



Climate-driven golden tides are reshaping coastal communities in Quintana Roo, Mexico

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ARTICLE INFO

Keywords:

Community structure
Seagrass
Sargassum
Biodiversity
Degradation
Mexico

ABSTRACT

Sargassum mats in Mexican bays reduce the biodiversity of coral and seagrass nursery habitats. Three bays in Quintana Roo, Mexico were chosen to determine the environmental stress caused by *Sargassum natans* and *S. fluitans* on coral, seagrass and fish populations. For both control sites, Yal Ku Lagoon and Half Moon Bay with little to zero *Sargassum* cover, benthic communities and the physico chemical characteristics of the waters were not impacted. In Soliman Bay, *Sargassum* mats cover large areas in the shallows and shore and smother the seagrass and corals. Under the *Sargassum* mats light and dissolved oxygen levels were significantly lower. Anoxic conditions were found, with levels as low as 0.5 mg/L for oxygen and a 73% decrease in light. Water temperature was 5.2 ± 0.1 °C (mean $\pm$ SE) warmer under the *Sargassum* mats. By determination of weight (grams per day) and growth (mm per day), the stress caused by *Sargassum* mats in Soliman Bay caused a seven-fold decrease in productivity of *T. testudinum* compared to other sites. Taxonomic diversity was also reduced with lower biomass and an altered species distribution. To improve these ecosystems, pre-emptive conservation management and protection must be priority for future ecosystem health and biodiversity.

1. Introduction

The Sargasso Sea is formed by large amounts of *Sargassum natans* and *S. fluitans* and has always been considered as the source of the golden tides of pelagic *Sargassum* washing up on most Caribbean coastlines. *Sargassum* sequesters 40 to 260 million tonnes of CO₂ per year [33]. Sixty million tonnes of that net primary production per year sinks to the deep ocean [33]. This represents 7% of the oceans' global net transport of CO₂ [33], enhancing uptake of atmospheric CO₂ and ocean carbon sinks [70]. In addition to significant carbon uptake, *Sargassum* provides habitats for spawning, nursery and feeding grounds [32]. Similar functions are found in mangrove forests [21], seagrass [6] and corals [7].

Since 2015, large mats of *S. natans* and *S. fluitans* smother Caribbean coastlines of Mexico. The smothering began after the formation of the Small Sargasso Sea in 2011 off the Brazilian coast [20,61]. Several hypotheses have been put forward regarding the conditions that lead to the creation of the Small Sargasso. Global climate change might have forced

part of the Sargasso Sea to move further south (Small Sargasso), bringing the *Sargassum* spp. closer to the Caribbean Sea (review from [36]). The changes in the distribution of the *Sargassum* is thought to be caused by a regime shift in changing ocean currents [61,69], increasing seawater temperatures and abnormal winds, brought about by climate change [13,28,36]. Sanchez-Rubio et al. [59] mapped long term distributional patterns of *Sargassum* and found that the changing climate altered the Atlantic Multidecadal Oscillation (AMO). The AMO is the variability in the North Atlantic sea surface temperatures over many decades. This led to higher occurrences of *Sargassum* under warmer AMO events due to a changing global climate [59].

Over the last few decades, the volume of *Sargassum*, forming large mats and washed up along the coastline has been steadily increasing. The *Sargassum* mats arrive in Mexican shallow bays and remain for several months each year. The mats degrade on beaches, at average volumes of 2360³ km⁻¹ [56], creating toxic leachate. These impacts reduce oxygen availability [9] and cause high levels of hydrogen sulfide, H₂S

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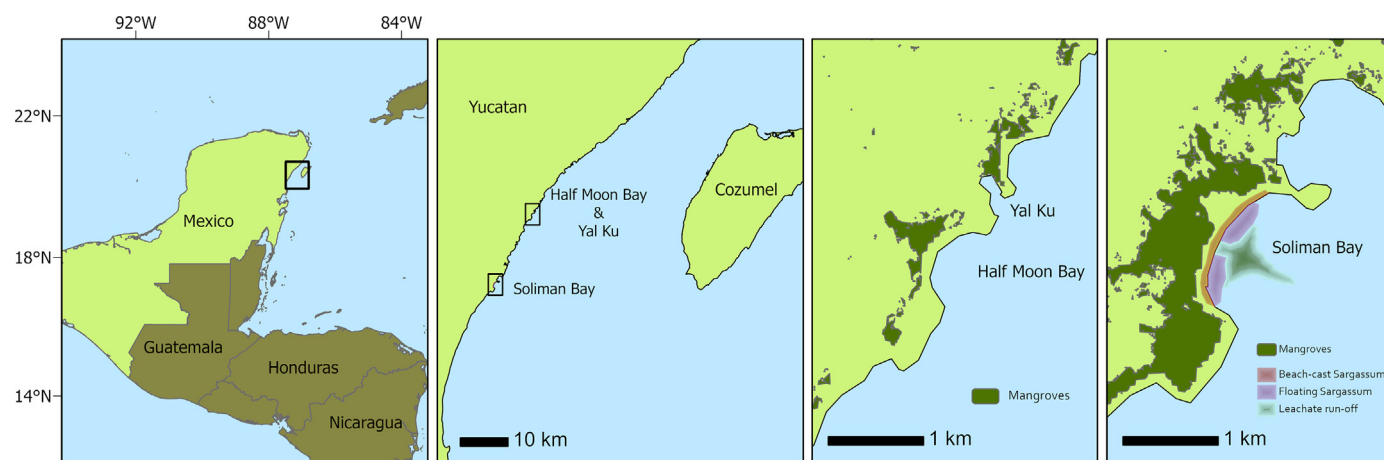


Fig. 1. Map illustrating country, region and site-specific scale of coastal bay localities. The area surveyed within each bay is highlighted. Many of the mangrove forests are established behind carbonate bedrock plateaus. A common geological feature in Caribbean Mexico.

[57] exacerbating devastation to the ecology, environment, and economy [5,36,57] of the site. Earlier studies have shown how seagrass and coral ecosystems in particular are the most affected by the *Sargassum* mats [5,66]. In Mexico, the health of seagrass and coral reef ecosystems play a crucial role to coastal tourism [19,39,55], which in Quintana Roo alone, it is worth \$10 billion per year [54]

In Mexico, seagrass meadows cover an area of 400,000 ha of coastal waters and the standing stock of stored carbon biomass in seagrass is estimated at 48 million tonnes [24]. This biomass supports fish populations and higher organisms in adjacent ecosystems [16]. Each year global seagrass loss continues at rates estimated at 7% [71]. Losses are due to poor water quality from reduced UV light and dissolved oxygen (DO_2) levels [49], similar to the environment caused by *Sargassum* mats and leachate. Coral reefs are also under threat from the smothering *Sargassum* mats and runoff from the degrading mats, which form a toxic leachate, visible as dark brown in the water [9]. The impacts on coral reefs and losses of hard coral cover cause declines in biodiversity, due to loss of habitat complexity and connectivity [12,18,41]. Losses of hard coral cover are often followed by an overgrowth of macroalgae, leading to an unstable state phase-shift [26]. The impacts from smothering mats of *Sargassum* and toxic leachate will lead to reductions in ecosystem resilience and loss of function [9,58,64], due to declines of seagrass productivity and hard coral cover.

Northwest of the Small Sargasso Sea we investigated the impact of *Sargassum* mats and its leachate on the seagrass, corals, and fish distribution in Soliman Bay, 10 km north of Tulum, Quintana Roo, Mexico. We also compared primary production rates of the seagrass, *Thalassia testudinum* and water quality in Soliman Bay against sites without impact from *Sargassum*, Yal Ku lagoon and Half Moon Bay, which had little to zero smothering from *Sargassum* (Fig. 1). Before *Sargassum* smothering occurred in Soliman Bay, seagrass and coral communities were healthy (D. Graham pers comm). We hypothesised that, (1) benthic community structure will have a greater diversity and abundance in areas without *Sargassum* mats compared to areas smothered by mats in Soliman Bay, (2) *Sargassum* mats and its leachate will reduce light intensity and dissolved oxygen levels, while increasing water temperature, and (3) *T. testudinum* growth rates and mass gain will be greater in sites without *Sargassum* mats.

2. Materials and methods

2.1. Sites used in the investigation

Three coastal shallow-water bays in Quintana Roo, Mexico were investigated between June and August 2018. Site selection was determined by the presence of coral, seagrass, and different levels of *Sar-*

Table 1

Site specific environmental variables across the three localities (mean $\pm$ SE).

Environmental variable	Yal Ku Lagoon	Half Moon Bay	Soliman Bay
Water depth (m)	1 to 3	1 to 4	1 to 3
Sea surface temperature (°C)	29.5 $\pm$ 0.2	29 $\pm$ 0.7	29 $\pm$ 0.2
Salinity (PSU)	34 $\pm$ 0.2	34 $\pm$ 0.4	35.1 $\pm$ 0.1

gassum cover (see Table 1 for environmental variables). Yal Ku lagoon and Half Moon Bay were control sites. In Half Moon Bay, some areas of the strandline had beach-cast *Sargassum* but high wave energy improved mixing of oxygen-rich water. Yal Ku lagoon (Fig. 1, 20.4095° N, 87.3055° W) has a 200 m-wide opening to the ocean, allowing the exchange of water between the ocean and the lagoon. The lagoon has benthic species including seagrass, *Halodule wrightii* and *T. testudinum*, and corals, *Siderastrea siderea* and *Agaricia* spp. *Sargassum* was not found in the Yal Ku lagoon. Half Moon Bay (Fig. 1, 20.3960° N, 87.3159° W) close to and South of Yal Ku lagoon is on the coast with a bay perimeter of 1.2 km. The distance from the strandline (spring high water) to the fringing coral reef at the outer edge of the bay is 500 m. The benthos of the bay has a rich biodiversity with thick beds of seagrass, *H. wrightii*, *T. testudinum* and *Syringodium filiforme*. Coral species include *S. siderea*, *Orbicella annularis*, *Porites ateroides*, and *Acropora palmata*. Soliman Bay (Fig. 1, 20.2867° N, 87.3754° W) is 15 km South of the Half Moon Bay and Yal Ku lagoon. The bay perimeter is 2.2 km, and the distance from the strandline to the fringing coral reef at the outer edge of the bay is 650 m. Extending away from the strandline to 200 m, there are large areas of seagrass beds of *H. wrightii*, *T. testudinum* and *Syringodium filiforme*. Throughout the bay, there are many habitat-forming benthic species including corals and sponges. Thick and large mats of *Sargassum* smother 50% of the Soliman Bay coast from May to November. The *Sargassum* mats increase in mass close to shore with an estimated live volume of 2970 m³. Large volumes, 2000 m³ of decaying *Sargassum* spp. end up on the shore forming a five-meter rotting band at the strandline, creating extensive toxic leachate and runoff, seen as cloudy dark brown water.

2.2. Seagrass *thalassia testudinum* growth and mass measurements in the three bays

Measurements of *T. testudinum* primary productivity was modeled on methods provided by the Caribbean Coastal Marine Productivity network [11]. Eight permanent quadrats (0.20 m x 0.20 m) were anchored into the sand in Soliman Bay, and five each in the Yal Ku and Half Moon Bay localities. Within the quadrats 38 (Yal Ku), 56 (Half Moon Bay) and 29 (Soliman Bay) seagrass leaves were used to measure leaf growth rate by puncturing the leaf at the base (where the white sheath begins) and

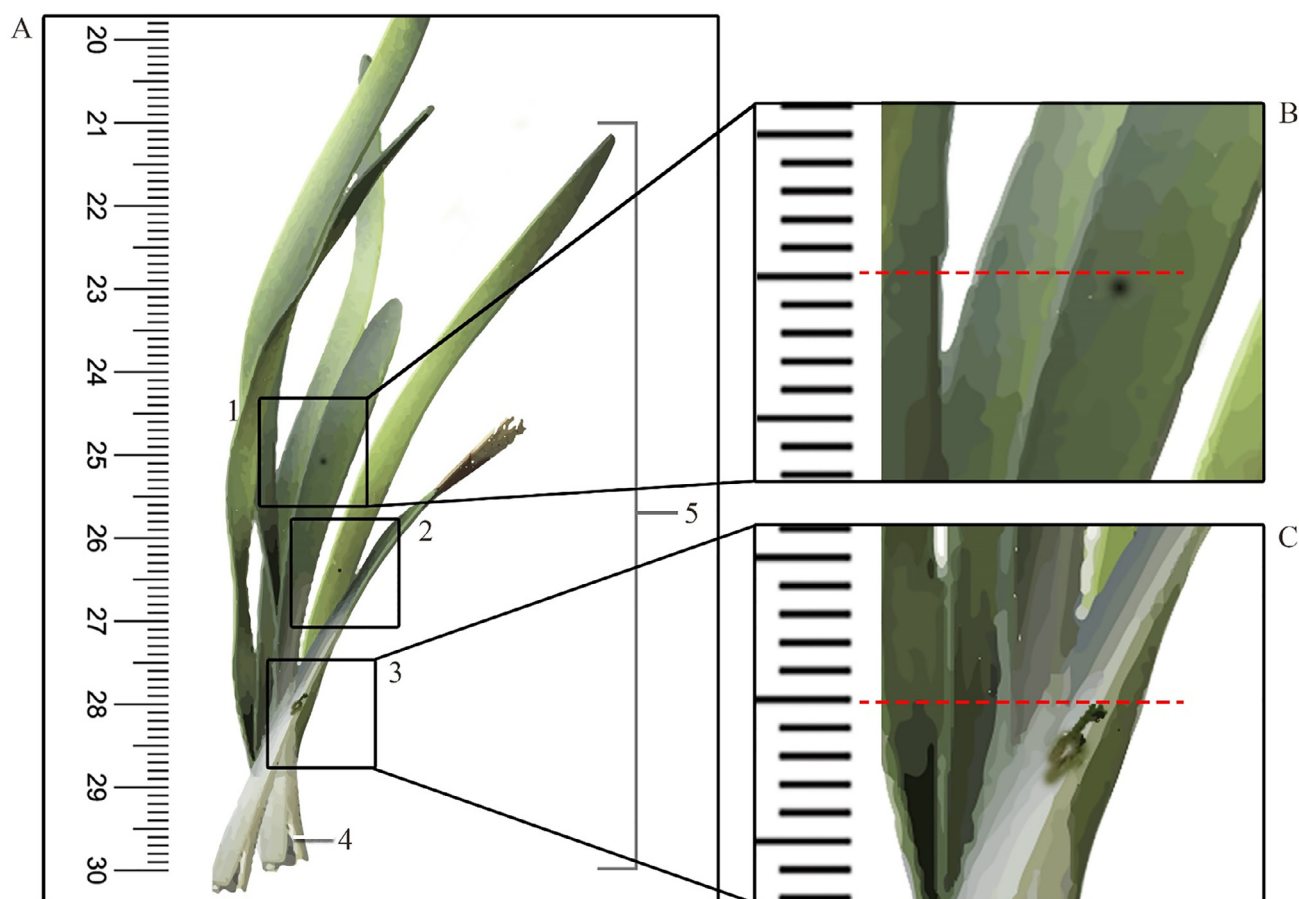


Fig. 2. An illustration highlighting the method for assessing growth of *Thalassia testudinum*. **A**, bundle of blades highlighted with, 1, a puncture mark on youngest blade; 2, a puncture mark on growing blade; 3, a puncture mark on old blade - the reference cut for the whole bundle; 4, white sheath; and 5, bundle. The distance between 1 and 3 and 2–3 are measurements for growth. **B**, a puncture mark visible on a young *T. testudinum* blade. **C**, a puncture mark visible on an old, seagrass blade. Red dotted lines indicate where all blades in the bundle were cut.

measuring the position of the puncture after several days (Fig. 2A). Due to changes in visibility and high wave energy, three quadrats from Soliman Bay and Yal Ku lagoon, and four quadrats from Half Moon Bay were recovered after 11 and 12 days respectively. *Thalassia testudinum* shoots were also collected at the same time for the leaf growth rate.

The seagrass leaves were washed and cleaned free of epiphytes. Each shoot contained two to three *T. testudinum* leaves. Since the oldest leaves do not grow when punctured [35] they were used as a comparative baseline for growth with the younger blades (Fig. 2B and Fig. 2C). Bundles were cut at the old leaf puncture marks and the younger leaves were cut at their puncture mark. The distance between the two cuts were considered the new growth (measurements taken in millimeters). All leaves were sun-exposed air dried for 5 days until visibly dry and remaining at a constant weight.

Dry weight mass (g) growth of *T. testudinum* in each quadrat was weighed using a Ohaus PA224 Analytical Balance. Since not all the leaves within the quadrat were punctured, we multiplied the growth by the ratio of collected bundles and then divided it by the number of punctured blades to get an approximation for the growth in the whole quadrat. All seagrass data were collected using Permit # SGPA/DGVS/05,809/17. To compare levels of dissolved oxygen in each site (DO_2 mg L) a HQ30d portable multi-parameter meter was used (LDO101, accuracy: ± 0.1 mg/L. HACH, Manchester, UK).

2.3. Community composition investigations in Soliman Bay

Within the three bays investigated, Soliman bay was the only bay with a thick layer of *Sargassum* with leachate, visible as dark brown

water (see Fig. 1). In total, six transects were conducted. Areas under the *Sargassum* mats and adjacent to the mats, three transects (165 m long) running parallel to the strandline were conducted at 20 m, 40 m, and 60 m distance from the shore. Community composition investigations were carried out with 12, 1 m² quadrats along the transect. In three transects in areas more than 100 m (>100 m) from the *Sargassum* mats, 10, 1 m² quadrats were surveyed. All species were identified to their lowest taxonomic classification. Benthic species, algae, seagrass and corals were quantified as a percent of a 1 m² sampling area. Fish species richness and abundance observations were conducted using underwater visual census and quantified as abundance m³ along each of the 165 m transects. Species were grouped into one of four broad taxonomic groups (from this point forward defined as ‘groups’): algae; seagrass; corals; fish.

2.4. Algal physiology

In order to determine the photosynthesis and respiration of the *Sargassum* mat, the thalli of *Sargassum fluitans* were incubated for 30 min in 50 mL closed- airtight oxygen chambers ($n = 5$). Incubations were conducted under natural light and dark conditions [53]. To correct for metabolism effects by other organisms, reference incubations without algae were conducted. Incubations were repeated in two different days. During the first day, incubations were at 13:00 h with a natural irradiance level of $2173 \mu\text{mol m}^{-2} \text{s}^{-1}$ (High PAR). The second day the incubations were started at 10:00 h with a natural irradiance level of $1524 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Low PAR). Irradiance was measured with a Quantitherm PAR/Temperature Sensor with a QTP1 probe (resolution:

1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 0.02 °C, respectively. Hansatech, Norfolk, UK). The chambers were used to determine gross photosynthesis (PG) and respiration (R). To measure respiration, chambers ($n = 5$) were covered with aluminium foil. The concentration of dissolved oxygen ($\text{O}_2 \text{ mg L}^{-1}$) and temperature (°C) were measured before and after the incubations using a HQ30D flexi oxygen meter (Hach Environmental). Primary production was calculated following Naumann et al. [45].

2.5. Water quality measurements in Soliman bay

Water temperature (°C) and light intensity (lx) measurements were made under the *Sargassum* mats, leachate (as defined by dark brown water) and surrounding areas, using two HOBO Pendant® Temperature/Light 64 K Data Loggers (± 0.5 °C, 1 min intervals). Light intensity measurements were also recorded (30 cm below the water surface) at 20 m, 40 m, and 60 m from the shore using a HOBO UA-002-64 Pendant Temp/Light data logger (accuracy: 0.47 °C, resolution: 0.1 °C. Tempcon, Arundel, UK).

Extra measurements were taken in the thickest part of the *sargassum* mat at 8 m, 4 m and zero m from the first clean area in the open ocean to shore. The depth of the mat using a transect tape (cm thickness) and DO_2 levels using a HQ30D flexi oxygen meter (Hach Environmental) were recorded ($n = 3$).

2.6. Statistical analyses

Within Soliman Bay species grouped into four groups, algae, seagrass, and corals (% m^2) and numbers of fish per m^3 in transects 20 m, 40 m, 60 m and >100 m from the strandline in areas under the *Sargassum* mats and adjacent to the mats were examined using non-parametric multivariate techniques contained in PRIMER 7 (PrimerE Ltd: Plymouth Routines in Multivariate Ecological Research, Version 7). All PRIMER 7 tests were based on square root transformed data in S17 Bray Curtis similarity matrices [15] with 9999 permutations or raw data and Type III sums of squares were used to calculate P -values due to the unbalanced design. The groups under the *Sargassum* mats and adjacent areas were tested for similarities using a permutational multivariate analysis of variance (PERMANOVA) main test. A PERMANOVA posthoc pairwise test examined similarities between groups using the variables of transects under the *Sargassum* mats or adjacent to them with areas and species abundance as factors.

To discriminate between the effects established by PERMANOVA, a non-metric multidimensional scaling (nMDS) plot was visually explored [4] to examine patterns of species distribution within Soliman Bay in the areas under the *Sargassum* mats and adjacent to the mats. Species under the *Sargassum* mats and in adjacent areas in Soliman Bay were assessed using Pearson rank correlation coefficients. Correlations of species $R = 0.5$ for the nMDS were plotted for visualization of results as an ordination. Pearson's correlation coefficient measures the strength and direction of the association between the species. An nMDS ordination identified the species within groups that best explain variation between areas and determine species distribution that contributed most to differences between areas. Species distributions were plotted using bubble plots for visualization. Differences between areas were also examined using an analysis of similarities (ANOSIM) test, analogous to a one-way ANOVA.

Similarity percentage analysis (SIMPER) was employed to examine groups within areas under the *Sargassum* mats and adjacent to the mats. The contribution of the groups in each area was visualised using bar graphs, highlighting community evenness between areas in Soliman Bay.

Using parametric tests contained within MINITAB (MINITAB Inc®, version 17.3.1), t -tests were used to examine differences of light intensity (lux) and temperature. A One-way ANOVA was used to examine relationships with light intensity (lux) at 20 m, 40 m, and 60 m under

the *Sargassum* mats; to examine *Sargassum* mat depth and oxygen content ($\text{O}_2 \text{ mg L}^{-1}$), and to examine differences of seagrass growth mm d^{-1} and mass g d^{-1} between localities. Values of seagrass tissue growth and mass between the three localities were visualized using Box Plots. Because of the unbalanced design, a Levene's test was used to check for equal variance ($P \geq 0.05$).

A Two-way ANOVA was used to examine differences between days with different intensity of Active Radiation (PAR) and the photosynthetic ability of *Sargassum* spp. with oxygen flux ($\text{O}_2 \text{ mg L}^{-1} \text{h}^{-1} \text{cm}^{-2}$) in Soliman Bay.

All count data were square-root transformed, and all measurement data were log-transformed, with the suitability of the transformations scrutinized by examining residuals. Post-hoc pairwise Tukey HSD comparison tests separated values into distinct subsets in all ANOVAs.

3. Results

3.1. Seagrass productivity in Yal Ku, Half Moon Bay and Soliman Bay

Growth rate (mm.d^{-1}) of the seagrass, *T. testudinum*, was significantly greater in the Half Moon Bay and Yal Ku lagoon compared to Soliman Bay, with $5 \pm 0.2 \text{ mm d}^{-1}$ ($n = 119$, mean $\pm$ SE), $7 \pm 0.3 \text{ mm d}^{-1}$ ($n = 35$, mean $\pm$ SE) and $2.9 \pm 0.1 \text{ mm d}^{-1}$ ($n = 42$, mean $\pm$ SE), respectively (Fig. 3 A, One-way ANOVA, sites vs. growth rate: $F_{2,193} = 32.2$, $p \leq 0.001$). Mass gained was also greater in Half Moon Bay and Yal Ku lagoon compared to Soliman Bay, $0.07 \pm 0.01 \text{ g d}^{-1}$ ($n = 4$, mean $\pm$ SE), $0.03 \pm 0.01 \text{ g d}^{-1}$ ($n = 3$, mean $\pm$ SE) and $0.01 \pm 0.004 \text{ g d}^{-1}$ ($n = 3$, mean $\pm$ SE) respectively (Fig. 3 B, One-way ANOVA, sites vs. mass gain: $F_{2,7} = 15.2$, $p \leq 0.01$). The interquartile ranges of *T. testudinum* growth rates per day and mass gained per day were lower in Soliman Bay.

Dissolved oxygen ($\text{DO}_2 \text{ mg L}^{-1}$) was greater from Half Moon Bay and Yal Ku lagoon, compared with Soliman Bay, with $8.9 \pm 0.01 \text{ DO}_2 \text{ mg L}^{-1}$ ($n = 18$, mean $\pm$ SE), $9 \pm 0.02 \text{ DO}_2 \text{ mg L}^{-1}$ ($n = 18$, mean $\pm$ SE) and $4.9 \pm 0.7 \text{ DO}_2 \text{ mg L}^{-1}$ ($n = 18$, mean $\pm$ SE) respectively (Fig. 3 C, One-way ANOVA, sites vs. DO_2 : $F_{2,51} = 31.4$, $p \leq 0.001$).

3.2. Spatial variation of macrobenthos in Soliman Bay

Biota within the quadrats ($n = 66$) in Soliman Bay corresponded to 4 groups (Table 2). Groups in areas under the *Sargassum* mats and leachate compared with areas next to the *Sargassum* mats had different compositions (PERMANOVA main test: $F_{6,216} = 18.3$, $p \leq 0.001$, Table 3).

Non-metric dimensional scaling (nMDS) confirmed the separation of the groups between areas under the *Sargassum* mats and adjacent to the mats within Soliman Bay (Fig. 4 A) (ANOSIM (R : 0.5, $p \leq 0.01$). A greater frequency of quadrats under the *Sargassum* mats contained macroalgae (Fig. 4 B and C). Two groups, algae and seagrass were found only in areas under the *Sargassum* and comparisons of their abundance in those areas were not significantly different (PERMANOVA pairwise test: $t = 5.2$, $P \geq 0.05$). Seagrass, algae, corals, and fish were found in areas adjacent to the *Sargassum* mats in Soliman Bay and were significantly different in their abundances (PERMANOVA main test: area vs. species abundance, $F_{1,43} = 6.6$, $p \leq 0.001$). Comparisons of abundances between all groups in areas adjacent the *Sargassum* were significantly different (PERMANOVA pairwise tests: $t = 1.9$ to 3.8, $P \leq 0.001$).

In areas under the *Sargassum* mats, contained attached algae and decaying seagrass, and the percent contribution was 70.3% and 29.7% respectively (SIMPER analysis). Algae, seagrass, fish, and corals were found in areas adjacent to the *Sargassum* mats, and the percent contribution was 11.2%, 45.3%, 27.6%, and 15.9% respectively (Fig. 5 A). A total of 20 species from four groups were found in areas adjacent to the *Sargassum* mats in Soliman Bay. A total of 7 species from two groups, seagrass and algae were found in areas under the *Sargassum* mats and leachate in Soliman Bay. The community structure in areas away from the *Sargassum* had greater evenness and species richness (Fig. 5 B and C).

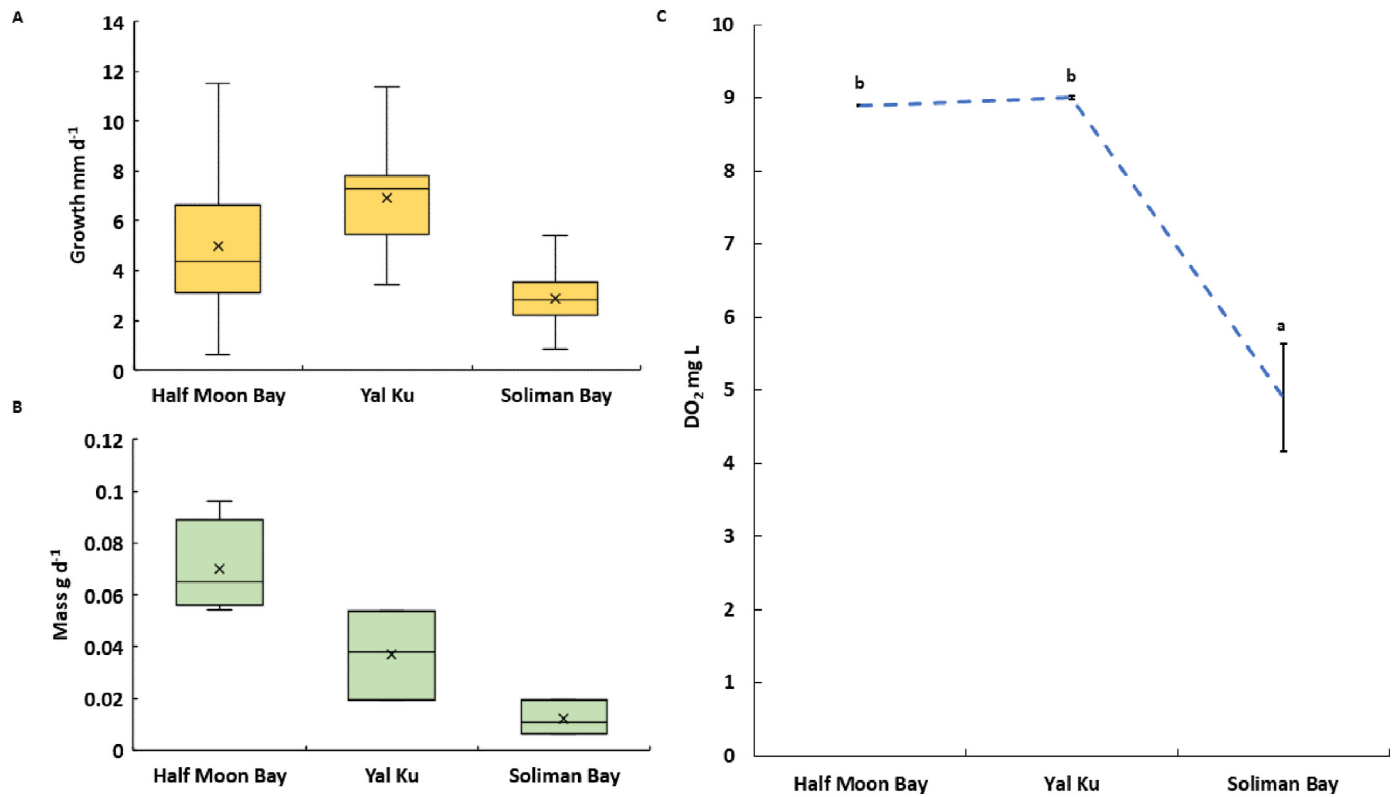


Fig. 3. Box plots illustrating interquartile ranges of, **A**, seagrass growth rate mm per day from three Mexican bays, One-way ANOVA, sites vs. growth rate- $F_{2,193} = 32.2$, $p \leq 0.001$. **B**, seagrass mass gain grams per day from three Mexican bays, One-way ANOVA, sites vs. mass gain- $F_{2,7} = 15.2$, $p \leq 0.01$. **C**, Dissolved oxygen recordings mg per litre from three Mexican bays, One-way ANOVA, sites vs. DO₂- $F_{2,51} = 31.4$, $p \leq 0.001$ (mean $\pm$ SE). *Letters above bars = Tukey's pairwise comparison tests.

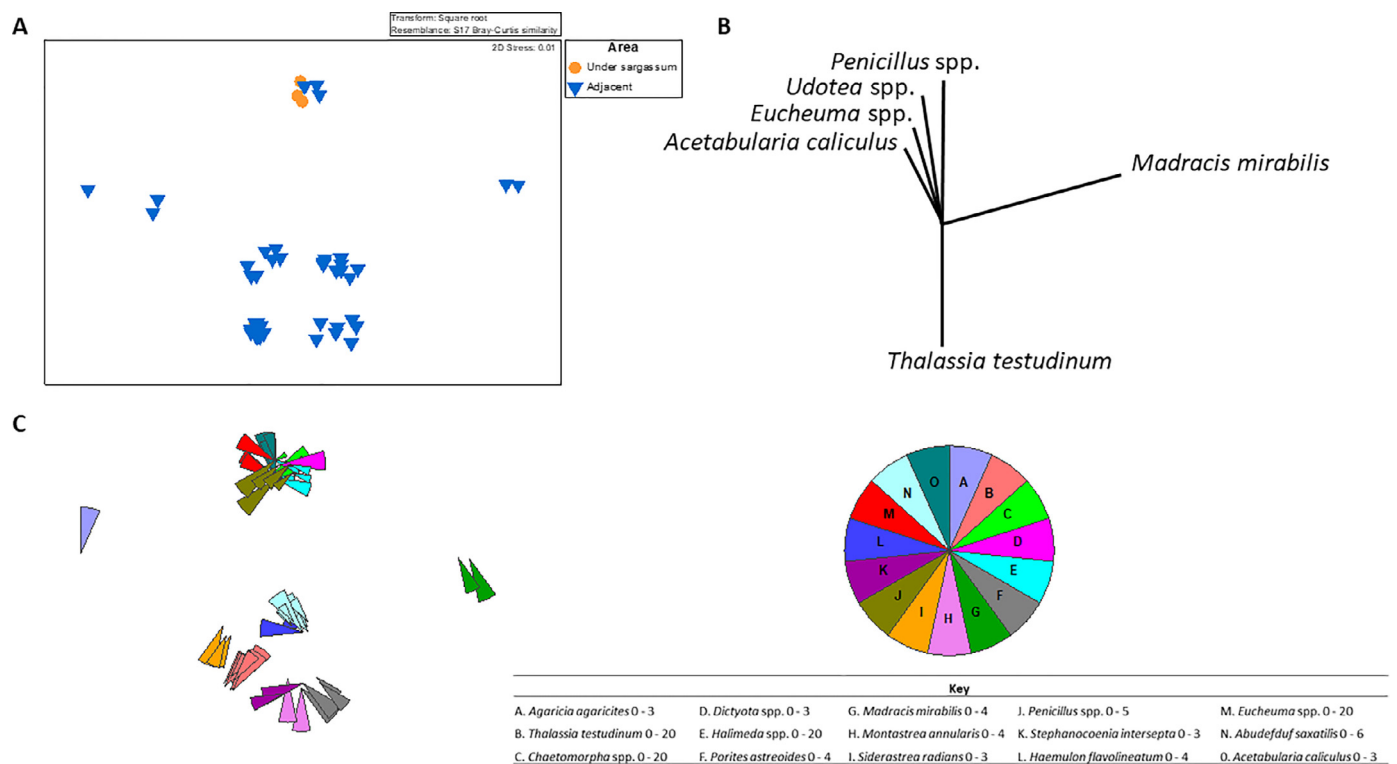


Fig. 4. Non-metric multidimensional scaling (nMDS) plot illustrating **A**, differences in distribution of groups from areas under the *Sargassum* mats and in adjacent areas in Soliman Bay (ANOSIM: $R = 0.5$, $p \leq 0.01$). **B**, vectors based on Pearson correlation (R) values = 0.50, illustrating the group most associated to each area. **C**, the size of the bubble symbol is proportional to the percentage surface area of algae, seagrass and corals, and abundance of fish within areas (see key for details).

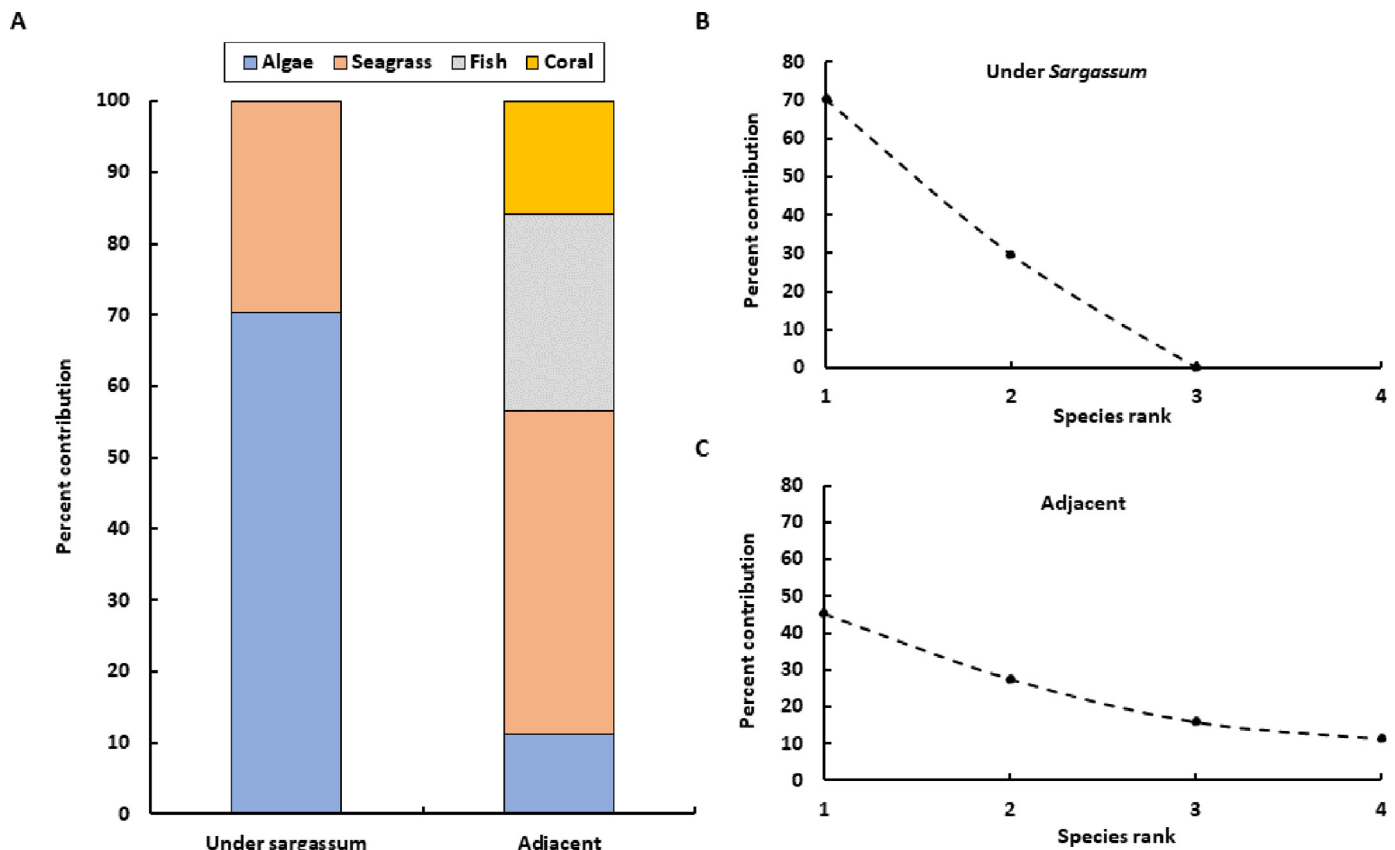


Fig. 5. **A**, community contribution (%) of organisms from one of four groups in quadrats ($n = 36$) (m^2) from areas under the *Sargassum* mats and in areas adjacent to the *Sargassum* mats in Soliman Bay. **B**, community evenness of species under the *Sargassum* mats, illustrating a high dominance with a rapid decline, and **C**, community evenness of species adjacent the *Sargassum* mats, illustrating a greater community evenness compared to areas under the *Sargassum*.

3.3. Light, temperature, and dissolved oxygen availability in Soliman Bay from *Sargassum*

Light intensity (measured at 30 cm below the water surface over two days, a high PAR and low PAR day) expressed as lux, was lower in areas of the thick *Sargassum* canopy and leachate, $13,553 \pm 2863.7$ lx ($n = 213$, mean $\pm$ SE). Areas adjacent to the *Sargassum* mats within Soliman Bay had higher lux values, with $42,468 \pm 4194.1$ lx ($n = 111$, mean $\pm$ SE) (Fig. 6 A, Paired t-test, lux vs. area: $P \leq 0.001$). Water temperature was 5.1 ± 0.1 °C (mean $\pm$ SE) warmer under the *Sargassum* mats, compared to adjacent areas in Soliman Bay, 33.5 ± 0.1 °C ($n = 240$, mean $\pm$ SE) and 28.7 ± 0.1 °C ($n = 111$, mean $\pm$ SE) respectively (Fig. 6 A, t-test, water temperature (°C) vs. area: $P \leq 0.001$).

In areas of the leachate, at 20 m, 40 m, and 60 m from the *Sargassum* mats lux values increased. The leachate became less visible with distance and lux was 6217 ± 833 lx ($n = 516$, mean $\pm$ SE), 5208 ± 752.7 lx ($n = 654$, mean $\pm$ SE) and $19,285 \pm 2769.7$ lx ($n = 245$, mean $\pm$ SE) respectively (Fig. 6 B, One-way ANOVA, distance from *Sargassum* (m) vs. lux: $F_{2,1412} = 30.3$, $p \leq 0.001$). A 73 % reduction in light was found in areas with leachate vs. clearer water.

The amount of oxygen flux varied between days due to light intensities in the water column. Day one had a high PAR (time of incubation 13:00 h), and day two had a low PAR (time of incubation 10:00 h). The net and gross photosynthesis (p_n and p_g) on day one was greater. Oxygen fluxes calculated for p_n , 10.9 ± 0.8 O₂ mg L⁻¹ h⁻¹ cm⁻² ($n = 5$, mean $\pm$ SE) and p_g , 13.9 ± 0.3 O₂ mg L⁻¹ h⁻¹ cm⁻² ($n = 5$, mean $\pm$ SE), compared to day 2 differed with p_n , 5.7 ± 1.6 O₂ mg L⁻¹ h⁻¹ cm⁻² ($n = 5$, mean $\pm$ SE) and p_g , 7.6 ± 1.6 O₂ mg L⁻¹ h⁻¹ cm⁻² ($n = 5$, mean $\pm$ SE), respectively (Fig. 7). In dark conditions, a *post-hoc* pairwise test highlighted no significant difference with oxygen flux, -3 ± 0.9 O₂ mg L⁻¹ h⁻¹ cm⁻²

($n = 5$, mean $\pm$ SE) and -2 ± 0.2 O₂ mg L⁻¹ h⁻¹ cm⁻² ($n = 5$, mean $\pm$ SE) for day one and day two, respectively (Fig. 7, Two-way ANOVA, Oxygen flux vs. day: $F_{1,26} = 10.5$, $p \leq 0.01$ and Oxygen flux vs. photosynthesis process: $F_{2,26} = 58$, $p \leq 0.001$).

From the middle of the *Sargassum* mat to the ocean-facing edge the mat thickness varied between 36.7 ± 3.5 cm ($n = 3$, mean $\pm$ SE) to 53 ± 5.7 cm ($n = 3$, mean $\pm$ SE) (One-way ANOVA, *Sargassum* mat thickness vs. area: $F_{2,6} = 3.9$, $p \geq 0.05$). Levels of dissolved oxygen (O₂ mg L⁻¹) at 8 m and 4 m from the ocean-facing edge were recorded at 0.5 ± 0.05 O₂ mg L⁻¹ ($n = 3$, mean $\pm$ SE) and 1.4 ± 0.2 O₂ mg L⁻¹ ($n = 3$, mean $\pm$ SE) respectively. Dissolved oxygen at the ocean-facing edge of the *Sargassum* mat was significantly different to levels further into the *Sargassum* mat, measured 8.5 ± 0.2 O₂ mg L⁻¹ ($n = 3$, mean $\pm$ SE) (dissolved oxygen vs. area: $F_{2,6} = 181.4$, $p \leq 0.001$).

4. Discussion

In this study we found that considerable quantities of *Sargassum* mats in Mexican coastal bays, Quintana Roo, create a trophic collapse of the flora and fauna. We found a distinct change from a high habitat complexity leading to reduced complexity and evenness, evidenced by the seven-fold decrease of *Thalassia testudinum* productivity and reduced abundance of coral bommies, with increases and high dominance of attached algae covering areas of the benthos in areas under the *Sargassum* mats. Analysis revealed that these impacts lead to reduced trophic levels in Soliman Bay. Corals and seagrass are ecosystem engineers [14,50]. amongst their many benefits they provide habitat and structure for many organisms, particularly juvenile and vulnerable species [42], therefore reductions of these groups lead to losses of biodiversity. A well-established habitat complexity with interconnected habitat mo-

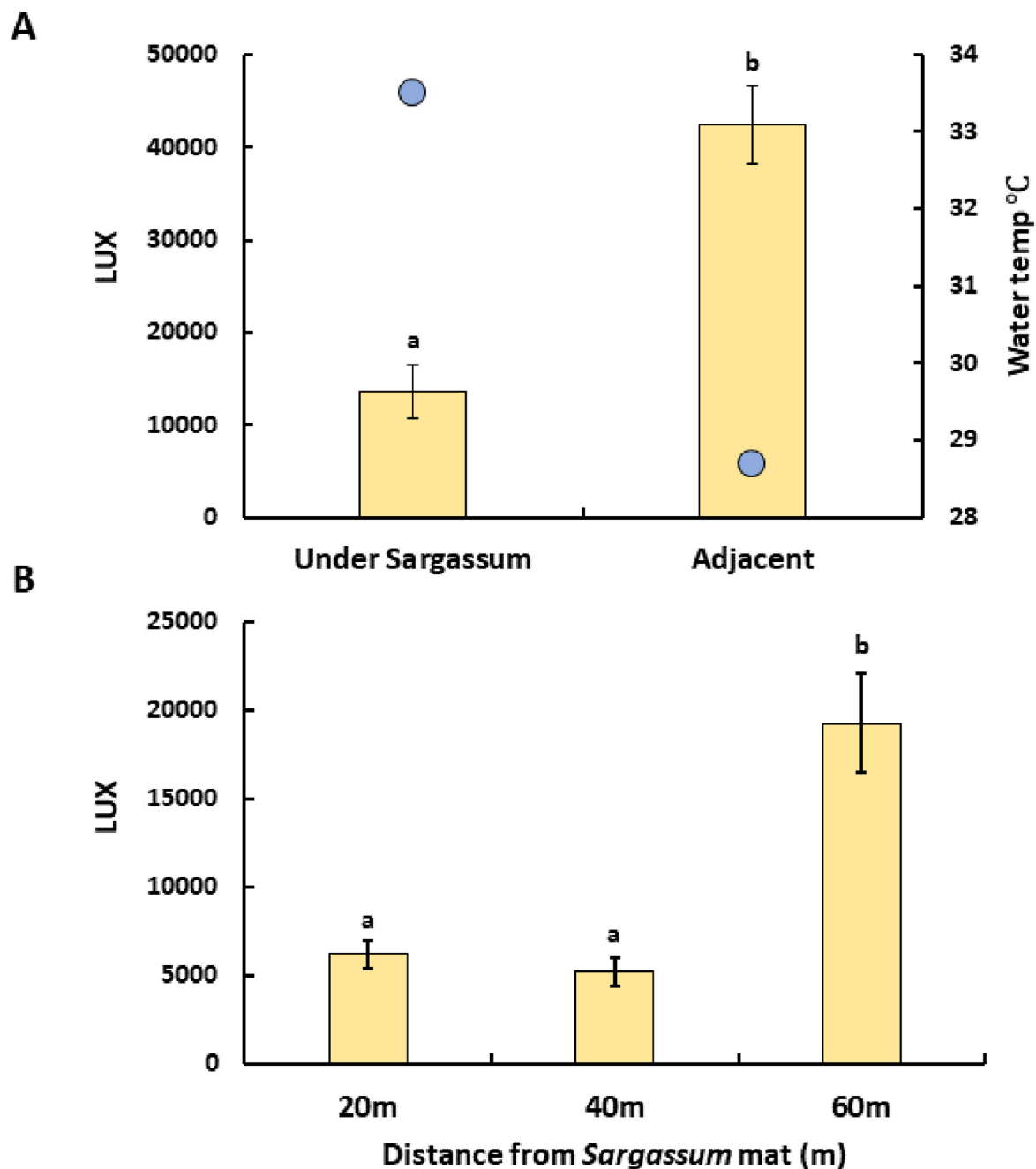


Fig. 6. Light intensity (lux) m² and water temperature (°C) readings measured at 30 cm below the water surface in areas under the *Sargassum* and adjacent areas in Soliman Bay. **A**, Area vs. lux and temperature (°C), Paired t-tests: $P \leq 0.001$ and $P \leq 0.001$ respectively. Temperature = blue dots **B**, distance from *Sargassum* (m) vs. lux, One-way ANOVA: $F_{2,1412} = 30.3$, $p \leq 0.001$. Mean $\pm$ SE. Letters above the bars = Tukey's pairwise test. .

saics will enable greater protection for vulnerable organisms [60]. The increase of niches provides a healthy ecosystem improving trophic subsidies and complex food webs [46,52]. Greater trophic levels within a food web drive the ecological structure through more interactions and transfer of energy [52]. The presence of *Sargassum* mats in Mexico impact food webs, alter the benthic structure and create changes throughout the ecosystem [58]. Other authors report on reduced species interactions and abundance due to impacts from *Sargassum* [5,57,58,66]. These losses are becoming more common in Mexico [37,68] with declines in habitat functionality and trophic diversity [17]. *Sargassum* blooms in Mexico lead to losses of nursery habitats, coupled with high fish mortalities and coastal dead zones [34]. This is the first study to detail direct

impacts to seagrass productivity due to decaying *Sargassum* mats and leachate.

Before the smothering and stranding of *Sargassum* in Soliman Bay the water was clear, with less algal cover coupled with minimal damage to corals and sea fans (D. Graham pers comm). In areas under and close to the *Sargassum* mats in Soliman Bay, there were dead seagrass beds covered in algae. The presence of seagrasses in the areas not affected by *Sargassum* mats supported greater trophic complexity than areas found in the impacted sites. This has also been reported from temperate seagrass meadows [72]. Seven species of hard corals and eleven species of fish were observed in areas away from the *Sargassum* mats. Additionally, the areas further away from the *Sargassum* mats had a lower cover of al-

Table 2

Species from quadrats identified within areas under the *Sargassum* mats and areas adjacent to the *Sargassum* mats in Soliman Bay. Note, fish species were categorized into one broad group, but trophic guilds ranged from herbivores to invertivores.

Group	Species
Algae	<i>Acetabularia caliculus</i>
	<i>Caulerpa</i> spp.
	<i>Chaetomorpha</i> spp.
	<i>Dasycladus vermicularis</i>
	<i>Dictyota</i> spp.
	<i>Eucheuma</i> spp.
	<i>Halimeda</i> spp.
	<i>Halophyllia minor</i>
	<i>Laurencia</i> spp.
	<i>Penicillus</i> spp.
	<i>Udotea</i> spp.
	<i>Syringodium filiforme</i>
	<i>Thalassia testudinum</i>
Coral	<i>Agaricia agaricites</i>
	<i>Madracis mirabilis</i>
	<i>Orbicella annularis</i>
	<i>Porites astreoides</i>
	<i>Siderastrea radians</i>
	<i>Siderastrea siderea</i>
	<i>Stephanocoenia intersepta</i>
Fish	<i>Abudefduf saxatilis</i>
	<i>Acanthurus bahianus</i>
	<i>Chaetodon capistratus</i>
	<i>Haemulon flavolineatum</i>
	<i>Halichoeres bivittatus</i>
	<i>Labrisomus guppyi</i>
	<i>Microspathodon chrysurus</i>
	<i>Stegastes adustus</i>
	<i>Stegastes fasciatus</i>
	<i>Stegastes leucostictus</i>
	<i>Thalassoma bifasciatum</i>

Table 3

Results from the PERMANOVA Pairwise tests, examining differences and similarities between areas under *Sargassum* mats and adjacent to the mats in Soliman Bay.

Area	Meters from strandline	t - value	Significance
<i>Sargassum</i> mat	20 vs. 40	0.7	≥ 0.05
	20 vs. 60	1.9	≥ 0.05
	40 vs. 60	1.7	≥ 0.05
Adjacent	20 vs. 40	0.9	≥ 0.05
	20 vs. 60	0.4	≥ 0.05
	40 vs. 60	0.8	≥ 0.05
	20 vs. >100	1.5	≥ 0.05
	40 vs. >100	1.7	≤ 0.05
	60 vs. >100	1.2	≥ 0.05
Both	20 vs. A.20	4.3	≤ 0.001
	20 vs. A.40	2.4	≤ 0.01
	20 vs. A.60	4.3	≤ 0.001
	40 vs. A.20	4.3	≤ 0.001
	40 vs. A.40	2.2	≤ 0.05
	60 vs. A.20	3.7	≤ 0.001
	60 vs. A.40	1.8	≤ 0.05
	60 vs. A.60	3.7	≤ 0.001
	20 vs. A.>100	6.3	≤ 0.001
	40 vs. A.>100	7.5	≤ 0.001
	60 vs. A.>100	6.7	≤ 0.001

A = adjacent to the mats.

gae, and the community structure was healthier. The increase of sessile benthic organisms created a greater habitat complexity, which supports high densities of species richness and biomass with an improved ecosystem resilience [8,23,48].

With reduced trophic subsidies the flow of energy through the ecosystem will be disrupted, leading to a trophic collapse. These reductions lead to top-down changes in community structure [10,58], as

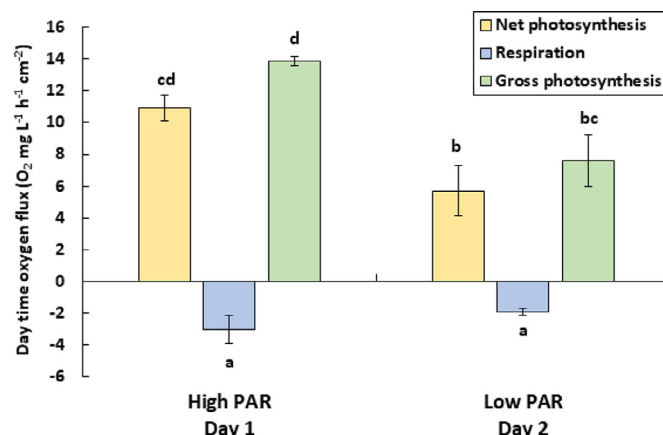


Fig. 7. Differences of oxygen flux. **A**, oxygen flux measurements over two days using chambers ($n = 5$ O₂ mg L⁻¹ h⁻¹ cm⁻²) during daytime with high and low Photosynthetically Active Radiation (PAR) (Two-way ANOVA, day vs. oxygen flux- $F_{1,26} = 10.5$, $p \leq 0.01$ and photosynthesis vs. oxygen flux- $F_{2,26} = 58$, $p \leq 0.001$). **B**, Oxygen measurements under the *Sargassum* mat at different distances from the *Sargassum*/ocean edge (One-way ANOVA, *Sargassum* mat thickness vs. area- $F_{2,6} = 3.9$, $p \geq 0.05$, and dissolved oxygen vs. area- $F_{2,6} = 181.4$, $p \leq 0.001$). Mean $\pm$ SE. Letters above the bars = Tukey's pairwise test.

seen with the high dominance of algal growth, with impacted seagrass beds in areas under the *Sargassum* mats in Soliman Bay. The change in seagrass community structure resulted in more generalist species, displacing the specialist species [58], such as the increase in algal coverage and communities found in this study. The loss of *T. testudinum* and coral will lead to greater impacts from storm events due to resuspension of sediments and coastal erosion [66]. Impact to seagrass habitats will also reduce carbon sequestration [47]. Reductions of carbon drawdown will decrease the transport of organic matter [2,48] and protection for juvenile fish [43,44] and invertebrates [38,72].

Seagrass loss also decreases ecological stability [27]. Toxic leachate from decaying *Sargassum* can reduce DO₂ levels to 1.0 mg L⁻¹ and pH to 7.4 [5,40,66]. Marine species have an optimum zone of tolerance [30]. Thus, due to the degraded environmental conditions caused by the *Sargassum* mats, occurrences of dead or moribund fish will increase. This is common with decomposing *Sargassum* [57]. Reduced pH exacerbates losses to the ecosystem structure and function, particularly to coral reefs. A reduced pH can also decrease species richness by more than 20%. Sunday et al., [63] found declines of coral biodiversity and reduced habitat complexity of up to 30% due to reduced pH. As the water quality deteriorates, this will reduce the settlement of coral larvae. Antonio-Martínez et al., [5] found *Acropora palmata* coral larvae had reduced dispersal and modified swimming behavior when exposed to *Sargassum* leachate [5]. This explains the absence of corals in areas close to the *Sargassum* mats and leachate. Rodríguez-Martínez et al., [57] noted 80 species of dead fish and invertebrates along the Mexican Caribbean coastline, including the keystone algivorous urchin *Diadema antillarum* [9]. These mortalities were due to the smothering effect of the *Sargassum* mats and leachate [57].

The *Sargassum* mats in Soliman Bay reduced the light intensity and decreased dissolved O₂ to levels fatal to organisms. The reduced O₂ was likely due to microbial respiration [3]. High levels of dissolved O₂ are vital for marine organism health and productivity. When levels fall below 4 mg L⁻¹ marine organism metabolisms are affected. When levels drop below 2 mg L⁻¹ high mortalities of fish and crustaceans occur [25,67]. We found low O₂ levels in areas under the *Sargassum* mats in Soliman Bay with readings less than 1 mg L⁻¹, which can be fatal to marine organisms. Studies in the Gulf of Mexico found that dissolved oxygen below 3.5 mg L⁻¹ causes losses of more than 80% of coral cover [29]. Combined with respiration from decomposition, we found that

water temperature was more than 4.5°C warmer under the *Sargassum* mats. The increase in temperature will also reduce dissolved O₂ [25]. Increased temperatures will reduce the biomass of taxonomic groups and reduce the transfer of energy between trophic levels in a food web [64]. In the adjacent land-locked mangrove forests of Soliman Bay, an extreme change in temperature is dealt with by resident fish populations. The fish can seek environmental buffering provided by the shade of the mangrove tree canopy. The fish become less stressed [22]. The seaward side of Soliman Bay is an open system and mobile fauna can seek areas away from the *Sargassum* mats, but only if they do not become trapped under the *Sargassum* canopy.

Environmental impacts reduce the growth and biomass of seagrass [57,62,66]. Losses of seagrasses have consequences for coastal productivity if atmospheric CO₂ sequestration rates and carbon sinks decline [2,47]. As a result, declining provisions of essential coastal ecosystem services will ensue ([65,31]). These impacts lead to economic losses in Quintana Roo, due to declines in tourism [19,39,54,55].

5. Conclusion

The Mexican tourist industry depends on healthy and functioning coastal marine ecosystems. Management priorities should focus on minimizing coastal impact from *Sargassum* stranding and smothering. Academic institutions, stakeholders, NGOs and local municipalities should work together to mitigate these impacts. Damage to the structure and function of seagrass beds and coral reefs compromise the community structure [1]. These changes alter species distributions [51], taxonomic diversity, biomass, and productivity. Rapid solutions are required to prevent further ecological, environmental, and economic losses to ameliorate impacts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank M. Martin, M. Kosek, G. Georgiou, and R. Johnson for support during field activities. Gratitude goes to Operation Wallacea, for providing research funding for IH. We also thank D. Graham for Soliman Bay beach assess and for historical site knowledge, and J. Ensley and M. Johnson for their help with logistics.

Literature cited

- [1] T.D. Ainsworth, C.L. Hurd, R.D. Gates, P.W. Boyd, How do we overcome abrupt degradation of marine ecosystems and meet the challenge of heat waves and climate extremes? *Glob. Change Biol.* 26 (2020) 343–354.
- [2] E.A. Aller, J.S. Eklöf, M. Gullström, U. Kloiber, H.W. Linderholm, L.M. Nordlund, Temporal variability of a protected multispecific tropical seagrass meadow in response to environmental change, *Environ. Model. Assess* 191 (2019) 774.
- [3] A.H. Altieri, R.J. Diaz, Dead zones—Oxygen depletion in coastal ecosystems, in: *World Seas—An Environmental Evaluation*, Academic Press, 2019, pp. 453–473.
- [4] M. Anderson, R. Gorley, K.P. Clarke, For PRIMER—Guide to Software and Statistical Methods, PRIMER-E, Plymouth, UK, 2008.
- [5] F. Antonio-Martínez, Y. Henaut, A. Vega-Zepeda, A.I. Cerón-Flores, R. Raigoza-Figueras, N.P. Cetz-Navarro, J. Espinoza-Avalos, Leachate effects of pelagic *Sargassum* spp. on larval swimming behavior of the coral *Acropora palmata*, *Sci. Rep.* 10 (2020) 1–13.
- [6] R.S.K. Barnes, Do different sympatric seagrasses support macrobenthic faunas of differing composition, abundance, biodiversity or patchiness? *Marine Environmental Research* (2020) 160, 104983.
- [7] S.G. Belford, D.A.T. Phillip, M.G. Rutherford, S. Schmidt-Roach, E.J. Duncan, Biodiversity of coral reef communities in marginal environments along the north-eastern coast of Trinidad, Southern Caribbean, *PAFMB* 2 (2019) 180017.
- [8] D.K. Bolton, E.L. Johnston, M.A. Coleman, G.F. Clark, Caught between a rock and a hard place: fish predation interacts with crevice width and orientation to explain sessile assemblage structure, *Mar. Environ. Res.* 140 (2018) 31–40.
- [9] N. Cabanillas-Terán, H.A. Hernández-Arana, M.Á. Ruiz-Zárate, A. Vega-Zepeda, A. Sanchez-Gonzalez, *Sargassum* blooms in the Caribbean alter the trophic structure of the sea urchin *Diadema antillarum*, *PeerJ* 7 (2019) e7589.
- [10] I. Cáceres, E.C. Ibarra-García, M. Ortiz, M. Ayón-Parente, Rodríguez-Zaragoza FA, Effect of fisheries and benthic habitat on the ecological and functional diversity of fish at the Cayos Cochinos coral reefs (Honduras), *Mar. Biodivers.* 50 (2020) 9.
- [11] CARICOMP, CARICOMP Methods Manual Levels I & II, in: *Methods for Mapping and Monitoring of Physical and Biological Parameters in the Coastal Zone of the Caribbean*, Bulletin of Marine Science, 2001, pp. 29–32.
- [12] C. Cattano, S. Agostini, B.P. Harvey, S. Wada, F. Quattrocchi, G. Turco, K. Inaba, J.M. Hall-Spencer, M. Milazzo, Changes in fish communities due to benthic habitat shifts under ocean acidification conditions, *Sci. Total Environ.* (2020) 138501.
- [13] V. Chávez, A. Uribe-Martínez, E. Cuevas, R.E. Rodríguez-Martínez, B.I. van Tussenbroek, V. Francisco, M. Estévez, L.B. Celis, L.V. Monroy-Velázquez, R. Leal-Bautista, L. Álvarez-Filip, Massive influx of pelagic *Sargassum* spp. on the coasts of the Mexican Caribbean 2014–2020—Challenges and opportunities, *Water (Basel)* 12 (2020) 2908.
- [14] P.Y. Cheung, Y. Nozawa, T. Miki, Ecosystem engineering structures facilitate ecological resilience—A coral reef model, *Ecol. Res.* (2021).
- [15] K.R. Clarke, P.J. Somerfield, M.G. Chapman, On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray–Curtis coefficient for denuded assemblages, *JEMBE* 330 (2006) 55–80.
- [16] K.J. Collins, A.M. Suonpää, J.J. Mallinson, The impacts of anchoring and mooring in seagrass, Studland Bay, Dorset, UK, *Underwater Technol.* 29 (2010) 117–123.
- [17] A. Dobson, D. Lodge, J. Alder, G.S. Cumming, J. Keymer, J. McGlade, H. Mooney, J.A. Rusak, O. Sala, V. Wolters, D. Wall, Habitat loss, trophic collapse, and the decline of ecosystem services, *Ecology* 87 (2006) 1915–1924.
- [18] N. Estrada-Saldívar, E. Jordán-Dalhgren, R.E. Rodríguez-Martínez, C. Perry, L. Álvarez-Filip, Functional consequences of the long-term decline of reef-building corals in the Caribbean—Evidence of across-reef functional convergence, *R. Soc. Open Sci.* 6 (2019) 190298.
- [19] B. Faber, C. Gaubert, Tourism and economic development—Evidence from Mexico's coastline, *Am. Econ. Rev.* 109 (2019) 2245–2293.
- [20] Jim Gower, Erika Young, Stephanie King, Satellite images suggest a new *Sargassum* source region in 2011, *Remote Sens. Lett.* 4 (8) (2013) 764–773.
- [21] I.W. Hendy, L. Michie, B.W. Taylor, Habitat creation and biodiversity maintenance in mangrove forests—Terrestrial bivalves as ecosystem engineers, *PeerJ* 2 (2014) e591.
- [22] I.W. Hendy, O. Burt, S. Clough, L. Young, S.M. Cragg, Mosquitofish avoid thermal stress by moving from open water to the shade of the mangrove *Rhizophora mangle*, *MEPS* 637 (2020) 103–116.
- [23] E. Hensel, J.E. Allgeier, C.A. Layman, Effects of predator presence and habitat complexity on reef fish communities in The Bahamas, *Mar. Biol.* 166 (2019) 136.
- [24] J.A. Herrera-Silveira, M.A. Pech-Cardenas, S.M. Morales-Ojeda, S. Cinco-Castro, A. Camacho-Rico, J.P. Sosa, J.E. Mendoza-Martínez, E.Y. Pech-Poot, J. Montero, C. Teutli-Hernandez, Blue carbon of Mexico, carbon stocks and fluxes—A systematic review, *PeerJ* 8 (2020) e8790.
- [25] J.P. Hobbs, C.A. McDonald, Increased seawater temperature and decreased dissolved oxygen triggers fish kill at the Cocos (Keeling) Islands, Indian Ocean, *J. Fish. Biol.* 77 (2010) 1219–1229.
- [26] T.P. Hughes, M.J. Rodrigues, D.R. Bellwood, D. Ceccarelli, O. Hoegh-Guldberg, L. McCook, N. Moltschniowskyj, S.M. Pratchett, R.S. Steneck, B. Willis, Phase shifts, herbivory, and the resilience of coral reefs to climate change, *Curr. Biol.* 17 (2007) 360–365.
- [27] E. Jankowska, L.N. Michel, G. Lepoint, M. Włodarska-Kowalczyk, Stabilizing effects of seagrass meadows on coastal water benthic food webs, *JEMBE* 510 (2019) 54–63.
- [28] E.M. Johns, R. Lumpkin, N.F. Putman, R.H. Smith, F.E. Muller-Karger, D.T. Rueda-Roa, C. Hu, M. Wang, M.T. Brooks, L.J. Gramer, F.E. Werner, The establishment of a pelagic *Sargassum* population in the tropical Atlantic—Biological consequences of a basin-scale long distance dispersal event, *Prog. Oceanogr.* 182 (2020) 102269.
- [29] M.A. Johnston, M.F. Nuttall, R.J. Eckert, R.D. Blakeway, T.K. Sterne, E.L. Hickerson, J.A. Embesi, Localized coral reef mortality event at east flower garden bank, gulf of Mexico, *Bull. Mar. Sci.* 95 (2) (2019) 239–250.
- [30] E. Kikuchi, F.R. De Grande, R.M. Duarte, T. Vaske-Júnior, Thermal response of demersal and pelagic juvenile fishes from the surf zone during a heat-wave simulation, *J. Appl. Ichthyol.* 35 (2019) 1209–1217.
- [31] F. Kurniawan, M.N. Arkham, A. Rustam, Y.P. Rahayu, N.S. Adi, L. Adrianto, A. Damar, An ecosystem services perspective for the economic value of seafood production supported by seagrass ecosystems—An exercise in Derawan Island, Indonesia, *IOP Conference Series—Earth and Environmental Science*, 414, IOP Publishing, 2020 No. 1.
- [32] D.D.A. Laffoley, H.S.J. Roe, M.V. Angel, J. Ardron, N.R. Bates, L.L. Boyd, S. Brooke, K.N. Buck, C.A. Carlson, B. Causey, M.H. Conte, The Protection and Management of the Sargasso Sea—The Golden Floating Rainforest of the Atlantic Ocean—Summary Science and Supporting Evidence Case, Sargasso Sea Alliance, 2011.
- [33] M.W. Lomas, N.R. Bates, K.N. Buck, A.H. Knap, Notes on “Microbial productivity of the Sargasso Sea and how it compares to elsewhere” and “The role of the Sargasso Sea in carbon sequestration—Better than carbon neutral? Sargasso Sea Alliance Report Series 6 (10) (2011).
- [34] Lopez C.B., Dortch Q., Jewett E.B., Garrison D. (2008) Scientific Assessment of Marine Harmful Algal Blooms
- [35] J.M. López-Calderón, H.M. Guzmán, G.E. Jácome, P.A. Barnes, Decadal increase in seagrass biomass and temperature at the CARICOMP site in Bocas del Toro, Panama, *Rev. Biol. Trop.* 61 (2013) 1815–1826.
- [36] C. Loume, J. Fortune, G. Gervais, Sargassum invasion of coastal environments—A growing concern, *Am. J. Environ. Sci.* 13 (2017) 58–64.
- [37] A.C.D.A. Mazzucco, P.S. Stelzer, A.F. Bernardino, Substrate rugosity and temperature matters: patterns of benthic diversity at tropical intertidal reefs in the SW Atlantic, *PeerJ* 8 (2020) e8289.

- [38] J.M. McDewitt-Irwin, J.C. Iacarella, J.K. Baum, Reassessing the nursery role of seagrass habitats from temperate to tropical regions—A meta-analysis, *MEPS* 557 (2016) 133–143.
- [39] G. Mendoza-González, M.L. Martínez, R. Guevara, O. Pérez-Maqueo, M.C. Garza-Lagler, A. Howard, Towards a sustainable sun, sea, and sand tourism—The value of ocean view and proximity to the coast, in: *Sustainability*, 10, 2018, p. 1012.
- [40] J.J. Milledge, P.J. Harvey, Golden tides—Problem or golden opportunity? The valorisation of Sargassum from beach inundations, *J. Mar. Sci. Eng.* 4 (2016) 60.
- [41] P.S. Morillo-Velarde, P. Briones-Fourzán, L. Álvarez-Filip, S. Aguiñiga-García, A. Sánchez-González, E. Lozano-Álvarez, Habitat degradation alters trophic pathways but not food chain length on shallow Caribbean coral reefs, *Sci. Rep.* 8 (2018) 4109.
- [42] R.M. Moussa, F. Bertucci, H. Jorissen, C. Gache, V.P. Waqalevu, V. Parravicini, D. Lecchini, R. Galzin, Importance of intertidal seagrass beds as nursery area for coral reef fish juveniles (Mayotte, Indian Ocean), *Reg. Stud. Mar. Sci.* 33 (2020) 100965.
- [43] I. Nagelkerken, C.V. Roberts, G. Van Der Velde, M. Dorenbosch, M.C. Van Riel, E.C. De La Morinière, P.H. Nienhuis, How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale, *MEPS* 244 (2002) 299–305.
- [44] I. Nagelkerken, K.B. Huebert, J.E. Serafy, M.G.G. Grol, M. Dorenbosch, C.J.A. Bradshaw, Highly localized replenishment of coral reef fish populations near nursery habitats, *MEPS* 568 (2017) 137–150.
- [45] M.S. Naumann, C. Jantzen, A.F. Haas, R. Iglesias-Prieto, C. Wild, Benthic primary production budget of a Caribbean reef lagoon (Puerto Morelos, Mexico), *PLoS ONE* 8 (2013).
- [46] A.M. Olson, M. Hessing-Lewis, D. Haggarty, F. Juanes, Nearshore seascape connectivity enhances seagrass meadow nursery function, *Ecol. Appl.* 29 (2019) e01897.
- [47] M.P. Oreska, K.J. McGlathery, L.R. Aoki, A.C. Berger, P. Berg, L. Mullins, The greenhouse gas offset potential from seagrass restoration, *Sci. Rep.* 10 (2020) 1–15.
- [48] J.M. Park, S.N. Kwak, Seagrass fish assemblages in the Namhae Island, Korea—The influences of seagrass vegetation and biomass, *J. Sea Res.* 139 (2018) 41–49.
- [49] C.T. Perry, M.A. Salter, K.M. Morgan, A.R. Harborne, Census estimates of algal and epiphytic carbonate production highlight tropical seagrass meadows as sediment production hotspots, *Front. Mar. Sci.* 6 (2019) 120.
- [50] C.M. Pinnell, G.S. Ayala, M.V. Patten, K.E. Boyer, Seagrass and oyster reef restoration in living shorelines—Effects of habitat configuration on invertebrate community assembly, *Diversity (Basel)* 13 (6) (2021) 246.
- [51] M.L. Pinsky, R.L. Selden, Z.J. Kitchel, Climate-Driven Shifts in Marine Species Ranges—Scaling from Organisms to Communities, *Annual Review of Marine Science* 12 (2020) 153–179.
- [52] D.M. Post, The long and short of food-chain length, *Trends Ecol. Evol.* 17 (2002) 269–277.
- [53] P.J. Ralph, R. Gademann, Rapid light curves—A powerful tool to assess photosynthetic activity, *Aquat. Bot.* 82 (2005) 222–237.
- [54] G.B. Reguero, F. Secaira, A. Toimil, M. Escudero, P. Díaz-Simal, M.W. Beck, C.D. Storlazzi, R. Silva, L.J. Losada, The risk reduction benefits of the mesoamerican reef in Mexico, *Front. Earth Sci.* 7 (2019) 125.
- [55] E. Robles-Zavala, A.G.C. Reynoso, The recreational value of coral reefs in the Mexican Pacific, *Ocean Coast. Manag.* 157 (2018) 1–8.
- [56] R.E. Rodríguez-Martínez, B. van Tussenbroek, E. Jordán-Dahlgren, Afluencia masiva de sargazo pelágico a la costa del Caribe mexicano (2014–2015), *Florcimientos Algaes Nocivos en México. Ensenada: CICESE* 2016 (2016) 352–365.
- [57] R.E. Rodríguez-Martínez, A.E. Medina-Valmaseda, P. Blanchon, L.V. Monroy-Velázquez, A. Almazán-Becerril, B. Delgado-Pech, L. Vásquez-Yeomans, V. Francisco, C.M. García-Rivas, Faunal mortality associated with massive beaching and decomposition of pelagic Sargassum, *Mar. Pollut. Bull.* 146 (2019) 201–205.
- [58] T. Salvaterra, D.S. Green, T.P. Crowe, E.J. O’Gorman, Impacts of the invasive alga *Sargassum muticum* on ecosystem functioning and food web structure, *Biol. Invasions* 15 (2013) 2563–2576.
- [59] G. Sanchez-Rubio, H. Perry, J.S. Franks, D.R. Johnson, Occurrence of pelagic *Sargassum* in waters of the US Gulf of Mexico in response to weather-related hydrographic regimes associated with decadal and interannual variability in global climate, *Fish. Bull.* 116 (2018).
- [60] M. Sheaves, Consequences of ecological connectivity—The coastal ecosystem mosaic, *MEPS* 391 (2009) 107–115.
- [61] M.N. Sissini, Barros de, M.B.B. Barreto, M.T.M. Széchy, M.B. de Lucena, M.C. Oliveira, J. Gower, G. Liu, E. de Oliveira Bastos, D. Milstein, F. Gusmão, J.E. Martinelli-Filho, The floating Sargassum (Phaeophyceae) of the South Atlantic Ocean—likely scenarios, *Phycologia* 56 (2017) 321–328.
- [62] S. Strydom, K. McMahon, G.A. Kendrick, J. Statton, P.S. Lavery, Seagrass *Halophila ovalis* is affected by light quality across different life history stages, *MEPS* 572 (2017) 103–116.
- [63] J.M. Sunday, K.E. Fabricius, K.J. Kroeker, K.M. Anderson, N.E. Brown, J.P. Barry, S.D. Connell, S. Dupont, B. Gaylord, J.M. Hall-Spencer, T. Klinger, Ocean acidification can mediate biodiversity shifts by changing biogenic habitat, *Nat. Clim. Change* 7 (2017) 81–85.
- [64] H. Ullah, I. Nagelkerken, S.U. Goldenberg, D.A. Fordham, Climate change could drive marine food web collapse through altered trophic flows and cyanobacterial proliferation, *PLoS Biol.* 16 (2018) e2003446.
- [65] R.K. Unsworth, L.M. Nordlund, L.C. Cullen-Unsworth, Seagrass meadows support global fisheries production, *Conserv. Lett.* 12 (2019) e12566.
- [66] B. van Tussenbroek, A. Héctor, A. Hernández, R.E. Rodríguez-Martínez, J. Espinoza-Avalos, H.M. Canizales-Flores, C.E. González-Godoy, M.G. Barba-Santos, A. Vega-Zepeda, L. Collado-Vides, Severe impacts of brown tides caused by *Sargassum* spp. on near-shore Caribbean seagrass communities, *Mar. Pollut. Bull.* 122 (2017) 272–281.
- [67] R. Vaquer-Sunyer, C.M. Duarte, Thresholds of hypoxia for marine biodiversity, *Proc. Natl. Acad. Sci. U.S.A.* 105 (2008) 15452–15457.
- [68] F. Vaz-Pinto, C. Olabarria, F. Arenas, Ecosystem functioning impacts of the invasive seaweed *Sargassum muticum* (Fucales, Phaeophyceae), *J. Phycol.* 50 (2014) 108–116.
- [69] M. Wang, H. Chuanmin, B.B. Barnes, G. Mitchum, B. Lapointe, J.P. Montoya, The great Atlantic *Sargassum* belt, *Science* 365 (2019) 83–87.
- [70] K. Watanabe, G. Yoshida, M. Hori, Y. Umezawa, H. Moki, T. Kuwae, Macroalgal metabolism and lateral carbon flows create extended atmospheric CO₂ sinks, *Biogeosciences* (2019) 1–25.
- [71] M. Waycott, C.M. Duarte, T.J. Carruthers, R.J. Orth, W.C. Dennison, S. Olyarnik, A. Calladine, J.W. Fourqurean, K.L. Heck, A.R. Hughes, G.A. Kendrick, Accelerating loss of seagrasses across the globe threatens coastal ecosystems, *Proc. Natl. Acad. Sci. U.S.A.* 106 (2009) 12377–12381.
- [72] M. Włodarska-Kowalczyk, E. Jankowska, L. Kotwicki, P. Balazy, Evidence of season-dependency in vegetation effects on macrofauna in temperate seagrass meadows (Baltic Sea), *PLoS ONE* 9 (2014).