aristotle lantern's muscle were lower than 3.5 (Post et al., 2007).

We performed a comparison USE and WSE between the niche width and overlap for *D. antillarum* by using Stable Isotope Bayesian Ellipses in R (SIBER) (Jackson et al., 2011) from the SIAR package (Parnell & Jackson, 2013). This procedure performs metrics based on ellipses and provides the standard ellipse corrected area (SEAc) used as the trophic niche breadth and the overlap between ellipses, presuming that values close to 1 exhibit a higher trophic overlap. Models were run with 200 000 iterations and a burn in of 50 000.

~~Prior to the statistical analyses, t~~The homogeneity and normality of variance were tested by performing a Kolmogorov-Smirnov and a Cochran's test (Zar, 1999). Nitrogen data followed the premises of parametric analysis, but the carbon data and biomass required a power transformation for reaching normality and homogeneity of variance (Box & Cox, 1964). We ran two-way ANOVA using the functions aov and glm from the Gaussian family to test the differences on the isotopic ratios of carbon and nitrogen values to compare the effect (WSE and USE) between sites and their interaction. Statistics were performed with ~~a~~ $\alpha < 0.05$ (R Core Team, 1.0.153, 2017).

Results

The dissolved oxygen values USE indicated that the effects of the leachates generated by the decomposition process, together with the organic material carried in their vegetal structures, ~~modified the~~reduced the values of dissolved oxygen in the benthic ecosystem~~, with negative consequences in the benthic structure~~. The reef lagoons of Mahahual, Xahuayxol and Xcalak displayed dissolved overall oxygen values ranged from 0.67mg l^{-1} at Xahuayxol to 7.05 mg l^{-1} at Xcalak. The overall values of dissolved oxygen displayed the lowest concentrations for section a

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near the shoreline (Figure 3). The lowest mean value was exhibited in Xcalak (1.0 ± 0.1mg l^{-1}) and higher values beyond offshore section c. The highest mean value was displayed for Xcalak (4.7 ± 0.4mg l^{-1}).

Analysis of macroalgal $\delta^{15}N$ and $\delta^{13}C$

Prior the stable isotope analysis was carried out, macroalgal biomass per site was considered to have additional information about the reliable sources used for the resources contribution to *D. antillarum*. Biomass data for benthic taxa displayed no significant differences between USE and WSE ~~*per effect*~~, but significant differences were found among localities (ANOVA, df=2, F=8.24, p<0.0001). Mahahual had the highest mean benthic biomass values (55.2 dry weight m^{-2}) followed by Xahuayxol with (38.8 dry weight m^{-2}) and Xcalak (16 dry weight m^{-2}±). WSE biomass average values for local benthic algae ranged from 3.01 dry weight m^{-2}±0.95 (*Codium* spp. at Xcalak) to 133.50 dry weight m^{-2}±30.29 (*Halimeda* spp. at Mahahual). USE values ranged from 7.75 dry weight m^{-2} ±5.4 (*Caulerpa* at Xcalak) to 145.99 dry weight m^{-2} ± 36.21 (*Halimeda* spp. at Mahahual, Table 1). Genus-level ~~Biomass~~ biomass of pelagic taxa showed no significant differences per site ~~neither at genus level~~, however *Sargassum fluitans* displayed the highest biomass values.

Pre- and with-Sargassum values ~~Based on the established categories WSE and USE~~ significant differences were found in overall benthic algae values of $\delta^{15}N$ (ANOVA, df=1, F=20.27, p<0.0001). Specifically,~~Therefore~~ under *Sargassum* blooms ~~USE~~ most of the algae exhibited isotopic signatures with significantly depleted $\delta^{15}N$ (Table 2).

As for $\delta^{13}C$ USE ratios fluctuated from -21.98 to -9.23‰ and WSE from -20.90 to -5.65‰. Considering only the algae presented in both sampling periods (WSE and USE) there was no significant difference in $\delta^{13}C$ among sites (ANOVA, df=2, F=0.55, p>0.05) neither was significant difference analysing the effect (ANOVA, df=1, F=1.14, p>0.05) and their interaction (ANOVA, df=2, F=0.86, p>0.05).

The overall algal $\delta^{15}N$ (WSE) fluctuated from 0.60‰ to 5.68‰. Xcalak displayed the highest mean value of $\delta^{15}N$ with turf (4.59±0.64 ‰). The overall macroalgal $\delta^{15}N$ (USE) fluctuated from 0.023 to 2.08‰. At Xcalak *Caulerpa* displayed the highest mean values of nitrogen with 2.02 ± 0.08 ‰ (Table 2). Local Turf USE displayed negative values and overall turf values fluctuated

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from -0.97‰ to 0.42‰. Xahuayxol displayed the most negative $\delta^{15}N$ mean value of local turf (-0.51±0.02‰).

USE overall pelagic *Sargassum* $\delta^{13}C$ values fluctuated from -17.95‰ to -15.24‰. *S. natans* exhibited the most negative mean values of $\delta^{13}C$ (-17.44 ±0.71‰) at Mahahual (Table 2). There was no difference in $\delta^{13}C$ among sites (ANOVA, df=2, F=0.05, $p>0.05$) but there were significant differences $\delta^{13}C$ between species (ANOVA, df=2, F=7.57, $p=0.01$). *Sargassum´*s associated turf $\delta^{13}C$ values fluctuated from -18.65‰ to -15.37‰. The most negative $\delta^{13}C$ mean value was displayed at Mahahual (-18.3± 0.5‰) for *Sargassum*'s associated turf.

Overall pelagic *Sargassum* $\delta^{15}N$ values ranged from -2.87‰ to -0.30‰. The less negative mean value was exhibited at Mahahual (-0.53±0.26‰) for *S. fluitans*. There was no significant difference for $\delta^{15}N$ among sites (ANOVA, df=2, F=3.90, $p=0.05$), but there was a remarkable trend to depleted $\delta^{15}N$ at Xcalak where *S. fluitans* displayed the lowest mean values of $\delta^{15}N$ (-2.51±0.52‰). Turf associated to floating *Sargassum* $\delta^{15}N$ values fluctuated from -0.42‰ to -1.17‰. The most depleted $\delta^{15}N$ was exhibited at Mahahual (-1.13±0.05‰) and the less negative mean value was displayed in Xahuayxol (-0.47±0.07‰).

Sea urchins

There were significant differences $\delta^{15}N$ among sites (ANOVA df=2, $F=6.473$, $p=0.005$) and the interaction between site*effect (USE and WSE) showed significant differences (ANOVA, df =2, F=7.321, $p=0.003$).

D. antillarum exhibited no differences among sites for $\delta^{13}C$ values $p>0.05$. However, we found significant differences analysing the USE and WSE effect (ANOVA df=1, F=5.301, $p=0.03$). The isotopic ratios of *D. antillarum* (USE) varied from 3.83‰ to 6.13‰ for $\delta^{15}N$, while $\delta^{13}C$ ranged from -9.41‰ to -13.62‰. Mahahual was the site with the highest average values for $\delta^{15}N$ 5.80 ± 0.30‰, while Xcalak displayed the lowest average value 4.38 ± 0.29‰. The isotopic ratios of *D. antillarum* (WSE) ranged from 4.69‰ to 6.16 for $\delta^{15}N$, while $\delta^{13}C$ fluctuated from -8.83‰ to -13.42‰. We found significant differences for $\delta^{15}N$ for sea urchins between sites (USE, ANOVA, df=2, F=6.47, $p<0.005$). Xcalak showed particularly low values Under *Sargassum* Effect (~~USE~~ average value 4.38 ± 0.29‰ *versus* WSE average value 5.44 ±0.36‰).

Nevertheless, $\delta^{13}C$ exhibited no significant differences although we noticed a negative trend in the values of $\delta^{13}C$ under *Sargassum* effect (USE).

SIAR~~, trophic levels and isotopic niches~~

Mixing models provided evidence for the contribution of different algal resources for three sites USE and WSE (Table 3). SIAR analysis showed that *D. antillarum* behaved as an opportunistic grazer under the *Sargassum* blooms, it is important to notice that there was a reduction of food sources USE. Nevertheless, the species displayed differential resource assimilation and pelagic *Sargassum*, despite of being one of the most abundant available resource, was not the most assimilated resource (Figure 4).

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Caulerpa was the most important resource for *D. antillarum* in Mahahual WSE (up to 37%), followed by Turf (up to 34%) and by *Halimeda* and *Udotea* (up to 29% for both). USE the most important resource was *Halimeda* (up to 44%) followed by *Caulerpa* and *Dictyota* (both up to 31% of contribution) *S. fluitans* and *S. natans* were no important sources (0-28% and 0-23% respectively), and turf associated to *Sargassum* blooms was the lesser assimilated resources by *D. antillarum* from 0 up to 22% (Table 3).

At Xahuayxol WSE *D. antillarum* showed *Caulerpa* was the most important resource for *D. antillarum* (from 2 up to 25%) and for the rest of algae there were very similar algal contribution (from 0 up to 23%). The main macroalgal contributor of USE was *Udotea* with up to 61%, followed by *Halimeda* and *Lobophora* (with up to 35% and 38% respectively) as secondary resources. Turf associated to *Sargassum* blooms showed evidence of low contribution (from 0 up to 21%) and *S. fluitans*, *S. natans* had negligible contribution to *D. antillarum* diet with a maximum of 17% of the proportional contributor (Table 3).

Turf was the main algal resources for *D. antillarum* in Xcalak WSE (up to 45%) followed by *Caulerpa*, *Codium* and *Padina* as secondary resources (close to 30% maximum of contribution); contrasting USE the main macroalgal contributors in Xcalak were *Penicillus* and *Caulerpa* with up to 39% and 40% respectively. Likewise *Dictyota* and *Sargassum polyceratium (*benthic *Sargassum)* were secondary resources up to 26% and 29%, respectively. The pelagic components in the other reef lagoons were negligible contributors for *D. antillarum* diet with just 18-23% of maximum contribution (Table 3, Figure 4).

Trophic Levels

The overall trophic level data for *D. antillarum* ~~(TL)~~ ranged from 1.97 to 3.22. The species exhibited significant differences among sites (ANOVA df=2, F=10.63, *p*=0.0004), also exhibited significant differences between WSE and USE (ANOVA, df=1, F=17.7, *p*=0.0003). Likewise calculating the interaction between site*effect (USE and WSE) there were significant differences (ANOVA, df=2, F=12.65, *p*=0.0001). The highest TL values were reported for Mahahual USE, while the lowest one was recorded in Xahauayxol WSE. At Mahahual TL mean value of *D. antillarum* was 2.35±0.18 WSE and 3.08 ±0.13 USE; at Xahuayxol TL mean value was 2.13±0.30 WSE and 2.49±0.27 USE and at Xcalak TL mean value was 2.62±0.15 WSE and 2.45±0.12 USE (Table 4).

Isotopic Niches

Table 5 shows data on isotopic niche breadth as measured by the corrected standard ellipse area (SEAc). The Stable Isotope Bayesian Ellipses in R (SIBER) analysis suggested a reduction in trophic niche particularly in Xcalak. This site showed the main difference in the trophic niche breadth with SEAc of 3.48 and 0.14 (WSE and USE respectively) overlap of isotopic niches between WSE and USE was found just in Xahuayxol; (Figure 5). SEAc was higher USE in this site with 3.57 versus 2.68 SEAc WSE (Figure 5).

Discussion

Our results provide evidence of the detrimental effect of *Sargassum* blooms ~~over the physical~~ on the physicochemical water properties and ecological processes in near-shore coral reef communities as recently has been shown in our study area (Rodríguez-Martínez, van Tussenbroek & Jordán-Dahlgren, 2016; van Tussenbroek et al., 2017; Cuevas, Uribe-Martínez & Liceaga-Correa, 2018). Particularly, the results give evidence of ~~over~~ the input of external carbon and nitrogen, related to *Sargassum* blooms on ~~towards~~ benthic communities with unfavorable and differential effect for nutrient fluxes in *D. antillarum*. These findings contribute to the growing recognition of the role of exogenous nutrient enrichment in modifying natural sources in a food web. Hence this leads to nutrient limitation of herbivorous sea urchins.

Sargassum onshore exhibit physical processes of fragmentation, decomposition and remineralization by bacteria, meiofauna and grazers (Colombini & Chelazzi, 2003). The algae-derived organic matter, product of that decomposition, has an effect on in situ oxygen availability (Haas et al., 2010). *Sargassum* blooms clearly showed a negative impact by hypoxia conditions

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found at the three studied reef lagoons (Figure 3). This ultimately could drive to the success of the communities' nitrogen fixation. Even in the section c (back reef) dissolved oxygen values for this study were lower than the standard values for coral reefs sites with areas dominated by algae (7.9 ± 0.5 mg l^{-1}) according to Haas et al. (2010) and values of 8.1 to 9.1 mg l^{-1} for Xahuayxol and Mahahual, respectively recorded by (Camacho-Cruz et al., 2019). This agrees with Kendrick et al. (2000) and Haas et al. (2010), who argued that benthic communities linked to reef lagoons are very susceptible to environmental degradation despite fluctuations in dissolved oxygen. ~~Oxygen is a critical element that structures benthic coral reef habitats (Nelson & Altieri, 2019).~~ ~~Oxygen is a critical element that structures can be structuring in benthic coral reef habitats (Nelson & Altieri, 2019).~~ Some benthic algae can be catalyzers of physical environment in reefs due to coral reef associated algae-derived organic matter (Wild et al., 2010). We considered that is likely that USE potentially lead to phase shifts in organic matter cycles, caused by changes in the oxygen dynamics, which were consistently reflected in the low isotopic signatures of the primary producers.

Isotopic variations in the algal resources

We found that the composition of benthic macroalgae assemblages were different before and with Sargassum~~between among both conditions (WSE and USE)~~. Sargassum ~~USE~~ conditions showed a clear reduction of algae composition and isotope values presented by clearly lower $\delta^{15}N$ values (Table 2). The fact that there were fewer available algal sources in the USE condition implies that the trophic chain becomes less complex as the interaction of primary consumers with their resources is reduced (Phillips & Gregg, 2003).

Overall $\delta^{13}C$ values ranged from -21.98 to -5.65‰ and agreed with the ranges reported by Fry & Sherr (1984). Those authors reviewed the $\delta^{13}C$ data of benthic algae, noting that values ranged between -30 and 5‰. $\delta^{15}N$ overall algae values fluctuated from 0.023 to 5.68‰. Despite these values agree with the variation reported in other studies like Owens (1987) and France (1995), we found USE very low, ergo according to Lapointe et al. (2005) and France et al. (1998). Lower limit values can be indicative of macroalgae living in oligotrophic reefs which experience N sources as nitrogen fixation. In the presence of *Sargassum*, anaerobic bacteria acquired

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Commented [kc31]: Unclear – do you mean reduction in species richness?

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significance comparable to ~~on~~ other benthic groups (Carpenter & Cox, 1974; Rooker, Turner & Holt, 2006), and could be the cause of the low macroalgal isotopic signatures, while high values of $\delta^{15}N$ of macroalgae are linked to land-based N enrichment sources. These are good indicators of anthropogenic nitrogen inputs ~~like enhancers of coral reef degradation (Umezawa et al., 2002)~~ such as ~~and temporal and spatial drivers of~~ sewage discharges (Risk et al., 2009; Lapointe et al., 2011).

France (1995) reported nitrogen ranges of marine macroalgae from -3 to 18‰. The inconsistencies in this pattern with values of $\delta^{15}N$ close to atmospheric signature of 0% suggest a fixation of nitrogen. Dorado et al. (2012) associated the depleted values of $\delta^{15}N$ with nitrogen fixation and its impact on the trophic position of consumers. So, temporal difference between values in this study WSE and USE might be explained by the influence of organic input derived from floating *Sargassum* dragged components. Although more evidence is required to confirm this statement, but in general, lower limit values of $\delta^{15}N$ in marine macroalgae are indicative of macroalgae living in oligotrophic reefs which experience nitrogen sources as nitrogen fixation. Hence, in the presence of *Sargassum*, the anaerobic bacteria took on importance on the benthos, being responsible for the low macroalgal isotopic signatures.

Trophic parameters of *D. antillarum* ~~**Sea urchin values, SIAR and Trophic level**~~

Our results supported the evidence that *Sargassum* blooms impacted $\delta^{15}N$ differentially among sites, as the ratios of $\delta^{15}N$ and $\delta^{13}C$ are determined by their resources (Phillips & Gregg, 2003). It was conspicuous that ~~the isotopic values of the algae were lower USE, while,~~ *D. antillarum* showed higher $\delta^{15}N$ values USE at Mahahual.

Although some available resources (e.g. *Dictyota* and turf) were present in both conditions (WSE and USE) the contribution of algae to the sea urchin tissues can display key information about how consumers assimilate habitat resources and this could exhibit information on the degree of disturbance (Layman et al., 2007b). So, it is possible that the ecological role of *D. antillarum* was different in each site and could be explained by the variation in the number of available resources and a differential assimilation (Table 3). The higher $\delta^{15}N$ values in the muscle of *D. antillarum* were due to the synergistic effect among the resource availability and the disturbance condition.

Pelagic sources may provide new sources of food and the possible nitrogen fixation carried out

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462 by turf attached to pelagic *Sargassum* undoubtedly brought a new source of organic matter to
463 basal trophic levels (Rooker et al. 2006). However those sources were not major contributors for
464 *D. antillarum* and appear to avoid the invasive pelagic macroalgae. This is consistent with the
465 feeding ecology by marine generalist herbivores (Boudouresque & Verlaque, 2001) and such
466 feeding response is in line with evidence from other sea urchin species in the face of other
467 invasive resources. The experiments carried out by Tomas et al. (2011) provide evidence that
468 some seaweed invaders were strongly avoided by *Paracentrotus lividus* and therefore escape
469 enemy control by reducing herbivore preference.
470
471 ~~Sea urchins are assumed as predominantly herbivorous with preference to algal turf and~~
472 ~~macroalgae (Macintyre, Glynn & Hinds, 2005). However under low availability of resources any~~
473 ~~other sources can be found in their diet as benthic invertebrates, even corals (Randall, Schroeder~~
474 ~~& Starck, 1964; Reaka-Kudla, Feingold & Glynn, 1996; Muthiga & McClanahan, 2007).~~ The
475 trophic level metric ~~of TL~~ is very useful because the classical ~~classifications that add organisms~~
476 ~~into~~ discrete trophic level definitions ~~s is~~are a reduction that ignores ~~the value of food web~~
477 ~~connections, the~~ omnivory and diet changes (Polis & Strong, 1996; Vanderklift, Kendrick &
478 Smit, 2006). The sea urchin *D. antillarum* has been considered as a generalist herbivore (Ogden
479 & Lobel, 1978; Sammarco, 1980; Solandt & Campbell, 2001; Weil, Torres & Ashton, 2005).
480 However, invertebrate samples in their stomach contents have been described for that species in
481 the Caribbean (Rotjan & Lewis, 2008; Rodríguez-Barreras et al., 2015, 2016).
482
483 The mean ~~TL~~ trophic level for *D. antillarum* exhibited at Mahahual was 2.35±0.18WSE up to
484 3.08±0.13 USE. Hence, WSE agreed with a herbivorous position. USE *D. antillarum* showed that
485 the species can occupy different trophic niches due to resource limitation. Under *Sargassum*
486 blooms, *D. antillarum* performed a position more related to omnivorous conditions, so the
487 estimated trophic level indicated a herbivorous behaviour tending to omnivory according to
488 Vander Zanden & Rasmussen (1999), who stated that primary consumers have a trophic position
489 of 2.0 (strictly herbivorous); but if organisms assimilate primary consumers, they are considered
490 in a TL of 3.0. The results for Mahahual are consistent with Andrew (1989) who argued that sea
491 urchins can take advantage through omnivory if variation exist in the availability of resources.
492 Our results suggest that *D. antillarum* behaves as facultative omnivore related to patterns of

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493 nutrient availability. $\delta^{15}N$ signatures for *D. antillarum* in Mahahual suggest a different carbon
494 source USE, but also anthropogenic nitrogen inputs, which seems coherent as this site has a high
495 eutrophication, being an area with elevated touristic demand (Martínez-Rendis et al., 2016; Arias-
496 González et al., 2017) plus the possible nitrogen fixation by anaerobic bacteria as an important
497 factor in the variation of available sources of food.
498
499 Regarding for the TL values exhibited for *D. antillarum* in Mahahual USE 3.08±0.13 versus
500 2.35±0.18 for WSE would place *D. antillarum* in an omnivorous position tending to carnivory.
501 Similar values were obtained in Mediterranean sea urchins as a strategy to avoid exclusion by
502 sympatric species (Wagensteen et al. 2011). However, we cannot state that *D. antillarum* is
503 carnivorous in Mahahual. This would require a more complete temporal study, and an adjustment
504 of a new $\delta^{15}N$ baseline of primary producers, considering that $^{15}N/^{14}N$ ratios can vary spatially
505 and temporarily (Jennings et al. 1997, Vanderklift et al. 2006).
506
507 The results for Xahuayxol showed also a trend to higher $\delta^{15}N$. However by analyzing the
508 condition of *D. antillarum* in Xahuayxol no significant differences were obtained. We can
509 assume that this locality that least changed in its foraging behavior position against the nutrients
510 modification and the species occupied a lower trophic level WSE. Meanwhile, Xcalak displayed
511 the opposite trend compared to Mahahual and Xahuayxol and USE *D. antillarum* trophic level
512 was lower than WSE. Our results suggest that for Xcalak the effect of *Sargassum* blooms was
513 completely modified and reduced the possibility of finding available resources, displayed a
514 trophic level around 2.5 between the two scenarios of *Sargassum* blooms. This corresponds to a
515 predominantly herbivorous ~~tending~~ to omnivorous condition. Moreover this was confirmed with
516 the isotopic niche breadth data where a reduced niche was observed for Xcalak (Fig. 3).
517
518 The rank found for *D. antillarum* in this study agreed with the study conducted by Rodríguez-
519 Barrras et al. (2015) in Puerto Rico where microinvertebrates were used as source of organic
520 matter by the sea urchin. Finally, TL values found in our results support the premise that
521 echinoids are able to modify their foraging behavior depending on the availability of resources
522 (Randall, Schroeder & Starck, 1964; Muthiga & McClanahan, 2007) and in this case (USE) was
523 not only explained by macroalgae.

It is important to remark that we analysed the most abundant species at the three localities and the most important shallow-bottom herbivore on Caribbean reefs (Carpenter, 1981; Hughes, 1994; Aronson & Precht, 2006; Kissling et al., 2014). One of the most dramatic events in the Caribbean resulted from the pathogen-driven reduction in the populations of *D. antillarum* (Lessios et al., 1984; ~~Cramer et al., 2018~~) with detrimental ecological consequences like coral-algal phase-shifts. The southern part of Quintana Roo is not an exception encompassing with the effects of the abrupt coastal development and watershed pollution as key drivers along the Costa Maya (Arias-González et al., 2017). For the Mexican Caribbean, there has been considerable variation in *D. antillarum* population data. Jordán-Garza et al. (2008) showed a high presence of *D. antillarum* with densities of more than 7 ind m^{-2} in several areas, including our study area. Jorgensen et al. (2008) reported densities of 12.6 nd m^{-2} after hurricane Dean. According to Maldonado-Sánchez (2018) population density of *D. antillarum* displayed <1 ind m^{-2} for five different habitats of the Parque Nacional Arrecifes de Xcalak (PNAX) reef lagoon (back reef, seagrasses, sandy bottoms and reef patches) and the fore reef. The back reef exhibited the highest abundance with an average of 0.5 ind m^{-2}. However for Mahahual, we registered an average density of 0.6 ind m^{-2} (unpublished data), because of the broad variability exhibited from *D. antillarum* populations in the back reef. It is necessary to strengthen the sampling effort to evaluate their population current status. A more comprehensive discussion would have to include the interactions with other herbivore/omnivore species, which coexist in each site and whether, and how they carry out the resource partitioning.

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Isotopic niche breadth

The ellipses provide ~~give us the~~ integrated information on~~of~~ the relationship between the availability of sources and the niche width~~amplitude (the relationship of the consumer with their consumed sources)~~. The results of Mahahual indicated that in USE. *D. antillarum* consumes different carbon and nitrogen sources (Fig.4).

Several studies (Lawrence, 1975; Carpenter, 1981; Sammarco, 1982; Hay & Fenical, 1988) noted that echinoids have the ability to adapt their foraging behavior depending on algae availability as well as their population density and site characteristics (Bak, Carpay & de Ruyter van Steveninck, 1984; Bak, 1994; Alvarado et al., 2016). We observed at Mahahual that USE *D.*

555 *antillarum* exhibited a broader trophic niche than WSE. Despite the limited resources this could
556 lead to trophic overlap and stronger habitat degradation. SIAR results showed a resource shift and
557 this could be explained in terms of omnivory as stated by France et al. (1998) “omnivory is a
558 prevalent attribute of aquatic food webs”.
559
560 The trophic niche of Xahuayxol reflects that there was no difference in the use of carbon and
561 nitrogen sources. It is noteworthy that for the case of Xcalak, the resulting isotopic niche of *D.*
562 *antillarum* was significantly smaller with *Sargassum* effect. This is consistent with the metric that
563 associates smaller niche amplitude with disturbed ecosystems (Layman et al., 2007b).
564
565 **Limitations of the study**
566
567 To assess the effect of differential management of *Sargassum* and to effectively evaluate the
568 effect of the management disposal, quantitative information on the beach disposal would be
569 necessary.
570 It is clear that ~~succession of~~ algae communities were modified due to *Sargassum*. Therefore, the
571 structuring role of sea urchins, and, considering that algae respond to a temporal variability
572 ~~naturally~~, it would be necessary to study changing gradients at different time scales. This would
573 provide us with more conclusive information about the effect of *Sargassum* spp. on the benthic
574 communities.
575
576 Metric values based on an instantaneous characterization of a single food web provide a limited
577 view of the food web. Therefore, ~~in order~~ to evaluate the trophic structure and consequently its
578 functional structure, the most promising evaluations would have to include a comparison of
579 multiple gradients, in order to examine the same food web on a longer temporal perspective. The
580 metrics used in this study allowed us to evaluate the variation of the isotopic signatures that
581 formed the trophic spectrum of *D. antillarum* under two different scenarios.
582 The deposited biomass ~~values~~ regarding to *S. fluitans* and *S. natans* did not include a
583 measurement of the total arrived *Sargassum* blooms. However, our results established a baseline
584 of the amounts that were more available for the echinoids, which inhabit in the back section of
585 the Caribbean shallow reefs.

It would be challenging to evaluate the ecological role of other coexisting species (*Echinometra viridis*, *E. lucunter* and *Eucidaris tribuloides*), and to include samples of micro-invertebrates. This could offer new clues to the connectivity between sympatric species, including trophic loops and successional states of algal communities (Camus, Daroch & Opazo, 2008) within the benthic communities of coral reefs.

Conclusions

The present study provides a first look how trophic parameters of *D. antillarum* were modified by the impact of pelagic *Sargassum* blooms in the Caribbean. The results indicated that the effects of the leachates generated by the decomposition process, the input of organic material and deposition in its vegetal structures modify the organic matter in the environment and hence the isotopic signatures. This has negative consequences in the benthic trophic structure, limiting the natural herbivory of *D. antillarum*. The source of available carbon and nitrogen was modified, and the isotopic signatures of macroalgae associated with the reef sites exhibited significantly lower values of $\delta^{15}N$. Consequently the trophic niches were changed and in the case of Xcalak, significantly reduced. However, feeding behavior preferences in *D. antillarum* was not driven by pelagic macroalgae masses.

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