ARTICLE IN PRESS

Marine Pollution Bulletin xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

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

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A R T I C L E I N F O

Keywords:
Algal bloom
Community shift
Coral mortality
Sargassum fluitans
Sargassum natans
Seagrass die-off

A B S T R A C T

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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http://dx.doi.org/10.1016/j.marpolbul.2017.06.057
Received 21 March 2017; Received in revised form 10 June 2017; Accepted 20 June 2017

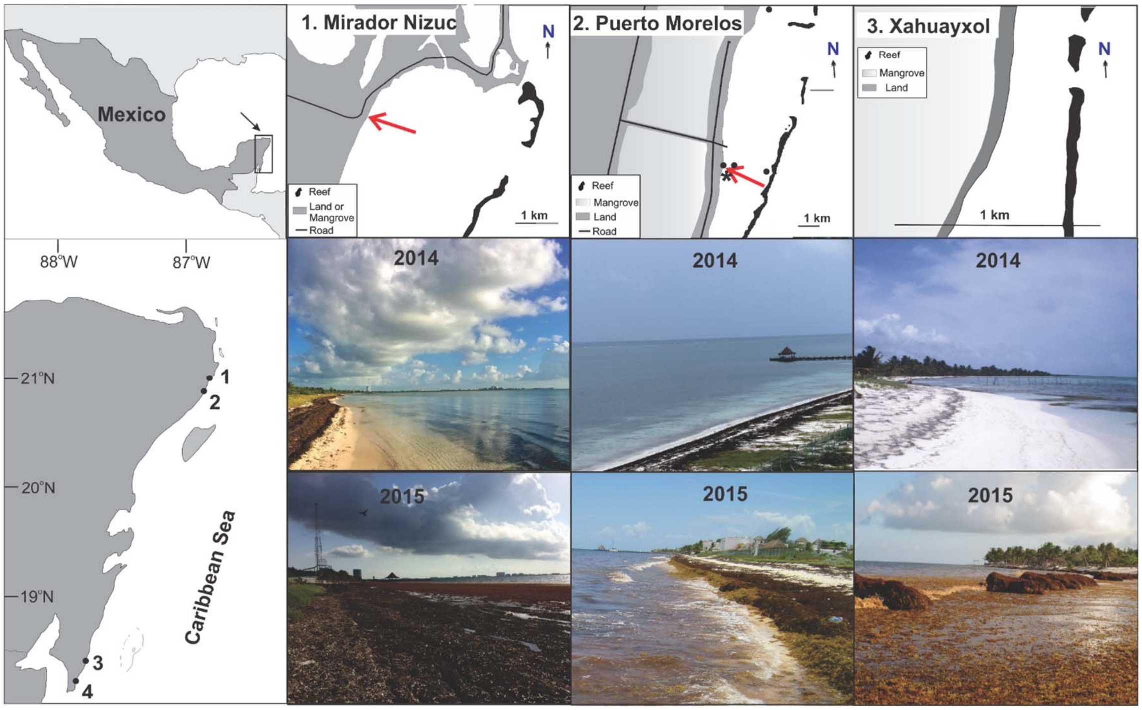

Fig. 1. Map indicating study sites: 1 Mirador Nizuc, 2. Puerto Morelos, 3. Xahuayxol, 4. Xcalak. Detailed maps are given for three of the four sites (general setting at site 3 and 4 were alike); arrows in detailed maps 1 and 2 indicate the position of the studied seagrass meadows, water quality was determined 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
δ^{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