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Research article

Motile macrofauna associated with pelagic *Sargassum* in a Mexican reef lagoon

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ABSTRACT

Buildup of decaying pelagic *Sargassum* on the beaches and coasts of the Mexican Caribbean during the massive arrivals of 2015 and 2018 had detrimental impacts on the environment and tourist industry. To avoid ecological and economic impacts from massive beaching of *Sargassum*, it would be better to remove the pelagic algal masses while still at sea. However, out at sea, pelagic *Sargassum* rafts constitute an ecosystem with a diversified associated fauna and their removal could impact this fauna. We conducted a survey on the motile macrofauna associated to pelagic *Sargassum* rafts in the Puerto Morelos reef lagoon, Mexican Caribbean. Pelagic *Sargassum* was sampled with nets at 2 m, 50 m and 500 m from shore, at four sites during the months of September, October and November 2018. The 108 samples contained 10,296 individuals belonging to 32 taxa distributed over eight Phyla. The main phyla were Arthropoda (48%), Annelida (41%) and Mollusca (15%). Fish abundance was low (10 individuals) with only five species, of which three are typically associated with *Sargassum* rafts and two are common in seagrass meadows and coral reefs. Species composition and abundance of motile macrofauna varied with month and zone; the nearshore zone had the lowest abundance but there was no difference in the abundance of the fauna associated with rafts 50 or 500 m offshore. Three of the four most abundant species (together accounting for 89% of the individuals) were species typically associated with pelagic *Sargassum*, and the fourth was an amphipod that was only registered once near shore. Although more studies over larger time and spatial scales are required, these results suggest that the removal of pelagic *Sargassum* within the reef lagoon may not have a significant effect on local populations of motile macrofauna.

1. Introduction

In 2014, pelagic *Sargassum* (*Sargassum fluitans* and *S. natans*) started to arrive in unusually large quantities to the Mexican Caribbean coast, reaching a peak in September 2015, when the Puerto Morelos Reef National Park (PMRNP) received ~2,360 m^3 algae km^{-1} coast (Rodríguez-Martínez et al., 2016). After a decrease during 2016 and 2017, the influx of *Sargassum* increased again in 2018, peaking in May at 8,793 $m^3 km^{-1}$ (CI: 8,848 $m^3 km^{-1}$) (unpublished data). Leachates and particulate organic matter from the beached decaying algal masses colored the usually clear near-shore waters murky brown, causing *Sargassum*-brown-tides that provoked mortality of nearshore seagrasses and fauna, and deterioration of the water quality of coastal ecosystems (Van Tussenbroek et al., 2017).

Since 2014, the management strategy of the government and hotel owners has been the removal of *Sargassum* from the beach, either manually or with machines. This strategy, however, was insufficient to remove all beached *Sargassum* in a timely manner and, when employed inadequately, resulted in beach erosion, as sand was removed with the beached algal masses (Rodríguez-Martínez et al., 2016) or destruction of sea turtle nests and hatchlings (Maurer et al., 2015).

In mid-2018, the Mexican government began placing interception barriers in coral reef lagoons to prevent the *Sargassum* for reaching the shore. This strategy, however, did not solve the ecological and economic problems because the algae were not removed from the barriers, so they were either transported to nearby areas by wind and currents, or died and sank in the coral reef lagoon. Currently, new techniques are being proposed to extract the *Sargassum* trapped on the interception barriers

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and from the sea, including the use of pumps and hoses, and *Sargassum* harvest boats. It is unknown, however, what species of fauna are harbored by the pelagic *Sargassum* arriving to the coast, or if species from the local fauna become opportunistic users of the algal masses. Therefore, the ecological impact of such techniques cannot be accurately determined.

The three dimensional structure of pelagic *Sargassum* masses in the Sargasso Sea, the Gulf Stream and the Gulf of Mexico provide habitat for motile (i.e. Crustacea, Mollusca, Annelida) and sessile organisms (i.e. algae, hydrozoa, Bryozoa, Cirripedia, sponges, fungi, bacteria, diatoms and protists) as well as nektonic fauna (e.g. fishes and turtles) (Timmermann, 1932; Prat, 1935; Fine, 1970; Coston-Clements et al., 1991; Thiel and Gutow, 2005; Trott et al., 2010; Laffoley et al., 2011; Martin, 2016). Over 100 species of fishes, four species of sea turtles (Coston-Clements et al., 1991), and over 145 invertebrate species (Trott et al., 2010) have been reported associated with pelagic *Sargassum* and of all these species, ten fish and invertebrate taxa are currently considered endemic to *Sargassum* (Coston-Clements et al., 1991; Laffoley et al., 2011). The fauna associated to the pelagic *Sargassum* arriving to the Caribbean Sea remains poorly studied because the massive influxes of this alga are a recent phenomenon. In addition, the associated fauna of the masses arriving to the shores may differ from that of the masses drifting in the open ocean, because some organisms use the floating masses as a temporal refuge (Fine, 1970). Therefore, information on the fauna associated with the pelagic masses at different distances from the shore is paramount for the establishment of best practices for removal of

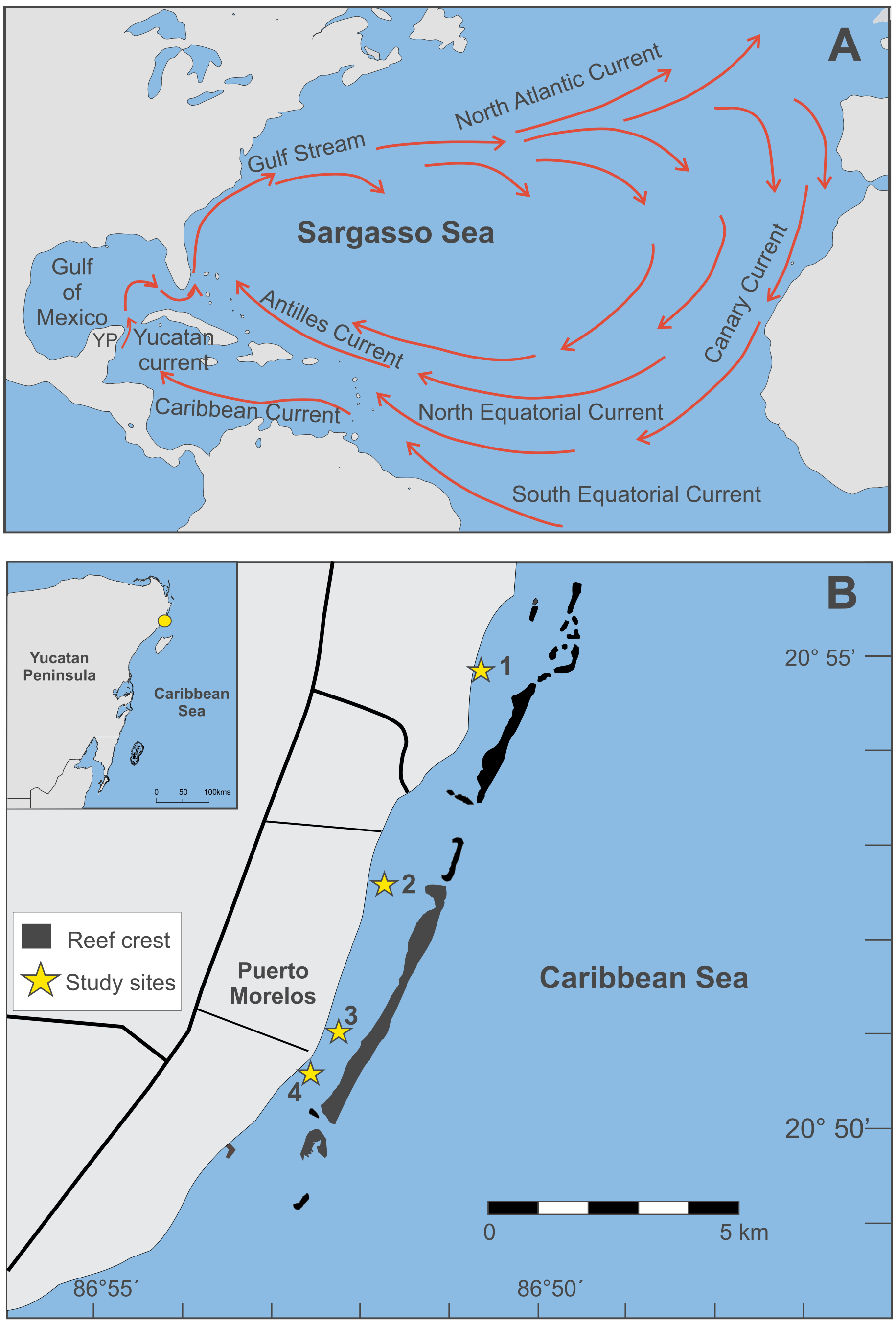

Fig. 1. (A) Schematic view of the major currents in the North Atlantic. (B) Location of Puerto Morelos Reef (yellow circle) in the eastern side of the Yucatan Peninsula and of the four study sites within the Puerto Morelos Reef lagoon. Fig. 1A modified from: Putman and He (2013) and Fig. 1B modified from: Monroy-Velázquez et al., 2017. Atlantic map image modified from Freepik (http://www.freepik.com).

pelagic algal masses from the sea.

The purpose of this study was to assess differences in abundance and diversity of the motile macrofauna community associated with pelagic *Sargassum* in a Mexican Caribbean reef lagoon in space (at different distances from the shore) and time (different sampling months), to provide data that aid in decision-making of the sustainability of collection of the pelagic algal masses before they impact the shore.

2. Materials and methods

2.1. Study sites

Puerto Morelos reef is located on the Mexican Caribbean coast (Fig. 1), characterized by its well-developed back-reef and crest zones. Between the reef crest and the shore, is a reef lagoon colonized by seagrasses and rooted macro-algae. The Yucatán current, a major branch of the Caribbean Current, flows northward along the narrow shelf (Fig. 1A). During the trade-wind season, superficial waters from those currents are transported into the reef area, importing pelagic masses of *Sargassum*. Prevailing winds are the easterly trade winds. Monthly average sea surface temperature ranges from 25.1 to 29.9 °C (Rodríguez-Martínez et al., 2010). From September to April, polar continental air masses ("nortes") generate strong northerly winds, reduce atmospheric and seawater temperatures, and increase turbidity, wave energy and ocean surf. The characteristics of this reef system have been described in several papers (Jordán-Dahlgren, 1979; Ruiz-Rentería et al., 1998; Rodríguez-Martínez et al., 2010; Van Tussenbroek, 2011).

2.2. Sampling method

Four transects perpendicular to the coast were selected within the Puerto Morelos Reef lagoon, with the following coastal coordinates: 1: 20°56′41″ N, 086°50′15″ W, 2: 20°52′05″ N, 086°52′00″ W, 3: 20°50′50″ N, 086°52′30″ W and 4: 20°50′37″ N, 086°52′42″ W (Fig. 1B). Along transects, samples were collected at three distances from the shore (<2 m, 50 m and 500 m) during the months of September, October and November 2018. The samples at 2 m from the shore were collected by wading, and samples at 50 m and 500 m offshore were taken from a small boat with an outboard engine. *Sargassum* clumps were collected in 30 cm-long dip nets with a 0.25 m^2 mouth opening and 0.5 mm mesh net. This mesh size is considered sufficient for capturing macrofauna such as amphipods and gastropods (Tanaka and Leite, 1998; Granados-Barba et al., 2002). Although fishes can be underestimated with this method (Moser et al., 1998), fishes were sampled and therefore included in the analyses of diversity and community structure. The few captured fishes were photographed and then released back to sea. All other specimens of fauna were placed in plastic bags with seawater, together with *Sargassum*, and immediately transported to the laboratory where they were placed in buckets filled with freshwater to induce osmotic shock (Granados-Barba et al., 2003), forcing the motile fauna to detach from the *Sargassum*. The samples were then sieved through a 0.5 mm mesh. The organisms were fixed in 70% ethanol, sorted, identified to the lowest possible taxonomic level and counted. Identifications followed LeCroy (2002), LeCroy (2004) and Winfield et al. (2007) for Amphipoda, Kensley and Schotte (1989) for Isopoda, Chace (1972) and Williams (1984) for Decapoda, Castillo-Rodríguez (2014) for Mollusca, de León-González et al. (2009) for Polychaeta, and Froese and Pauly (2011) for fish. The clumps of *Sargassum* were weighed (wet weight) after removal of excess water with a cloth. The three samples from a single site and time were pooled. The abundance of the motile macrofauna was standardized to number of organisms per wet kilogram of *Sargassum*.

2.3. Statistical analysis of motile macrofauna communities

Possible relations in motile macrofauna specific composition among months and zones were summarized in Venn diagrams. Using iNEXT (iNterpolation and EXTrapolation) analysis (Hsieh et al., 2016), we verified that sampling effort was sufficient to detect >95% of the motile macrofauna taxa predicted to exist at the sampling stations at time of collection (Supplementary Fig. 1). The test statistic iNEXT is calculated using the abundance and richness of the sampled fauna, in relation to the number of taxa represented by only one or two individuals. It can be considered as a proxy for understanding sample completeness. The test statistic iNEXT was also used to obtain Shannon-Wiener diversity index (H').

To visualize differences in the dominant taxa across months and zones, we constructed a heatmap. A non-metric multidimensional scaling (MDS) plot was constructed using the Bray-Curtis similarity measure on the abundance data after fourth-root transformation (Clarke and Gorley, 2015). Previously, the significance of the clusters was tested with a similarity profile analysis (SIMPROF), which tests the null hypothesis that the set of samples contains no multivariate structure to further examine (Clarke et al., 2008). Smooth envelopes were drawn around each of the cluster groups for two slices defined by SIMPROF at similarity levels of 20% and 40%. PRIMER 6 (PRIMER-E Ltd) software was used to carry out these analyses. Differences in the abundance of individuals among zones and months were tested using non-parametric ANOVAs based on the Kruskal-Wallis rank procedure, as violations of assumptions of normality, homoscedasticity and outliers in the dataset precluded the use of parametric tests.

We compared the motile macrofauna communities associated to pelagic *Sargassum* from four regions (Sargasso Sea, Gulf Stream, NW Gulf of Mexico, and Caribbean Sea; Fig. 1A) using data from 126 taxa reported in six studies (Weis, 1968; Fine, 1970; Stoner and Greening, 1984; Muñoz, 2013; Huffard et al., 2014; the present study). For this comparison, we combined results from a cluster analysis and an MDS plot using the Kulczinsky (P/A) similarity measure on a presence-absence matrix (Clarke and Gorley, 2015). The significance of the clusters was tested with a similarity profile analysis (SIMPROF). In the resulting MDS, smooth envelopes were drawn around each of the cluster groups for three slices at similarity levels of 20%, 40%, and 60%. The rest of the analyses were done in R (R Core Team, 2016) employing libraries: ggplot2 (Wickham, 2009), plyr (Wickham, 2014), lsr (Navarro, 2015), gplots (Warnes et al., 2009), vegan (Oksanen et al., 2017) RColorBrewer (Neuwirth, 2011), and pgirmess (Giraudoux, 2013). In all analyses $\alpha = 0.05$. Throughout the text, results are expressed as mean ± SD unless otherwise stated.

A reproducible record of all statistical analyses is available on GitHub (https://github.com/rerodriguezmtz/MacrofaunaSar). This includes all underlying data and R code for all analyses.

3. Results

In total, 108 samples of *Sargassum* with a total wet weight of 14.8 kg were collected in the three zones in the Puerto Morelos Reef lagoon during the surveys between September and November 2018 (Table 1). *Sargassum fluitans* morph III was the dominant algal species (65%), followed by *S. natans* morph I (15%), whereas *S. natans* morph VIII had a low relative abundance (4%). Dislodged benthic species of *Sargassum* were also collected and represented 16% of the samples weight. We found no relationship between *Sargassum* weight (n = 36 replicates, weight range: 62–1905 g) and the number of motile macrofauna individuals in the samples ($r^2 = 0.0114$, $F_{1, 34} = 1.402$, $P = 0.2446$).

In total, 10,296 specimens of motile macrofauna consisting of 32 taxa in eight Phyla were collected from the *Sargassum* samples (Table 1); 19 taxa were identified to species level, four to generic level, and nine to higher taxonomic levels (Fig. 2, Supplementary Table 1). Arthropoda was the most speciose and abundant phylum, with 18 taxa (16 belonging to the subphylum Crustacea) and 4,393 individuals. Annelida was the second most abundant phylum with 4,234 individuals, but was represented by only one species, the polychaete *Platynereis dumerilii*. The

Table 1
Abundance of motile macrofauna in pelagic *Sargassum* collected in three zones within the Puerto Morelos Reef lagoon from September to November 2018. N: number of individuals collected, Sarg (g): weight of *Sargassum* collected with nets, Ind kg-1: number of individuals per kilogram.

Zone	Site	September			October			November			Total N
		N	Sarg (gr)	Ind kg^{-1}	N	Sarg (gr)	Ind kg^{-1}	N	Sarg (gr)	Ind kg^{-1}	
2 m	1	17	530	32.1	610	693	880.2	2292	179	12,804.5	2919
	2	16	1300	12.3	41	170	241.2	243	195	1246.2	300
	3	5	1400	3.6	30	685	43.8	125	152	822.4	160
	4	4	1680	2.4	90	1905	47.2	227	63	3603.2	321
50 m	1	238	410	580.5	289	213	1356.8	202	62	3258.1	729
	2	41	110	372.7	382	395	967.1	181	96	1885.4	604
	3	116	90	1288.9	425	310	1371.0	321	183	1754.1	862
	4	142	280	507.1	220	505	435.6	132	88	1500.0	494
500 m	1	124	160	775.0	704	310	2271.0	600	86	6976.7	1428
	2	80	80	1000.0	395	275	1436.4	274	185	1481.1	749
	3	162	440	368.2	515	592	869.9	357	161	2217.4	1034
	4	72	160	450.0	378	480	787.5	246	161	1528.0	696
Total		**1017**	**6640**		**4079**	**6533**		**5200**	**1611**		**10,296**

phylum Mollusca was represented by four taxa and accounted for 15.2% of the collected organisms, whereas the phyla Nemathelminthes, Nemertea, Platyhelminthes and Sipuncula jointly contributed with 0.9% of the collected organisms. The Phylum Chordata was represented by five fish species, but accounted for only 0.1% of the collected organisms. Among all taxa collected, six species (*Idotea metallica, Stephanolepis hispidus*, *Sygnathus pelagicus*, *Litiopa melanostoma*, *Scyllaea pelagica* and *Gnesioceros sargassicola*) represent new records for the Mexican Caribbean Sea.

The phyla Arthropoda, Annelida and Mollusca dominated throughout the study in the three zones, contributing overall with 99% of the individuals collected, but their relative abundance varied with month and zone (Fig. 3). In September, Annelida dominated in the 2 m zone and Arthropoda in the 50 m and 500 m zones; in October, all zones were dominated by Annelida, followed by Arthropoda, whereas in November, Arthropoda dominated the 2 m zone, Mollusca the 50 m zone and Annelida the 500 m zone (Fig. 3).

By month, taxa richness was highest in November (N = 26), followed by October (N = 19) and September (N = 18), whereas diversity was higher in November (H' = 6.060) followed by September (H' = 4.357) and October (H' = 3.840). A Venn diagram illustrated that only 12 of the 32 taxa recorded occurred in all three months (Fig. 4a). The highest number of unique taxa was found in November (N = 9) (Fig. 4a). Comparisons among zones showed that motile macrofauna taxa richness was similar among the three zones (2 m: 24 taxa, 50 m: 22 taxa, 500 m: 23 taxa), but the composition of the assemblages was heterogeneous and only 16 taxa were shared among them (Fig. 4b). The highest number of unique taxa was found in the 500 m zone (N = 5). Diversity was higher in the 2 m zone (H' = 5.065) followed by the 50 m zone (H' = 5.030) and 500 m zone (H' = 4.505).

The 2-D MDS ordination plot had a good stress value (0.09). Cross-checking results from this ordination against those from the cluster analysis and SIMPROF test (Clarke and Gorley, 2015) (Fig. 5) shows that, at 20% similarity, the samples formed only two groups: one consisting of the four September samples taken at 2 m from the shore, and the other group consisting of all the other samples. At 40% similarity, however, three of the four October samples taken at 2 m from the shore formed a third group. Nevertheless, these results confirm that there was a high similarity in the composition of the pelagic *Sargassum* invertebrate community collected throughout the reef lagoon between September and November 2018, except in samples taken very close to the shoreline in September and October.

The abundance of individuals of motile macrofauna varied significantly with month (Kruskal-Wallis test, H = 19.84, df = 2, $p < 0.01$), with significantly higher values (multiple comparison test, $p < 0.05$) in November (3256.4 ± 3431.6 Ind kg^{-1}) than in September (449.4 ± 416.8 Ind kg^{-1}) and October (892.3 ± 655.4 Ind kg^{-1}) (Fig. 6a). No significant differences were recorded in the abundance of individuals among the three zones (Kruskal-Wallis test, H = 5.41, df = 2, p = 0.067) (Fig. 6b).

The polychaete *Platynereis dumerilii* was the dominant species in all zones and months, followed by the decapod *Latreutes fucorum* and the mollusk *Litiopa melanostoma* (Fig. 2). These three species accounted for 74% of the individuals collected. The abundance varied significantly with month for *P. dumerilii* (Kruskal-Wallis test, H = 16.689, df = 2, $p < 0.001$) and *L. melanostoma* (H = 21.007, df = 2, $p < 0.001$), with significantly lower values in September than in October and November for both species (multiple comparison tests, $p < 0.05$), whereas no significant differences were recorded among zones for either species (Kruskal-Wallis tests, $p > 0.05$). The abundance of *L. fucorum* did not vary significantly with month (Kruskal-Wallis = 3.956, df = 2, p = 0.1384) but it did with zone (Kruskal-Wallis = 14.254, df = 2, $p < 0.001$), with significantly lower values in the 2 m zone than in the 50 m and 500 m zones (multiple comparison test, $p < 0.05$). Another abundant species was the amphipod *Nototropis minikoi*, which represented 15% of all collected individuals, but its abundance was high only in the 2 m zone in November, when 97% of the individuals of this species were collected (Fig. 2).

Results of the comparison of the motile macrofauna associated to pelagic *Sargassum* in different regions by different authors (Supplementary Table 2) show that the community recorded in 1966 by Weis (1968) in the Gulf Stream (labeled as S4) separated from the rest of the communities at all levels of similarity chosen (20, 40 and 60%), whereas that recorded by Muñoz (2013) in the Gulf of Mexico (labeled as S6) separated from the rest at 40% similarity (Fig. 7). All communities differed at the 60% level, except S2 and S5, which correspond to a single study conducted in 1981 at the Sargasso Sea and the Gulf Stream, respectively, by Stoner and Greening, 1984.

4. Discussion

The pelagic *Sargassum* that arrived massively to the Puerto Morelos Reef lagoon sustained a rich community belonging to eight phyla, represented by 27 taxa of invertebrates and five taxa of fish. The number of taxa found in the present study was lower than that reported for the Sargasso Sea in the 1960's (N = 56, Fine, 1970) but higher than that reported recently in this Sea (N = 21, Stoner and Greening, 1984; N = 23, Huffard et al., 2014). The number of taxa was similar to that reported for the Gulf of Mexico (N = 35, Muñoz, 2013) and higher than that reported for the Gulf Stream (N = 16, Weis, 1968; N = 15, Stoner and Greening, 1984) (Table 2). Of the 32 taxa recorded in Puerto Morelos, only 19 were identified to species level. Of these, 17 had already been reported for the Caribbean Sea, 12 for the Mexican Caribbean, and nine for the Puerto Morelos Reef National Park (Table 3). The six newly recorded species for the Mexican Caribbean Sea (*Idotea metallica*, *Stephanolepis hispidus, Syngnathus pelagicus, Litiopa melanostoma, Scyllaea*

Fig. 2. Fig. 2. Relative abundance heatmap of motile macrofauna taxa associated to pelagic *Sargassum* in three zones (2 m, 50 m, 500 m) in Puerto Morelos Reef lagoon collected in September, October and November 2018. Color scale shows the proportion of each taxa within each zone and sampling month. White squares indicate zero counts. Taxa in black correspond to Arthropoda, in green to Mollusca, in red to Annelida, in blue to Chordata, in orange to Platyhelminthes, in ochre to Nematoda, in lilac to Nemertea and in grey to Sipuncula.

pelagica and *Gnesioceros sargassicola*) typically spend their life cycle associated to pelagic *Sargassum* in different regions of the world (Table 3), although they have also been observed associated to floating masses of other algal species or abiotic substrata (i.e. garbage) (Thiel and Haye, 2006).

The dominant phyla of motile macrofauna associated to *Sargassum* collected in Puerto Morelos (Arthropoda, Annelida and Mollusca) are consistent with reports from other regions (Butler et al., 1983; Muñoz, 2013; Huffard et al., 2014; Martin, 2016), but the relative abundance of these phyla varied with study. In our study, Arthropoda and Annelida co-dominated, while in the Sargasso Sea, the Gulf Stream and the Gulf of Mexico most authors report a clear dominance of Arthropoda (Table 2). The identity and relative abundance of the dominant species in Puerto Morelos also differed from those reported for other regions where pelagic *Sargassum* accumulates (Table 2). In our study there was a clear dominance of the polychaete *Platynereis dumerilii* (41%), followed by the shrimp *Latreutes fucorum* (18%) and the mollusc *Litiopa melanostoma* (15%). Even though these three species are common inhabitants of pelagic *Sargassum* (Butler et al., 1983; Huffard et al., 2014; Martin, 2016), their relative abundance differed from that in other regions (Table 2). In the Sargasso Sea, for example, a co-dominance of *L. fucorum* (17%), *Hemiaegina minuta* (16%) and *Carpias minutus* (= *Janira minutus)* (12%) was recorded in the late 1960's (Fine, 1970), a co-dominance of *L. melanostoma* (25%), *L. fucorum* (23%) and *Planes minutus* (12%) in the early 1980's (Stoner and Greening, 1984), and a dominance of *L. fucorum* (87%) in 2011 (Huffard et al., 2014). In the Gulf Stream, different authors have also reported the dominance of different species. For example, Weis (1968) found a co-dominance of *Bittium* sp. (32.1%), *L. fucorum* (28.3%) and *Rissoa* sp. (14.3%), whereas Stoner and Greening, 1984 found a clear dominance of *L. fucorum* (68%). For the

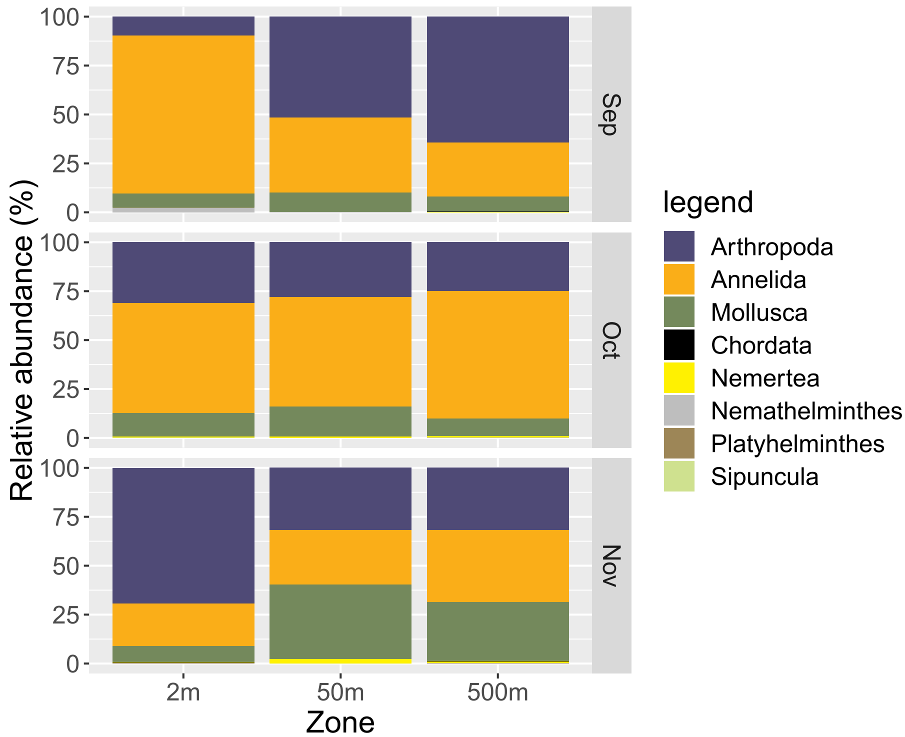

Fig. 3. Relative abundance (%) of eight phyla of motile macrofauna associated to pelagic *Sargassum* in three zones within the Puerto Morelos Reef lagoon in September, October and November 2018.

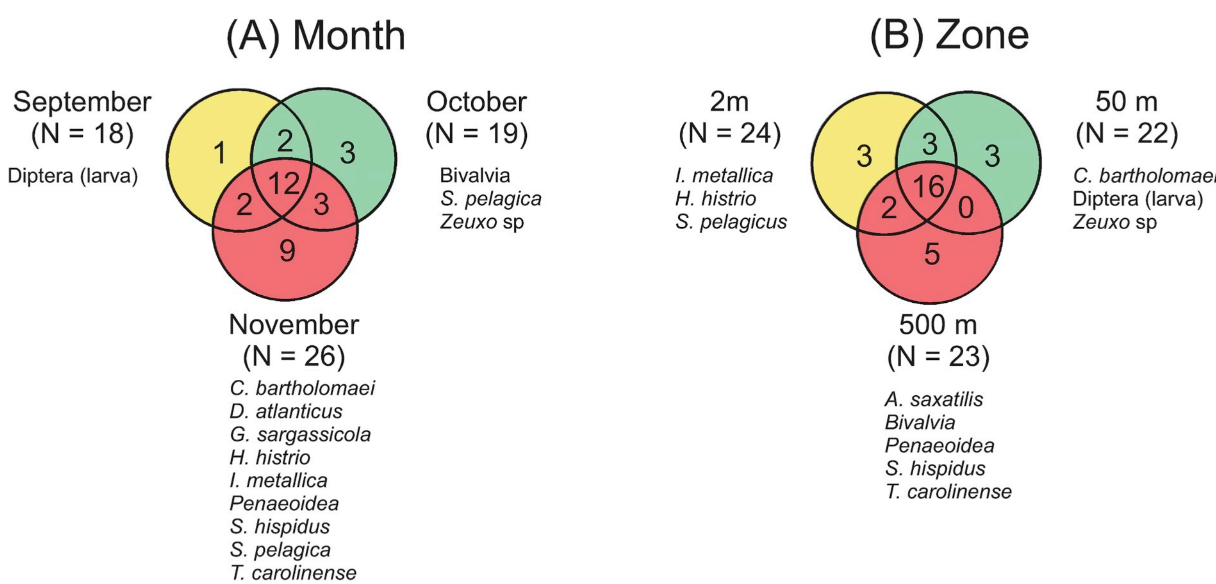

Fig. 4. Venn diagrams illustrating the unique and shared species of motile macrofauna associated to pelagic *Sargassum* among (A) months (September, October and November 2018) and (B) zones (2 m, 50 m and 500 m from the shore) within the Puerto Morelos Reef lagoon, Mexico.

Gulf of Mexico, Muñoz (2013) reported a co-dominance of *Palaemonetes intermedius* (35%), *Sergestes* sp. (27%) and *Palaemonetes vulgaris* (17%). In addition, our comparison of the communities associated to *Sargassum* in four regions as reported in six studies, suggests that both the composition and relative abundance of these communities are highly variable in time and space, possibly as a result of separate colonization events of *Sargassum* rafts, as proposed by Fine (1970).

Of the three species that dominated the *Sargassum* collected in Puerto Morelos, *P. dumerilii* and *L. fucorum* are generalist species that can also be found associated to other macrophytes, and *L. melanostoma* has a circumtropical distribution, mostly associated to floating objects and pelagic environments, although this species can also be found in benthic vegetation (Rosenberg et al., 2009).

All individuals of the five species of fish that were collected from pelagic *Sargassum* in Puerto Morelos were in juvenile stages and their abundance was very low. Three of these species (the *Sargassum* fish *Histrio histrio*, the planehead filefish *Stephanolepis hispidus* and the *Sargassum* pipefish *Syngnathus pelagicus*) were represented by only one or two individuals. These species are commonly associated to pelagic *Sargassum*, mostly in the Sargasso Sea and the Caribbean (Adams, 1960),

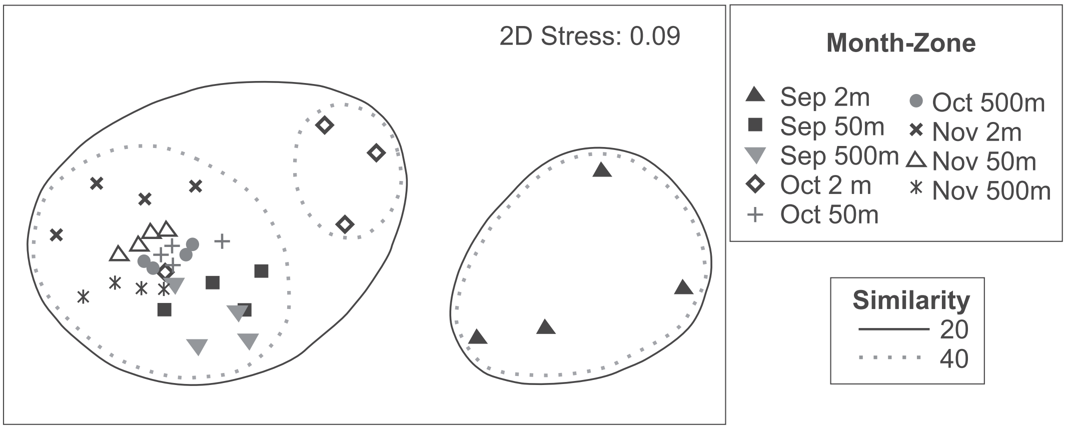

Fig. 5. Motile macrofauna community structure in samples from floating *Sargassum* taken at three zones (i.e., distances from the shore: 2 m, 50 m, 500 m) in four sites within the Puerto Morelos reef lagoon in three months (September, October November 2018). Non-metric multidimensional scaling plot showing groups of samples within 20% (solid line) and 40% (dotted line) similarity contours given by sequence of SIMPROF tests on a previous hierarchical clustering. Analyses were done using Bray-Curtis similarity and fourth root transformations. Each symbol denotes a sample.

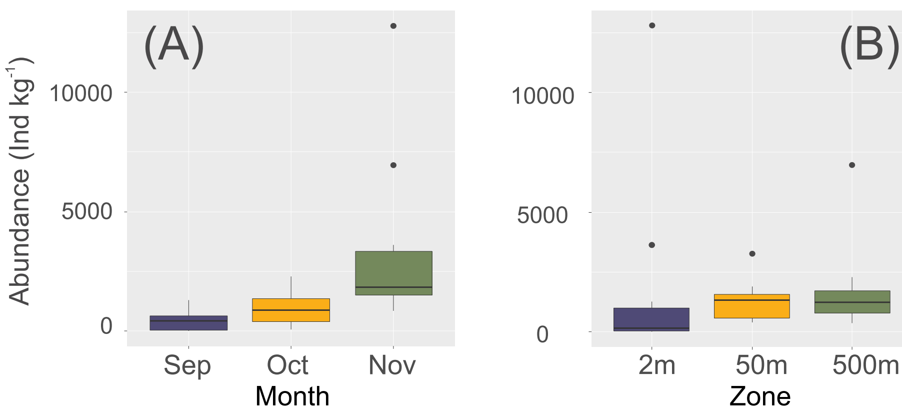

Fig. 6. Abundance (Ind kg^{-1}) of motile macrofauna associated to floating *Sargassum* by (a) Month and (b) Zone (distance to the shore).

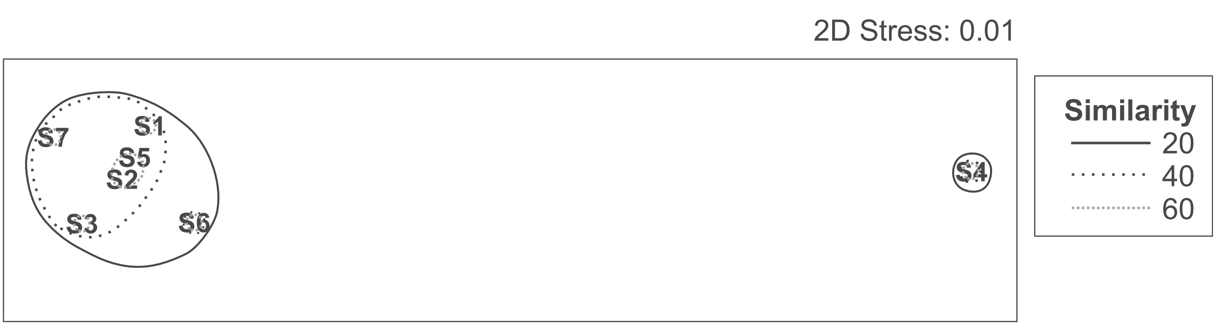

Fig. 7. Invertebrate community structure in samples from floating *Sargassum* reported in seven studies conducted in four regions (Sargasso Sea (S1–S3), Gulf Stream (S4, S5), Gulf of Mexico (S6), and Caribbean (S7)). Non-metric multidimensional scaling plot showing groups of samples within 20% (solid line), 40% (dotted line) and 60% (segmented line) similarity contours given by sequence of SIMPROF tests on a previous hierarchical clustering. Relative abundance data were transformed to presence-absence data in PRIMER. Analyses were done using Kulczynski (P/A) Index. S1: Fine (1970), S2 and S5: Stoner and Greening, 1984, S3: Huffard et al. (2014), S4: Weis (1968), S6: Muñoz (2013), S7: the present study.

as they depend on these algae for food and shelter (Dooley, 1972), although their abundance tends to be higher in areas distant to the coast (Wells and Rooker, 2004). Juveniles of *Stephanolepis hispidus* are pelagic and seek protection in the floating masses of *Sargassum*, but as they reach 50–100 cm in length they become benthic (Fine, 1970). Adults of this species have been observed in sandy and muddy bottoms and seagrass meadows, and although they are commonly found in shallow waters, they have also been recorded to depths of 293 m (Scott and Scott, 1988). The other two fish species recorded in our samples, *Abudefduf saxatilis* and *Carangoides bartholomaei*, are common inhabitants of seagrasses in the juvenile phase and of coral reefs in their adult phase. Therefore, the presence of juveniles of these species in the masses of *Sargassum* might suggest that they were using this alga as a temporal refuge.

The abundance of motile macrofauna in pelagic *Sargassum* in the Puerto Morelos Reef lagoon varied with month and distance to the shore. The lowest abundance recorded in September in the zone closest to the shore (2 m) could reflect a deterioration of the water quality near the

Table 2
Relative abundance of Phyla of motile macrofauna associated to pelagic *Sargassum* in studies conducted in the Sargasso Sea (SS), the Gulf of Mexico (GM), the Gulf Stream (GS), and the Caribbean Sea (Car).

Region	SS	SS	SS	GS	GS	GM	Car
Year	1968–69	1981	2011	1966	1981	2011–12	2018
Sample size	10,879[a]	888	2,420	371	900	6,364	10,296
Phylum (N)	7	5	4	5	5	6	8
Taxa (N)	58	21	23	16	15	35	32
Relative abundance							
Arthropoda	65.8%	58.9%	98.5%	40.4%	90.1%	89.4%	42.7%
Annelida	5.7%	3.7%	0.02%	2.2%	3.7%	3.2%	41.1%
Mollusca	9.1%	26.2%	1.4%	47.2%	1.4%	3.8%	15.2%
Chordata	2.3%	1.2%	0.1%	7.8%	2.6%	1.5%	0.1%
Platyhelminthes	10.5%	10%	–	2.4	2.2%	2.1%	0.1%
Other	6.6%	–	–	–	–	–	0.8%
Dominant taxa	*Latreutes fucorum* (16.8%), *Hemiaegina minuta* (16.4%), *Janira minuta* (11.5%)	*Litiopa melanostoma* (25.1%), *Latreutes fucorum* (22.5%), *Planes minutus* (11.8%)	*Latreutes fucorum* (87%)	*Bittium* sp. (32.1%), *Latreutes fucorum* (28.3%), *Rissoa* sp. (14.3%)	*Latreutes fucorum* (67.8%), *Bagatus minutus* (10.0%)	*Palaemonetes intermedius* (35%), *Sergestes* sp. (27%), *Palaemonetes vulgaris* (17%)	*Platynereis dumerilii* (41%), *Latreutes fucorum* (18%), *Litiopa melanostoma* (15%)
Source	Fine (1970)	Stoner and Greening 1984	Huffard et al. (2014)	Weis (1968)	Stoner and Greening 1984	Muñoz (2013)	This study

[a] Only motile species were considered.

Table 3
Distribution of motile macrofauna species associated to pelagic *Sargassum* in Puerto Morelos Reef lagoon between September and November 2018. Car: Caribbean, PNAPM: Puerto Morelos Reef National Park, SS: Sargasso Sea, GM: Gulf of Mexico, WA: Western Atlantic, Afr: Africa, Bra: Brasil.

Phylum	Species	This study	Car[a]	Car Mex[b]	PNAPM[c]	SS[d]	GM[e]	CG[f]	WA[g]	Afr[g]	Bra[g]
Annelida	*Platynereis dumerilii*	*	*	*	*	*		*			
Arthropoda	*Biancolina brassicacephala*	*	*	*	*	*	*				
	Discias atlanticus	*	*	*	*		*			*	
	Idotea metallica	*					*		*		
	Latreutes fucorum	*	*	*	*	*	*	*	*	*	*
	Leander ternuicornis	*	*	*	*	*	*	*	*	*	*
	Nototropis minikoi	*	*	*			*				
	Portunus sayi	*	*	*		*	*	*	*	*	
	Probopyrinella latreuticola	*	*	*		*	*				
	Sunamphitoe pelagica	*	*	*		*	*	*	*	*	
	Tozeuma carolinense	*	*	*	*		*				
Chordata	*Abudefduf saxatilis*	*	*	*	*	*	*	*	*	*	
	Carangoides bartholomaei	*	*	*	*	*	*	*	*		
	Histrio histrio	*	*	*	*	*	*		*		
	Stephanolepis hispidus	*					*		*		
	Syngnathus pelagicus	*	*				*	*			
Mollusca	*Litiopa melanostoma*	*	*			*	*				
	Scyllaea pelagica	*	*			*	*		*		
Platyhelminthes	*Gnesioceros sargassicola*	*	*			*	*		*	*	
		19	17	12	9	13	16	8	11	7	2

[a] Chace (1972), Abele and Kim (1986), Robins and Ray (1986), Markham et al., (1990), Smith (1997), de León-González et al., 2009, Matsuura et al., (2015), Martin (2016).
[b] Chace (1972), Abele and Kim (1986), Markham et al., (1990), Monroy-Velázquez (2000), Román-Contreras and Martínez-Mayén 2009.
[c] INE , 2000, Monroy-Velázquez (2000).
[d] Stoner and Greening, 1984, Huffard et al., 2014.
[e] Winfield and Ortíz (2008), Muñoz (2013), Martin (2016).
[f] Martin (2016).
[g] WoRMS.

coast due to the formation of *Sargassum*-brown-tides caused by decomposition of beach-cast *Sargassum*, which was more notorious in September than in the other months. These brown tides deplete oxygen, leading to the mortality of seagrasses and fauna (Van Tussenbroek et al., 2017; Rodríguez-Martínez et al., 2019). Therefore, it is likely that, as the algae get closer to the coast, the associated motile fauna either dies or abandons the substrate upon detecting the deterioration in water quality. The higher abundance of motile macrofauna associated to pelagic *Sargassum* in October and November of 2018 was possibly related to a decrease in the volume of the algae arriving to Puerto Morelos and to more intense beach cleaning efforts, which reduced the amount of decaying algae.

Of the 19 identified species associated to pelagic *Sargassum* collected within 500 m from the shore in Puerto Morelos reef lagoon, only nine were previously reported for the area, and these taxa occurred in low abundance. Accidental capture of vertebrate taxa (fish or turtles) is of special concern when capturing pelagic *Sargassum* while still drifting at sea, firstly because if collected in large numbers, this may potentially affect their population sizes, and secondly because incidental capture of iconic animals such as turtles may influence the public opinion on the (desirable) management strategy of capture at sea. However, we did not find adult vertebrates in our samples, and only a few juvenile fishes. We hypothesize that either near-shore mats do not harbor many vertebrates, or the vertebrates move further down the drifting mat and thus avoid capture as they perceive an approaching boat, as has been reported for boats that harvest the canopies of the giant kelp *Macrocystis pyrifera* in the Pacific Ocean (Limbaugh, 1955). It is important to emphasize that our collections were made near the shore in Puerto Morelos reef lagoon, and further studies on associated fauna in off-shore pelagic mats are required to assess management strategies for the capture of *Sargassum* in the open ocean. Although more studies are required in other periods and areas, as well as on the populations of the trapped juvenile fish, the findings of this study indicate that removal of *Sargassum* within reef lagoons may not have a significant effect on the local populations of motile macrofauna, and may thus be suggested as a sustainable management strategy as far as this fauna is concerned.

5. Conclusions

The pelagic *Sargassum* that arrives massively to the Puerto Morelos reef lagoon provides habitat to at least 27 taxa of motile macrofauna and is used as a refuge by at least five species of fish, two of which are typically associated to pelagic *Sargassum* and two of which are common dwellers of seagrasses and coral reefs. Species composition and abundance of motile macrofauna varied among months and zones, with the nearshore zone having generally the lowest abundance. In contrast, the abundance of the fauna associated with *Sargassum* rafts did not differ between 50 m and 500 m offshore. Three of the four most abundant species (jointly accounting for 89% of the individuals) were species typically associated with pelagic *Sargassum*, and the fourth was an amphipod that was only registered once in the nearshore zone. Although more studies over greater time and spatial scales are required, these results suggest that removal of pelagic *Sargassum* within the reef lagoon may not have a significant effect on the local populations of motile macrofauna.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2019.109650.

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