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Severe impacts of brown tides caused by *Sargassum* spp. on near-shore Caribbean seagrass communities

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ABSTRACT

From mid-2014 until the end of 2015, the Mexican Caribbean coast experienced a massive influx of drifting *Sargassum* spp. that accumulated on the shores, resulting in build-up of decaying beach-cast material and near-shore murky brown waters (Sargassum-brown-tides, Sbt). The effects of Sbt on four near-shore waters included reduction in light, oxygen (hypoxia or anoxia) and pH. The monthly influx of nitrogen, and phosphorus by drifting *Sargassum* spp. was estimated at 6150 and 61 kg km^{-1} respectively, resulting in eutrophication. Near-shore seagrass meadows dominated by *Thalassia testudinum* were replaced by a community dominated by calcareous rhizophytic algae and drifting algae and/or epiphytes, resulting in 61.6–99.5% loss of below-ground biomass. Near-shore corals suffered total or partial mortality. Recovery of affected seagrass meadows may take years or even decades, or changes could be permanent if massive influxes of *Sargassum* spp. recur.

From 2011 until 2016, the Caribbean Sea experienced an unprecedented massive influx of drifting *Sargassum* spp. consisting of the species *Sargassum fluitans* and *S. natans* (Franks et al., 2011; Smetacek and Zingone, 2013). Both species had been reported before for the Caribbean Sea, but in low abundances and at irregular intervals (Suppl. Table 1), and their arrival was possibly due to seasonal export from the Sargasso Sea in the NW mid-Atlantic; known as the Sargasso Loop System (Frazier, 2014). However, during 2011, there was an ocean-scale accumulation of drifting *Sargassum* spp. that by 2012 extended throughout the North Atlantic Recirculation Region (NARR, Johnson et al., 2013; Smetacek and Zingone, 2013; Oyesiku and Egunyomi, 2014). The origin of the new massive influx of *Sargassum* spp. into the Caribbean Sea was most likely not directly related to the Sargasso Sea (Franks et al., 2011; Sissini et al., 2017), but to an area off the coast of Brazil fed by *Sargassum* spp. that had bloomed in the NARR (Gower et al., 2013; Johnson et al., 2013; Franks et al., 2016; Sissini et al., 2017). Unusually large quantities of drifting *Sargassum* spp. started to arrive at the Mexican Caribbean coast in 2014, but the influx was especially massive during 2015.

Smetacek and Zingone (2013) used the term "golden tides" for drifting masses of *Sargassum* spp., due to their brown-yellow color that resembles gold. In the open ocean, this seaweed provides habitat for fish, invertebrates, sea turtles and seabirds, and it serves as spawning and nursery areas for many organisms, some of commercial importance (Laffoley et al., 2011; Pendleton et al., 2014). However, beaching of massive quantities of drifting *Sargassum* spp. resulted in a build-up of decaying beach-cast material that colored the usually clear near-shore waters murky brown, due to leachates and organic particles. Golden tide does not apply to these decayed masses washed ashore; therefore, we prefer the term Sargassum-brown-tide (Sbt) when near-shore coastal waters are affected by the massive onshore build-up of seaweed.

During peak times of beaching of *Sargassum* spp. to the Mexican coastline in July and August 2015, on average 9726 m^3 of seaweed accumulated per month per km of coastline (Rodriguez-Martínez et al., 2016). During this time, over 4400 workers were employed to remove the seaweed from the sections of beach important for tourism; however, ~90% of the coastline was not considered to be essential for the tourist industry, and there the beach-cast seaweed was not removed (Rodriguez-Martínez et al., 2016). When left onshore, the masses of decayed algae on the beaches affected human health and the tourist industry (Doyle and Franks, 2015; Rodriguez-Martínez et al., 2016). In addition to economic and health hazards, the decaying algal masses

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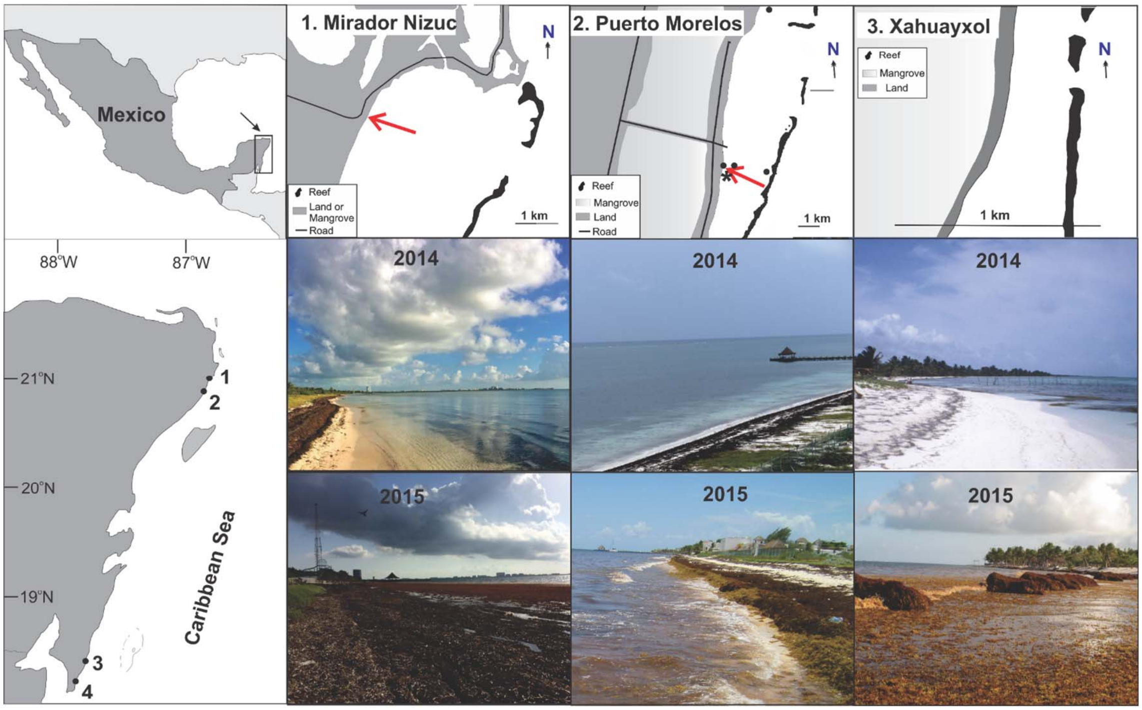

Fig. 1. Map indicating study sites: 1 Mirador Nizuc, 2. Puerto Morelos, 3. Xahuayxol, 4. Xcalak. Detailed maps are given for three of the four sites (general setting at site 3 and 4 were alike); arrows in detailed maps 1 and 2 indicate the position of the studied seagrass meadows, water quality was determined throughout the area of detailed of site 3 and 4. Photos of the coasts before (darker areas in the sea are seagrass meadows) and during the Sargassum-brown-tide (Sbt) in 2015 are also presented. *Position of coral monitoring site, •Positions of stations monitored for K_d and nutrient availability after 1 year. Note differences in scales of the detailed maps.

Table 1
Summary of general site information and types of measurements taken at these sites. Wilma: hurricane Wilma (Oct. 2005, force 4), Sbt Sargassum-brown-tide, At Sites 3 and 4, measurements were always made throughout the reef lagoon. [a]At Site 2, 1 year after Sbt, water transparency and C, N, P content in *T. testudinum* were measured at 3–4 stations throughout the reef lagoon. ORP oxidation/reduction potential, B-B Braun-Blanquet estimation of abundance, ND not determined. See Suppl. 1 for details on the methods used at each site.

	Site 1	Site 2		Site 3	Site 4
	Mirador Nizuc	Puerto Morelos	Puerto Morelos	Xahuayxol	Xcalak
		Zone 1	Zone 2		
General information					
Position	21°01′32″N 86°48′40″W	20°52′03.6″N 86°52′01.8″W	20°52′03.3″N 86°52′01.1″W	18°30′00″N 87°45′30″W	18°16′20″N 87°50′00″W
Depth of affected area	0.1–2.5 m	0.5–2.0 m	2.0–3.0 m	0.1–0.6 m	0.1–0.7 m
Exposure	Wave-protected	Moderately exposed	Moderately exposed	Wave-protected	Wave-protected
Impacted by Wilma	Not visibly	Severely (Zone 1)	Not visibly	Not visibly	Not visibly
Sbt period	July 2015–May 2016	July–Oct 2015	July–Oct 2015	April–Summer 2015	April–Summer 2015
Measurements environment					
Illuminance	ND	ND	Before Sbt (Feb. 2013) Before Sbt (Jun. 2015)	ND	ND
Oxygen	ND	ND	During Sbt (Aug. 2015)	During Sbt (Aug. 2015)	During Sbt (Aug. 2015)
pH		ND	During Sbt (Aug. 2015)	During Sbt (Aug. 2015)	During Sbt (Aug. 2015)
ORP				During Sbt (Aug. 2015)	During Sbt (Aug. 2015)
Organic content of sediment	ND	Before Sbt (Feb. 2013) After Sbt (Oct. 2016)	Before Sbt (Feb. 2013) After Sbt (Oct. 2016)	ND	ND
$\delta^{15}N$ in seagrass and algae	ND	ND	Before Sbt (Feb. 2013) Before Sbt (June 2015) After Sbt (Oct. 2015)	ND	ND
Water transparency[a]	ND	ND	1 year after Sbt (Sep. 2016)	ND	ND
C, N, P content in *T. testudinum*[a]	ND	ND	Before Sbt (2010–2014) 1 year after Sbt (Sep. 2016)	ND	ND
Measurements seagrass community					
Transects (B-B)	Before Sbt (Nov. 2008) After Sbt (May 2016)	ND	ND	ND	ND
Biomass	Before Sbt (Nov. 2008) After Sbt (May 2016)	ND	Before Sbt (Feb. 2013) After Sbt (Oct. 2015)	ND	ND
Density	ND	Before Sbt (Feb. 2013) Before Sbt (June 2015) After Sbt (Oct. 2015)	Before Sbt (Feb. 2013) Before Sbt (June 2015) After Sbt (Oct. 2015)	ND	ND
Coral mortality	ND	ND	Before Sbt (Aug. 2013) After Sbt (Aug. 2016)	ND	ND

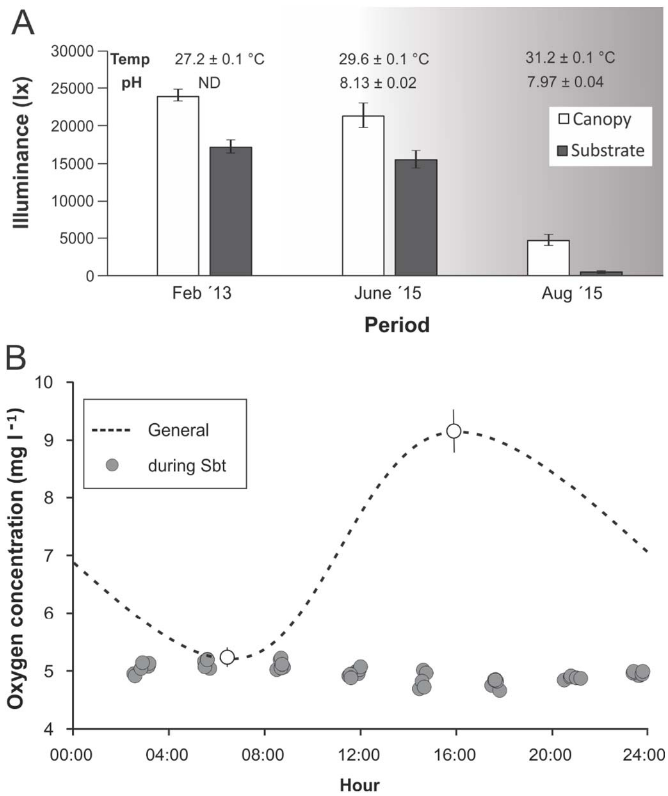

Fig. 2. Environmental conditions at Puerto Morelos. A. Average (± SE) illuminance just above the seagrass canopy (canopy) and at the level of the sediment (substrate). The average (± SE) temperature and pH (measured during 24 h) is indicated above the bars. The shaded area indicates approximate period of the Sargassum-brown-tide. B. Oxygen concentration during Sbt (8–12 August 2015) above the seagrass zone 2 at Puerto Morelos. General: Oxygen concentration above a seagrass bed in Puerto Morelos adapted from minimal and maximal values by Haas et al. (2010) measured during July–August 2008.

Table 2
Sediment (% organic matter of Dry Weight) and nitrogen (%N DW and $\delta^{15}N$ in plant tissues) conditions before and after Sargassum-brown-tide (Sbt) at Puerto Morelos, Mexico. $N = 4$ for sediments, and $N = 3$ for plant tissues. Values are average ± 95% C.I. *T. testudinum*: *Thalassia testudinum*, *H. incrassata*: *Halimeda incrassata*.

	Before Sbt	Just before Sbt	After Sbt
	Feb. '13	June '15	Oct. '15
Zone 1			
Sediment organic matter (%)	0.28 ± 0.30	–	9.74 ± 1.72
Zone 2			
Sediment organic matter (%)	1.03 ± 0.36	–	14.49 ± 4.30
T. testudinum - % N	1.30 ± 0.09	–	2.26 ± 0.06
H. incrassata - % N	0.69 ± 0.03	0.70 ± 0.08	0.98 ± 0.01
T. testudinum - $\delta^{15}N$	4.22 ± 0.51	–	3.41 ± 0.19
H. incrassata - $\delta^{15}N$	5.76 ± 0.08	5.25 ± 0.91	2.88 ± 0.99
Sargassum spp. - $\delta^{15}N$	–	2.05 ± 1.23	–

also potentially posed an environmental threat to the coastal ecosystems.

The shallow seas along the Mexican Caribbean coasts, especially those within reef lagoons, are colonized by well-established seagrass communities (Van Tussenbroek, 2011). Unlike seaweeds, seagrasses have an extensive below-ground root-rhizome system that allows them to form vast underwater meadows that serve to maintain water clarity, aid in nutrient recycling, reduce exposure to bacterial pathogens, and stabilize the sediments and thereby the beaches. In addition, they sustain diverse and abundant faunal communities, thereby supporting fisheries, and mitigate the effects of global climate change through carbon sequestration (Orth et al., 2006; Barbier et al., 2011; Fourqurean et al., 2012; Lamb et al., 2017).

In this study, we assessed the effects of Sargassum-brown-tides on four near-shore seagrass communities along the Mexican Caribbean coastline: two sites were in the northern sector (1. Mirador Nizuc and 2. Puerto Morelos), and two in the southern sector (3. Xahuayxol and 4. Xcalak; Fig. 1). The vegetation in the seagrass meadows at all sites consisted of seagrasses with rhizophytic algae, with a few multispecies assemblages of scleractinian corals, sponges, or gorgonians in areas with rocky substratum. The beach-cast material was not removed from any of these sites during the period of maximal *Sargassum* influx. Data obtained at different times from various research or monitoring projects were used to obtain a general picture of the impact of the Sbt (Table 1, Supplement 1). Some data on the benthic communities were obtained 2–7 years before the Sbt, but seagrass meadows in reef lagoons in the Mexican Caribbean tend to be stable, with only small seasonal or inter-annual fluctuations in abundance of the principal species (Van Tussenbroek, 2011); thus, any major changes are likely induced by major disturbance such as the Sbt. In addition, the sites were visited months (Xahuayxol, Xcalak), weeks (Mirador Nizuc) or days (Puerto Morelos) before the Sbt, and the extension and the general aspect of the seagrass meadows had not changed visibly over time until the Sbt. All sites (except the near-shore shallow water of Puerto Morelos), had well-developed seagrass meadow extending from ~1 m from the coastline up to ~150 m into the sea (Mirador Nizuc) or until the reef crests, which are ~300–600 m or ~800–1200 m off-shore at Xahuayxol or Xcalak, respectively. The well-developed seagrass meadow at Puerto Morelos also extends to the reef crest, ~2 km offshore, but the near-shore zone from the beach-line until ~50–70 m was buried below a 0.5–1.0 m thick layer of sand by hurricane Wilma (Oct. 2005), and still recovering. At this site, two zones were established; Zone 1 was in this impacted near-coastal fringe, and Zone 2 was ~20 m further off-shore, where the vegetation received little impact from hurricane Wilma. In addition, scleractinian corals within the seagrass meadow ~100 m offshore (20°52′05.1″ N, 86°51′57.8″ W) have been monitored since 2009.

The Sargassum-brown tides caused acute high loads of organic material and increased turbidity, but the degree of impact varied among the sites. The impact was least severe at Puerto Morelos (Zone 2) where the illuminance was reduced 28 to 31-fold in comparison to values obtained in February 2013 and June 2015, respectively (Fig. 2). In this zone, dissolved oxygen (DO) levels remained at ~5 mg l^{-1} during the 24 h cycle, whereas this value is usually registered above seagrass meadows early in the morning and rises to > 9 mg l^{-1} during the day (Fig. 2). After the Sbt, the organic matter content of the sediments increased 15 and 35-fold at Zone 2 and Zone 1, respectively (Table 2) and both *Thalassia testudinum* and *Halimeda incrassata* had decreased $\delta^{15}N$ in their tissues, resembling that of the arriving *Sargassum* spp., which on average had 7.53 mg N and 0.075 mg P dry g^{-1} (Table 2). At Xahuayxol and Xcalak, masses of drifting *Sargassum* spp., 0.5–0.6 m thick, accumulated at 50 m and 25 m from the shoreline respectively (Suppl. Fig. 1). DO at these sites ranged from 0.67 to 7.05 mg l^{-1} with lowest concentrations near the shoreline and higher values offshore. Both pH and oxidation/reduction potential (ORP)

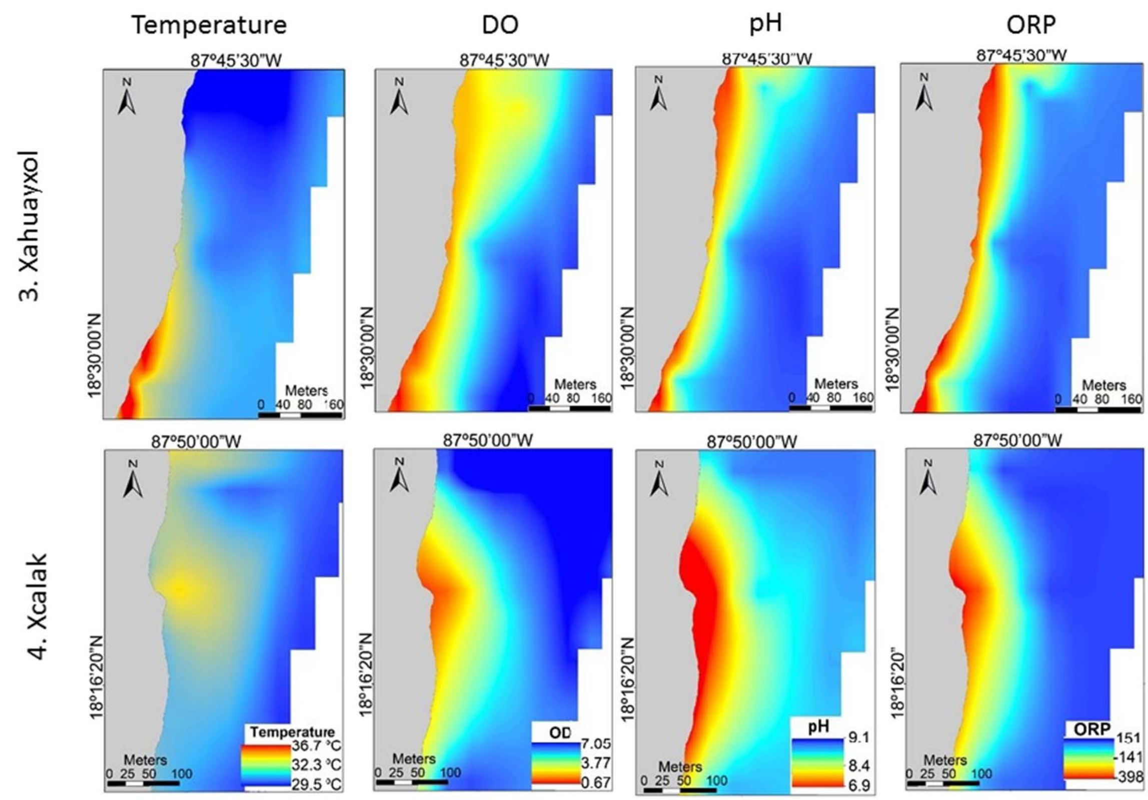

Fig. 3. Spatial distribution maps based on isoline maps for hydrological variables measured in situ and ammonium concentration measured in water samples at sites 3 and 4 of the southern Mexican Caribbean. Temperature (°C), DO dissolved oxygen (mg l^{-1}), pH and ORP oxidation/reduction potential (mV).

Table 3
Average values (± SE, $N = 3$) for the parameters measured at the two sites in the Southern Mexican Caribbean. Zone 1: with drifting (decomposing) *Sargassum* spp., Zone 2: without *Sargassum* spp., but with brown water from leachate and POM, Zone 3: no visible presence of Sargassum-brown-tide.

Site/zone	Temperature (°C)	Dissolved O_2 (mg l^{-1})	pH	ORP (mV)
Xahuayxol				
Zone 1	32.2 ± 0.8	1.8 ± 0.4	8.0 ± 0.2	− 268.8 ± 59.3
Zone 2	31.4 ± 0.2	2.8 ± 0.4	8.7 ± 0.1	− 96.0 ± 34.4
Zone 3	31.1 ± 0.2	4.3 ± 0.5	8.9 ± 0.1	− 3.0 ± 8.7.4
Xcalak				
Zone 1	32.2 ± 1.4	1.0 ± 0.1	7.4 ± 0.2	− 356.2 ± 12.5
Zone 2	31.9 ± 0.6	3.5 ± 0.7	8.4 ± 0.1	− 130.8 ± 54.4.9
Zone 3	30.7 ± 0.3	4.7 ± 0.4	8.7 ± 0.1	55.7 ± 25.2

depicted a similar spatial distribution pattern as DO; pH ranged from 6.9 to 9.1 and ORP from − 398 to 151 (Fig. 3). Three zones were distinguished (from shore towards the sea): 1) zone with drifting masses of *Sargassum* spp., with extremely low DO, reduced pH, and negative REDOX values, 2) zone without drifting *Sargassum* spp., but with the water colored brown by organic particles and leachates, with higher values for DO, pH and ORP than those found in zone 1, but still lower than normal values, and 3) no visible presence of Sbt (Table 3).

One year after the massive influx of *Sargassum* spp., water transparency (expressed as light attenuation coefficient K_d) at the four stations distributed throughout Puerto Morelos lagoon was below usual levels (Table 4, Paired *t*-test: $t = 11.12$, df = 2, p = 0.008). *T. testudinum* showed a significant increase in P content after Sbt (%P DW, Nested ANOVA F = 4.77, df = 1 p = 0.029), although not at all

Table 4
Water transparency (measured as K_d light attenuation coefficient) and nutrient availability (%N and %P DW in leaf tissues of *T. testudinum*) at different sites in Puerto Morelos reef lagoon (see Fig. 1), one year after Sargassum-brown-tide (Sbt, Sept. 2016). Data collected previously at the same sites are mentioned for comparison (K_d from Enríquez and Pantoja-Reyes, 2005, N = 4–6, year 2006). C, N and P content before Sbt from samples taken between 2010 and 2014. N = 3 for all parameters, except for K_d before Sbt. Values are average ± SE.

Variable	Site	Before Sbt	After Sbt
K_d	Coast	0.42 ± 0.05 m^{-1}	0.51 ± 0.11
	Mid-lagoon-1	0.20 ± 0.01 m^{-1}	0.27 ± 0.02
	Mid-lagoon-2	0.19 ± 0.01 m^{-1}	ND
	Reef	0.24 ± 0.01 m^{-1}	0.33 ± 0.02
%C	Coast	37.43 ± 0.07	37.10 ± 2.13
	Mid-lagoon-1	36.15 ± 1.29	34.82 ± 2.89
	Mid-lagoon-2	34.37 ± 1.54	34.76 ± 2.26
	Reef	37.49 ± 0.50	34.25 ± 1.61
%N	Coast	1.93 ± 0.07	2.13 ± 0.09
	Mid-lagoon-1	1.95 ± 0.03	1.86 ± 0.22
	Mid-lagoon-2	1.91 ± 0.08	1.89 ± 0.17
	Reef	1.82 ± 0.11	1.68 ± 0.07
%P	Coast	0.14 ± 0.01	0.31 ± 0.06
	Mid-lagoon-1	0.12 ± 0.01	0.11 ± 0.01
	Mid-lagoon-2	0.15 ± 0.02	0.12 ± 0.01
	Reef	0.15 ± 0.02	0.25 ± 0.10

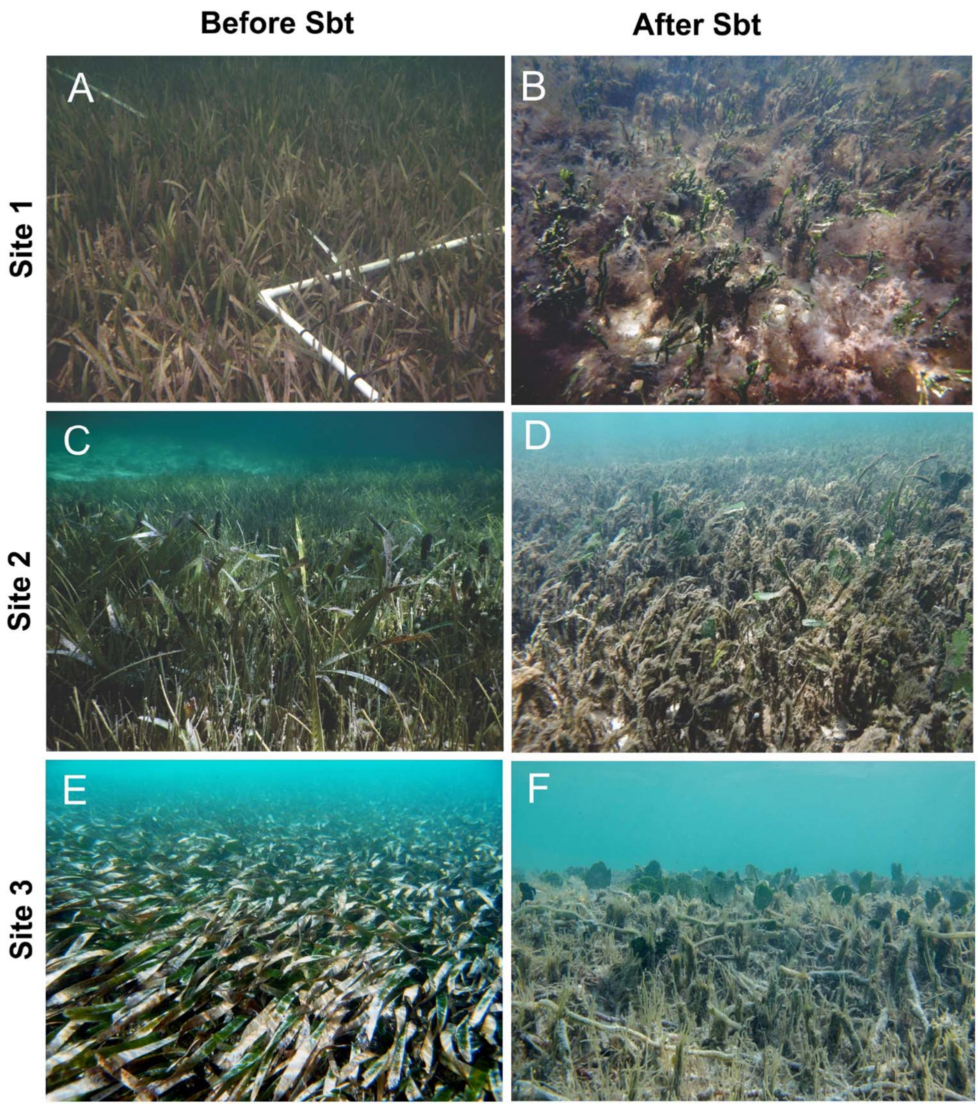

Fig. 4. Seagrass meadows before and after Sargassum-brown-tide at Site 1 Mirador Nizuc (A. November 2008, B. May 2016), Site 2 Puerto Morelos (C. September 2013, D. October 2015) and Site 3 Xahuayxol (E. September 2006, F. December 2016).

stations ($F = 27.7$, $df = 6$, $p < 0.001$ for site within Sbt; Table 4) in comparison with periods before the Sbt. Neither C content (%C DW, $p = 0.268$ for Sbt), nor N content (%N DW, $p = 0.868$) were significantly different before and after the Sbt (Table 4).

At Mirador Nizuc (Site 1), the most notable differences between 2008 and 2016 were the loss of the seagrass *T. testudinum* ($Z = -4.573$, $p < 0.0001$, $N = 66$), and the increase in the abundance of the algae *Halimeda* spp. ($Z = 4.617$, $p < 0.0001$, $N = 66$) and of drift/epiphytic algae ($Z = 6.420$, $p < 0.0001$, $N = 66$; Fig. 4, Suppl. Fig. 2). By 2016, a large section of the seagrass meadow formerly dominated by *T. testudinum*, ~5700 m^2 in size (corresponding to ~47% of the studied meadow), was completely lost and replaced by *Halimeda* spp. (mainly *H. incrassata*) and drift/epiphytic algae (Fig. 5). Only a small section at 20–30 m off-shore, in a very shallow area (depth ~0.3–0.5 m) appeared to remain unaffected. The seagrass *H. wrightii* disappeared completely from this area ($Z = -2.675$, $p < 0.007$, $N = 66$; Fig. 5, Suppl. Fig. 2), while significant reductions in area were also recorded for the seagrass *S. filiforme* ($Z = -2.403$, $p = 0.016$, $N = 66$) and spongy algae ($Z = -2.070$, $p = 0.038$, $N = 66$), which typically accompanied *T. testudinum* at low abundances (Braun Blanquet category 0.1–1). The relative abundance of the brush-like algae, distributed throughout the study area in low densities during both study periods, was also significantly lower in 2016 ($Z = -3.238$, $p < 0.001$, $N = 66$). The total above-ground biomass did not change significantly after the Sbt ($t = 1.966$, $df = 7$, $p = 0.09$), although the composition of the species changed from a domination of *T. testudinum* to a *Halimeda* spp. dominated community. The below-ground biomass of the community, however, changed from 1236.4 to 6.1 dry g m^{-2}, which represented a 99.5% reduction ($t = 6.135$, $df = 7$, $p < 0.001$), due to the loss of seagrasses (Fig. 6). Like Mirador Nizuc, the reef lagoons at Xahuayxol and Xcalak, are relatively wave-protected. Although there were no quantitative data for the seagrass meadows before or after the Sbt for these sites, local knowledge of the previous extension of the seagrass meadows and photographic records indicate that like Mirador Nizuc, these sites lost their near-shore seagrass meadows as far as ~50 m off-shore.

The effects of Sbt on the seagrass community in Puerto Morelos, although notorious, were less severe than those at the other three more

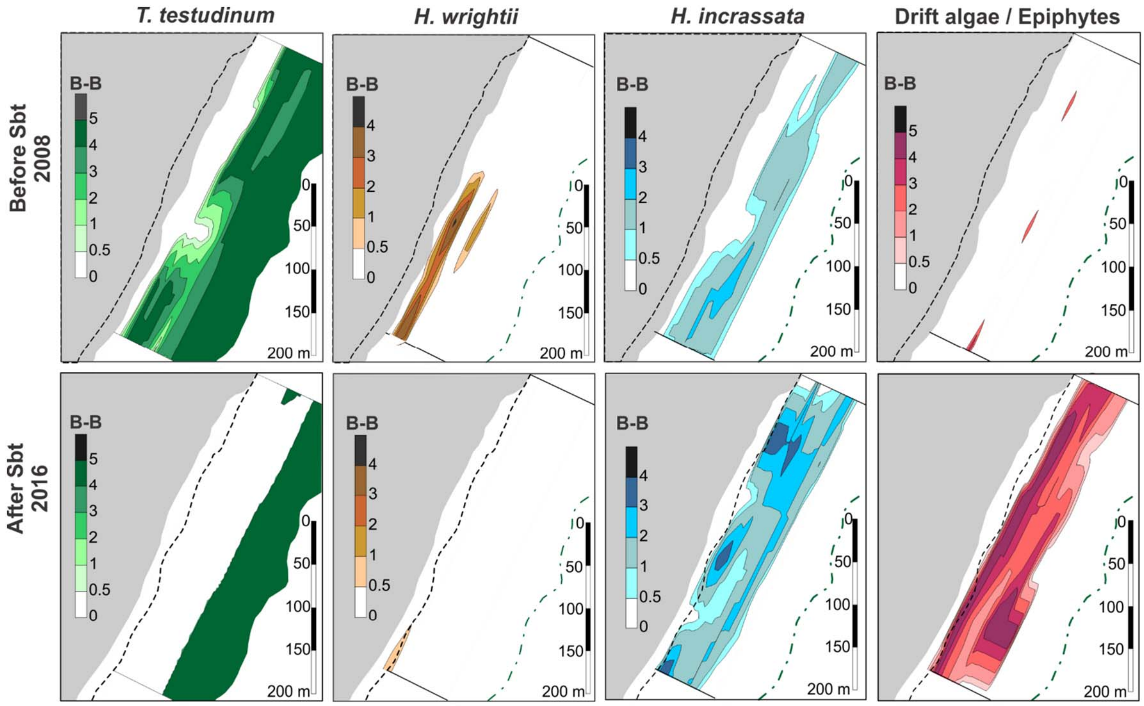

Fig. 5. Maps of approximate areas covered by the seagrasses *Thalassia testudinum*, *Halodule wrightii*, the calcareous alga *Halimeda incrassata* and drift/epiphytic algae at Mirador Nizuc in 2008 (before the Sbt) and 2016 (after the Sbt). B-B: The abundance as Braun-Blanquet scale (B-B): 0.5 (scale r: rare and +: few individuals), 1 (various individuals or cover up to 5%), 2 (many individuals or cover 6–26%), 3 (cover 26–50%), 4 (cover (51–75%), 5 (cover 76–100%).

wave-protected sites. In the nearshore Zone 1, with sparse seagrass vegetation, densities of *H. wrightii* and *Caulerpa* spp. significantly increased after Sbt, although their distribution was patchy resulting in large variations in densities (Table 5). In Zone 2, ~20 m further offshore, the effect of Sbt was more notable (Wald Chi-squared = 130.446, df = 16, $p < 0.001$) with significantly lower densities of *T. testudinum*, *S. filiforme*, *H. wrightii* and *Halimeda* spp. after the Sbt (Fig. 4, Suppl. Fig. 3). Total above-ground biomass increased significantly ($t = 3.053$, df = 14, $p = 0.009$) after the Sbt mainly due to the increase of (calcified) biomass of calcareous rhizophytic algae. Below-ground biomass reduced significantly ($t = 5.625$, df = 14, $p < 0.001$) by 62% (from 674.7 to 258.6 dry g m^{-2}), mainly due to the loss of the *T. testudinum* and *S. filiforme* (Fig. 6).

The coral colonies in the seagrass meadows belonged mostly to sediment-tolerant species, and were small (< 30 cm) with a semi-hemispherical growth form. In the survey conducted before the Sbt (2013), a total of 50 scleractinian coral colonies, belonging to six species, were recorded at the monitoring site; *Dichocoenia stokesii* was the dominant species ($N = 17$), followed by *Siderastrea siderea* ($N = 8$), *Pseudodiploria clivosa* ($N = 8$), *P. strigosa* ($N = 7$), *Porites astreoides* ($N = 7$) and *Montastraea cavernosa* ($N = 3$; Fig. 7). Colony sizes ranged from 9 to 74 cm with a mean of 25.7 cm (SE = 1.9). Although corals in the Puerto Morelos reef system have been affected by disease and bleaching episodes in the last two decades (Rodriguez-Martínez et al., 2010), the colonies in the monitoring site showed low rates of total loss (~10–12% per 3–4 years) and stable partial mortality (on average 9–10% of dead tissue per colony) between 2009 and 2013 (before Sbt). However, by August 2016, eight months after the Sbt, 27% of the coral colonies had died, all of them belonging to *P. astreoides*, *D. stokesii* and *P. clivosa* (Fig. 7). The mean partial mortality of the remaining colonies was 20.2 % (SE = 5.1), which was significantly higher ($V = 89$, $N = 34$, $p < 0.01$) than the mean of 9.3 % (SE = 3.2) recorded before the Sbt in 2013. The coral species that presented the higher partial mortality were the same as those that lost the higher number of colonies (Fig. 7, Suppl. Fig. 4). In 2016, the dead areas of surviving coral colonies were colonized by turf algal-sediment mats, macro-algae and ascidians.

Combining the findings of all study sites, the following scenario of impact on near-shore seagrass communities can be developed (Fig. 8); although the degree of impact may vary among locations. Near-shore drifting *Sargassum* spp., in combination with leachates and particulate organic matter released from the beach-cast material, caused severe reduction of light reaching the seagrass canopy. Seagrasses, and specially *Thalassia testudinum* with its well-developed below-ground rhizome-root system, requires high light to maintain a positive carbon-balance (Fourqurean and Zieman, 1991; Kenworthy and Fonseca, 1996). The seagrasses in the sargassum-tidal area at Puerto Morelos normally receive 1200 μmol quanta $m^{-2}s^{-1}$ around noon (unpubl. data, van Tussenbroek). This was reduced approximately 30-fold during the peak of the Sbt, which is well below the level of the compensation irradiance of 100–130 μmol quanta $m^{-2}s^{-1}$ for whole plants during the summer (Herzka and Dunton, 1998). Thus, during the Sbt, *T. testudinum* never attained a positive carbon balance, and even though seagrasses can survive short periods of negative carbon-balance using carbohydrate reserves from their rhizomes, prolonged periods of light reduction will deplete these reserves. In addition, the accumulation of organic material caused hypoxia (at Puerto Morelos) or approaching anoxia (at Xahuayxol and Xcalak, and probably also at Mirador Nizuc),

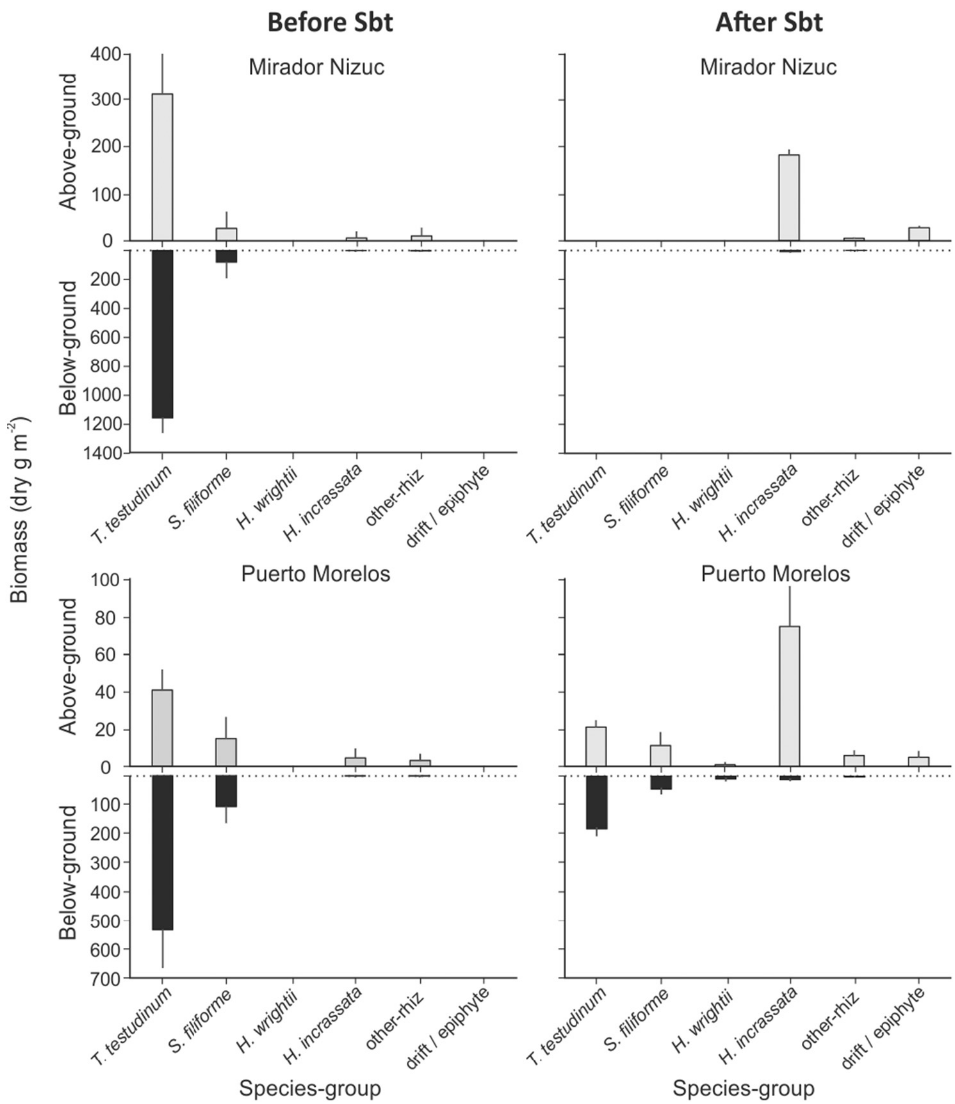

Fig. 6. Average (± SE) biomass of seagrasses and algae at Mirador Nizuc and Puerto Morelos sites in zones with dense seagrass before and after the Sargassum-brown-tide (Sbt). Other rhiz: other rhizophytic algae (brush-like algae and *Udotea* spp. combined). Mirador Nizuc; before Sbt: Nov. 2008, after Sbt: May 2016. Puerto Morelos; before Sbt: Nov. 2012-Feb. 2013, After Sbt: Oct. 2015. Note differences in Y-axes. N = 4–5 for Mirador Nizuc, and N = 8 for Puerto Morelos.

Table 5
Average density (± SE, N = 8) of the species groups in the two zones at Puerto Morelos, before and after the Sargassum-brown-tide (Sbt), together with the results of the contrast between pairs of sampling periods determined with the General Linear Model (df = 1). *** < 0.0001, ** < 0.01, * < 0.05, NS: not significant. ND: not determined due to small sample size. *T. testudinum*, *Thalassia testudinum*; *S. filiforme*, *Syringodium filiforme*; *H. wrightii*, *Halodule wrightii*.

	Density (no. ind. m^{-2})			2013 vs. 2015 post-Sbt	2015 pre-Sbt vs. 2015 post-Sbt
	2013	2015 before Sbt	2015 after Sbt	(Wald χ^2)	(Wald χ^2)
Zone 1					
T. testudinum	12.0 ± 7.1	18.5 ± 7.0	11.0 ± 5.4	0.000^{NS}	0.008^{NS}
S. filiforme	105.0 ± 46.0	146.5 ± 44.5	106.5 ± 50.6	0.000^{NS}	0.221^{NS}
H. wrightii	5.0 ± 5.0	28.5 ± 16.0	445.0 ± 204.9	26.747***	23.966***
Caulerpa spp.	44.0 ± 14.2	9.0 ± 9.0	414.5 ± 220.3	18.965***	22.717***
spongy algae	0	0	1.0 ± 1.0	ND	ND
brush-like algae	31.0 ± 8.3	20.0 ± 7.6	28.0 ± 9.2	0.001^{NS}	0.009^{NS}
Halimeda spp.	81.0 ± 14.1	24.0 ± 12.4	173.5 ± 25.9	1.182^{NS}	3.088^{NS}
Udotea spp.	27.5 ± 6.7	10.5 ± 3.4	81.5 ± 11.4	0.403^{NS}	0.696^{NS}
Zone 2					
T. testudinum	244.0 ± 20.8	216.5 ± 13.5	114.0 ± 17	7.444**	4.628*
S. filiforme	936.0 ± 99.4	632.5 ± 59.6	520.0 ± 96.9	76.227***	5.575*
H. wrightii	0	0	145.5 ± 68.2	9.325**	9.325**
Caulerpa spp.	0	0	2.0 ± 2.0	ND	ND
spongy algae	43.5 ± 6.4	23.0 ± 4.8	45.0 ± 9.3	0.001^{NS}	0.213^{NS}
brush-like algae	47.0 ± 7.6	21.5 ± 2.9	81.0 ± 13.4	0.509^{NS}	1.559^{NS}
Halimeda spp.	103.0 ± 12.6	58.0 ± 12.4	280.0 ± 42.7	13.800***	21.708***
Udotea spp.	62.0 ± 7.8	22.5 ± 5.7	90.5 ± 10.7	0.358^{NS}	2.037^{NS}

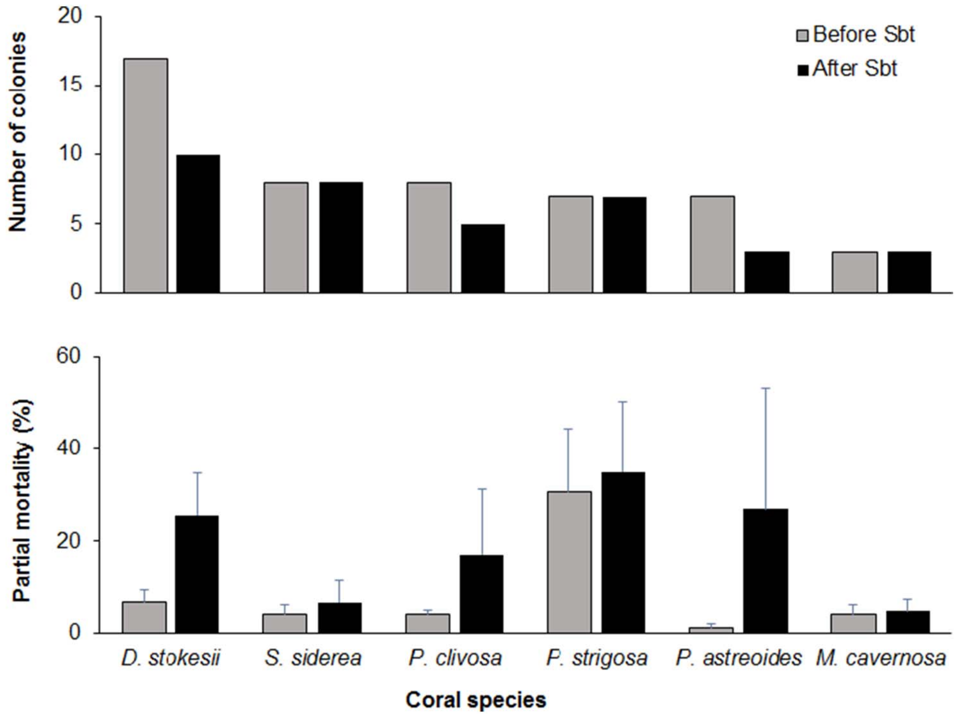

Fig. 7. Number of coral colonies and mean partial mortality (% of dead tissue of surviving colonies ± SE) of six scleractinian coral species in a monitoring site within the Puerto Morelos reef lagoon before (2013) and after (2016) the Sargassum-brown-tide (Sbt). See text for species names of the corals.

most likely due to bacterial activity in the decomposing weed (Valiela et al., 1997). Increased organic load, caused by algal mats combined with depleted oxygen, may have caused sulfide intrusion in the seagrass tissues inducing decreased performance and mortality of the plants (Borum et al., 2005; Mascaró et al., 2009). The higher temperature below the drifting mats of *Sargassum* spp. probably exacerbated the negative effects of decrease in light, accumulation of organic matter and eutrophication, due to higher metabolic demands of the plants (Burkholder et al., 2007; Lee et al., 2007, Martínez-Lűscher and Holmer, 2010); in addition, concentrations of toxic sulfide increase with temperature (Martínez-Lűscher and Holmer, 2010). The synergy of these processes caused profound changes in the plant community. Especially notable were the loss of seagrasses and the increase in epiphytes/drift algae and rhizophytic calcareous algae (mainly *Halimeda* spp.), especially in areas previously dominated by *T. testudinum*. Loss of *T. testudinum* was also obvious from the presence of exposed dead rhizomes, which suggest that the sediments eroded after the seagrass die-off. Even in Zone 1 at Puerto Morelos, which did not have a well-developed seagrass community before the Sbt, the increases in the abundance of *H. wrightii* and of algae belonging to the genus *Caulerpa* were striking. Scleractinian corals growing close to the shore in the seagrass meadow within Puerto Morelos reef lagoon were also affected by the Sbt, with colonies suffering total or partial mortality. Some coral species (*D. stokesii*, *P. astreoides* and *P. clivosa*) appeared to be more affected than others (*S. siderea*, *P. strigosa* and *M. cavernosa*). Similar effects of the Sbt have also been reported by Silva et al. (2016) on corals colonizing the structures of an artificial reef in the northern section of Puerto Morelos reef lagoon.

In addition to loss of near-shore seagrass meadows and associated fauna including corals, the Sbt caused increased nutrient loads into coastal systems. Nutrients inputs, as result of the Sbt, were taken up by the primary producers as indicated by $\delta^{15}N$ in *T. testudinum* and *H. incrassata* being like the value of the drifting *Sargassum* spp. (Table 1). During peak time of influx of *Sargassum* spp. (July–December 2015), the monthly influx of N in *Sargassum* spp. to coastal waters was more than that entering the system from land-based sources during a complete year. For example, in August 2015, an average of 9726 m^3 (corresponding with ~817 × 10^3 kg) of *Sargassum* spp. was removed per km coastline from the Mexican Caribbean beaches (Rodriguez-Martínez et al., 2016). Using the N and P content of *Sargassum* spp. from this study, the monthly influx of N was 6200 kg km^{-1} coastline, and for P this was 61 kg km^{-1}. Whereas Hernández-Terrones et al. (2011) estimated the average monthly influx of nutrients from the aquifer to the sea (surface rivers are absent due to the karstic nature of the Yucatan peninsula) for the same coastline at 200 kg N km^{-1} and 6–18 kg P km^{-1}. Thus, during the peak period of massive influx of *Sargassum* spp., the monthly N and P imports by *Sargassum* spp. were respectively ~30 and ~3–10 times the usual inputs into the sea through ground-water discharge. Likely, not all the N and P returned to the sea, but the import during this period was significant even if only a small fraction remineralized. The increased eutrophication was still noticeable in Puerto Morelos after 1 year. For example, in September 2016, a year after the Sbt at Puerto Morelos, visibility in the water was still reduced in relation to previous records. Carbonate systems, such as Puerto Morelos reef lagoon, are P limited (Short et al., 1990; Fourqurean et al., 1992; Carruthers et al., 2005); as such, eutrophication will be easy to detect using the phosphorus content in plant tissue. Indeed, the P content in *T. testudinum* at the coastal and reef stations did increase after the Sbt (Table 3). The effects of the organic and nutrient load due to the massive influx of drifting *Sargassum* spp. on the extensive seagrass beds in reef lagoon is most likely gradual, but may accelerate the shifts in community composition towards faster-growing and less-deep rooting vegetation as has already been observed over the few last decades (Rodriguez-Martínez et al., 2010; Van Tussenbroek, 2011), due to eutrophication caused by contaminated groundwater discharges (Carruthers et al., 2005; Hernández-Terrones et al., 2011).

Seagrasses in near-shore waters are especially important for coastal protection and maintaining water clarity. The seagrass canopy baffles the waves allowing for the deposition of fine particles, and this baffling capacity is directly related to the proportion of the canopy that occupies the water column (Koch et al., 2009). Loss of below-ground tissues (Fig. 6) not only changes the biogeochemistry of the sediments (Enríquez et al., 2001), but also reduces nutrient cycling capacity (McGlathery et al., 2007) and carbon sequestration of the system (Fourqurean et al., 2012). Below-ground structures also play an important role in fixation of the sediments, which can be significant even

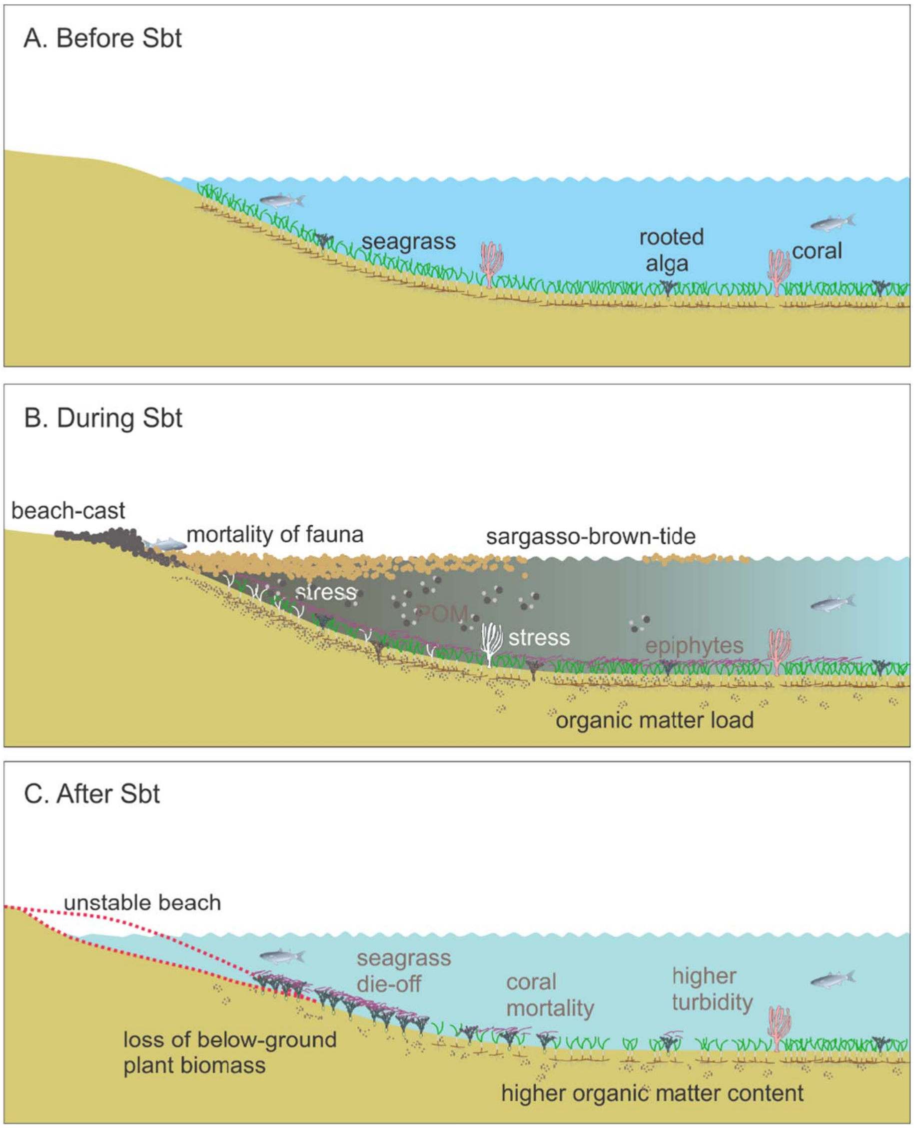

Fig. 8. Effects of Sargassum-brown-tide (Sbt) on near-shore seagrass communities typical of the Mexican Caribbean coastline. A. Before the Sbt: a well-developed seagrass meadow almost reaching the coastline with clear waters and healthy corals and other fauna. B. During the Sbt; leachates and particulate organic matter (POM) of beach-cast seaweed color the water and increase the organic matter in the sediments; seagrass and corals are under stress due to reduced light and organic matter load causing anoxia or hypoxia, and increased epiphyte growth. C. After the Sbt, near-shore seagrasses and some coral colonies are lost. Increased organic matter in sediments and higher turbidity of water, and unstable beaches or beach erosion due inadquate removal practices of the beach-cast weeds and loss of near-shore seagrass meadows.

if the canopy is almost absent (Christianen et al., 2013). Seagrasses, and specially *T. testudinum*, are deeply rooted, and therefore are much more resistant to removal by storms and hurricanes than macroalgae (Cruz-Palacios and van Tussenbroek, 2005). Thus, it is expected that coastlines that were affected by the Sbt and lost *T. testudinum* will have more turbid waters with less stable shorelines, and will be more vulnerable to impacts of storms or hurricanes.

Recovery of the near-shore seagrass meadows along the Mexican Caribbean coastline affected by the Sbt in 2015–2016 is likely to be slow. Dawes et al. (1997) reported that full recovery of *T. testudinum*, removed artificially from small areas (0.25 × 2 m) within a well-developed meadow, took up to 7.6 years and the recolonization in these small areas occurred through vegetative expansion from the seagrasses at the edges of the cut areas. However, if large sections of seagrass meadows are removed, recovery will take much longer (most likely decades) as has been shown in the coastal Zone 1 at Puerto Morelos, where the meadow was buried during hurricane Wilma in 2005. Even after 10 years, the seagrass community had not recovered and was still mainly colonized by rhizophytic algae and the pioneering seagrass species *H. wrightii*. The seagrass *S. filiforme* and the climax species *T. testudinum* were still only present in very low abundances. The longer-term effects of eutrophication due to nutrient input by Sbt are more difficult to assess. The well-flushed Puerto Morelos lagoon (Coronado et al., 2007) has shown a decrease in transparency and an increase in tissue nutrient content of seagrasses one year after the Sbt, suggesting that the imported organic material and nutrients by this seaweed had not yet been removed from the system. If the frequency of periodic disturbances is higher than the time of recovery of the system, then the system will change permanently. Thus, if the massive influxes of *Sargassum* spp. become recurrent, with frequencies of one to several decades, disappearance of near-shore well-developed seagrass beds due to Sargassum-brown-tides can be expected, with detrimental consequences for coastal stability and other ecosystem services. With the information of this study, it is possible to define coastal areas where long-term accumulation of *Sargassum* spp. is likely, and these areas should be prioritized for removal if massive beaching of this seaweed occurs again. Removing beach-cast *Sargassum* spp. will prevent the harmful effect on nearshore marine communities, but removal from the beaches causes beach erosion, as inevitably sand is taken away together with the algal masses (Rodriguez-Martínez et al., 2016; Suppl. Fig. 6). Thus, guidelines for appropriate removal and disposal practices are urgently required. Considering the potential damage Sbt can inflict, not only to the tourist industry, but also to the long-term health of the coastal ecosystems, it is essential to know whether these events will be recurring. This knowledge will aid in setting-up proper action plans, not only to ameliorate the immediate economic impact, but also to preserve the coastal ecosystems and their services.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.marpolbul.2017.06.057.

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