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# A baseline assessment of the epiphytic community associated with pelagic sargassum in the Tropical Atlantic



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# ABSTRACT

Pelagic sargassum, historically endemic to the North Atlantic where it accumulated in the Sargasso Sea, has now expanded to other accumulation regions namely in the North Equatorial Recirculation Region (NERR) of the Tropical Atlantic. To date, efforts to understand the biological community associated with pelagic sargassum have largely focussed on the motile organisms with very little attention given to the epiphytic flora and fauna, particularly for sargassum from the NERR. This study: (1) assesses the species composition and abundance (percentage cover) of epiphytes associated with the three prevalent forms (Sargassum fluitans III, S. natans I, S. natans VIII) of pelagic sargassum arriving in Barbados over summer and winter months and; (2) uses a backtracking algorithm to determine if differences in the composition of epiphyte species are linked to putative sub-origins within the NERR. Overall, epiphyte diversity was relatively low, comprising just six species of fauna, and an unidentified filamentous alga. However, there were significant differences in the epiphytic community associated with the three prevalent morphotypes. Based on percent cover, the bryozoan, Membranipora tuberculata, was the dominant species observed on S. fluitans III and S. natans I; while S. natans VIII was predominantly occupied by the hydroid, Aglaophenia latecarinata. This research provides the first quantification of the epiphytic community associated with pelagic sargassum in the Eastern Caribbean as it transitions from open Tropical Atlantic Ocean into the Caribbean Sea and will provide a useful baseline for monitoring potential change over time. The results corroborate with previous studies from elsewhere that suggest distinct differences in the epiphytic communities hosted by different sargassum morphotypes. We found no evidence that differences in epiphytic community composition were linked to sub-origin within the NERR, indicating that sargassum morphology is likely a stronger determinant of epiphyte composition than any environmental differences encountered between sub-origins and their associated transport pathways.

#### 1. Introduction

Pelagic *Sargassum* spp., a uniquely holopelagic ecosystem, supports rich faunal communities (Weis, 1968; Dooley, 1972; Butler et al., 1983; Schell et al., 2016; Monroy-Velázquez et al., 2019; Martin et al., 2021) by providing habitat, shelter from predation and foraging opportunities. For centuries this floating ecosystem was largely confined to the North Atlantic, specifically the Sargasso Sea, where it became the subject of scientific curiosity (Parr, 1939; Butler et al., 1983; Niermann, 1986). Since 2011 however, a 'new' population of pelagic *Sargassum* spp. has established itself in the North Equatorial Recirculation Region (NERR) of the Tropical Atlantic (Gower et al., 2013; Franks et al., 2016; Wang et al., 2019) about which much less is known. The NERR is loosely

bounded by the South Equatorial Current (SEC) and the North Equatorial Counter Current (NECC) and is an area of highly complex dynamic ocean currents (Skliris et al., 2022). Bloom events here are now confirmed as the source of unparalleled inundation events along the coasts of Caribbean and West African countries (Franks et al., 2016; Wang et al., 2019) where they are causing multiple negative cross-sectoral impacts (UNEP-CEP 2021). The blooms have primarily been attributed to ocean eutrophication, climate change and modes of natural variability in ocean circulation and climate, although uncertainties regarding the drivers of these blooms still remain (e.g. Johns et al., 2020; Lapointe et al., 2021; Skliris et al., 2022).

Early descriptions by Parr (1939) suggested that pelagic Sargassum spp. in the North Atlantic consisted of two species, Sargassum natans and

\* Corresponding author. *E-mail addresses:* w2005361@wmu.se (K.S.T. Alleyne), fn@wmu.se (F. Neat), hazel.oxenford@cavehill.uwi.edu (H.A. Oxenford).

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Received 29 December 2022; Received in revised form 12 February 2023; Accepted 13 February 2023 Available online 15 February 2023 0304-3770/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/). *S. fluitans* (hereafter simply referred to as 'sargassum'), with as many as six morphotypes (*S. fluitans* III, X and *S. natans* I, II, VIII, IX). Sargassum in the Tropical Atlantic appears to be predominantly composed of three morphotypes (*Sargassum fluitans* III, *S. natans* I, *S. natans* VIII) (Schell et al., 2015; García-Sánchez et al., 2020; Machado et al., 2022). Since the initial bloom, research on the negative impacts to nearshore ecosystems (van Tussenbroek et al., 2017; Chávez et al., 2020), fisheries (Ramlogan et al. 2017; Oxenford et al., 2019), tourism (Chávez et al., 2020; Bartlett and Elmer, 2021) and human health (Resiere et al., 2019, 2021) during mass accumulation and decomposition of sargassum has been well documented.

Within recent years, the concept of 'threat or opportunity' has helped to develop a now, rapidly growing interest in utilizing sargassum and turning it into business opportunities (Desrochers et al., 2020; Amador-Castro et al., 2021). Mass sargassum influxes into the Caribbean from the Tropical Atlantic are considered the new 'normal' for the region (Desrochers et al., 2020) and will likely be the major driver of future inundations and innovations in the Caribbean. Efforts to valorize sargassum have drawn much attention to the clinging and free-swimming biodiversity associated with sargassum rafts (Monroy-Velázquez et al., 2019; Martin et al., 2021; Goodwin et al., 2022) given the unknown effects of large-scale in-water harvesting on this ecosystem. However, very few studies have focused on the epiphytic biodiversity associated with sargassum originating from the NERR, and these have looked only at hydroids (Govindarajan et al., 2019; Mendoza-Becerril et al., 2020). Studies from the Sargasso Sea (Weis, 1968; Rackley, 1974; Ryland, 1974; Butler et al., 1983; Niermann, 1986; Calder, 1995) provide valuable insights into the epiphytic community associated with sargassum and identify hydroids ( $\sim$  14 species) as major components of that community. Studies on epiphytic species composition and variation of sargassum originating from the NERR are needed to improve our understanding of the ecology of this recently established sargassum population, including differences among the most frequently occurring morphotypes and examine the possibility of sargassum acting as a host for invasive epiphytic species (Mendoza-Becerril et al., 2020). Moreover, the capacity of epiphytes for long range transport (Calder, 1991) suggests that observed differences (if any) in epiphytic community composition could potentially be indicators of different sargassum sub-origins within the NERR and could indicate different transport pathways for invasives. Exploring potential origins of beached sargassum and differences in sargassum among origins and their transport pathways is important for understanding the factors responsible for the continued proliferation and extensive variability of sargassum in the Tropical Atlantic.

In this study, the three prevalent morphotypes of sargassum stranding in Barbados were analyzed to determine: (1) the occurrence and percent coverage of epiphytes; (2) differences in composition of epiphytes among sargassum morphotypes; and (3) assess whether or not epiphytic assemblages are linked to sub-origins within the NERR. We hypothesize that epiphytic assemblage will vary among, the three basibionts, *S. natans* I, *S. natans* VIII and *S. fluitans* III given their structural differences and their ability to host different motile organisms (Martin et al., 2021). We further hypothesize that differences in epiphytic assemblage on a given morphotype will occur as a result of their sub-origins and associated transport pathways within the NERR.

#### 2. Materials and methods

## 2.1. Sample collection and epiphytic assessment

Newly beached, wet, sargassum was collected from Conset Bay (13°10'47"N 59°27'57"W) on the east coast of Barbados during July and August of 2021 and February and March of 2022. Prevalent morphotypes (*Sargassum fluitans* III, *S. natans* I and *S. natans* VIII) of sargassum, identified following Parr (1939) and Schell et al. (2015) using gross morphological features (Fig. 1) were separated for epiphytic assessments.

A total of 510 sargassum specimens (170 of each morphotype) were used to describe the occurrence and percentage cover of epiphytes. This was done by selecting ten thalli of each sargassum morphotype for examination on 17 sampling occasions. Selected thalli were placed between two acrylic plates each marked with a  $1 \times 1$  cm square grid and epiphyte cover on thalli was estimated following Mendoza-Becerril et al. (2020) as shown in Fig. 2 and briefly described here.

Epiphyte cover was estimated by: (1) counting the number of grid squares occupied by sargassum with and without epiphytes on both sides of the plates; and (2) counting the number of squares occupied by each of the observed epiphyte species on both sides of the plates. Epiphyte percentage cover was calculated by dividing the number of squares occupied by epiphytes by the total number of squares occupied by sargassum. This was first done for all epiphytes (regardless of species) and then again for each individual epiphyte species. Under dissecting  $(\times 10 \text{ magnification})$  and compound microscopes ( $\times 40 \text{ magnification})$ , epiphytic fauna were identified to species-level using morphological descriptions provided in Rackley (1974), Morris and Mogelberg (1973), Oliveira et al. (2006) and Schuchert (2012). Specifically, hydroid identification was achieved with examination of colony structure, polyp formation and the presence and shape of hydrothecae. For Bryozoans the shape, size and formation of colonies were used for identification. Epiphytic flora were simply recorded as filamentous algae. Photographs of some species were also sent to the Universidad Nacional Autónoma de México for assistance with species identification.



Fig. 1. General appearance of the three pelagic sargassum morphotypes collected at Conset Bay, Barbados.



**Fig. 2.** Schematic of the method of measuring epiphytic cover found on pelagic sargassum samples. Adopted from the methodology described in Mendoza-Becerril et al. (2020).

#### 2.2. Backtracks

To determine if the observed epiphytic community was linked to sargassum sub-origins within the NERR each collection day was backtracked using IDL 8.8.1 programming software (https://www.l3harris. com/all-capabilities/idl). Backtracks were achieved through application of the 'Centre for Resource Management and Environmental Studies (CERMES) forecast model' developed for use in forecasting sargassum influxes to the Eastern Caribbean islands (Johnson et al., 2020; Marsh et al., 2022). The model is constructed from a Global Drifter Program (GDP) dataset consisting of: year, day, hour, longitude, latitude, east-current, west-current and drogue-on/drogue-off flag from 1979 to 2020, interpolated to a 1/12th degree resolution grid by year-day for 365 days. The model also incorporates a windage of 0.5 % applied to the drifter dataset. The exact steps taken to achieve the GDP data set and develop the tracking methodology used in this study can be found in Johnson et al. (2020). In this study, sargassum was tracked back 365 days from Conset Bay, Barbados to determine the putative origin of each sample within the NERR. Tracks were simulated by the model using 100 particles launched simultaneously from the collection location, applying sub grid-scale turbulent motions (Lagrangian Stochastic Model) to each particle's current component:

$$\mathbf{u}' = \mathbf{u} + 0.1 * \text{current speed} * \mathbf{P}$$
(1)

where u' is an adjusted current component and P(1) is a normal (Gaussian) random distribution with a mean of zero and a standard

# deviation of one.

#### 2.3. Statistical analyses

Epiphyte composition between different sub-origins was assessed with the use of Multivariate Analysis of Variance (MANOVA) using epiphytic counts as sampling units. Prior to running the MANOVA the data were Hellinger-transformed using the decostand function of the "vegan" package (Oksanen et al., 2018) in R (R Core Team, 2022). The MANOVA was followed by a Permutational Multivariate Analysis of Variance (PERMANOVA) to test for an effect of sub-origin and/or morphotype. Within the PERMANOVA epiphytic counts were used as the response matrix data and sub-origins and morphotypes as independent factors. This test was conducted using the adonis function of the "vegan" package in R.

#### 3. Results

#### 3.1. Sample collection and epiphytic assessment

A total of 510 sargassum specimens, *S. fluitans* III (n = 170; specimen mean wet weight = 19.4 g  $\pm$  2 SD), *S. natans* I (n = 170; specimen mean wet weight = 11.2 g  $\pm$  3 SD) and *S. natans* VIII (n = 170; specimen mean wet weight = 19.5 g  $\pm$  2 SD) were collected on the east coast of Barbados during summer (July and August 2021; 9 collections) and winter (February and March 2022; 8 collections).

The epiphytic community associated with sargassum arriving in Barbados had a relatively low species richness consisting of six species of fauna from six identified families, and unidentified filamentous alga considered here as a single taxon. The bryozoan *Membranipora tuberculata* was the predominant species observed and covered approximately one third of sargassum thalli overall (Table 1). Four of the six faunal species identified were hydroids, with *Aglaophenia latecarinata* being the predominant hydroid observed followed by *Clytia noliformis*, *Obelia dichotoma* and *Plumularia strictocarpa*. Other observed species include the tube-worm *Spirorbis spirorbis* and an unidentified filamentous green alga belonging to the family Chlorosarcinaceae (Table 1; Fig. 3; Supplementary Fig. 1).

#### 3.2. Backtracks

Collected samples were backtracked to two putative sub-origins/ transport pathways within the NERR. Sub-origin/transport pathway A is located close to the equator  $(0-7^{\circ}N)$  and travels along northeast Brazil before arriving in Barbados (hereafter referred to simply as sub-origin A). Sub-origin/transport pathway B is located further north  $(10-15^{\circ}N)$ and travels a relatively direct westerly route to Barbados (hereafter referred to as sub-origin B). Sub-origins align with and are named after those identified in the unpublished works of Alleyne et al. (2023, In press) (Fig. 4).

Epiphyte percentage cover of sargassum samples originating from sub-origin A and sub-origin B were very similar (F = 0.080, p = 0.969) with sargassum from each group having, on average, approximately 56 % epiphytic cover. Irrespective of sub-origin, *S. natans* I hosted the lowest abundance of epiphytes, albeit not significant; whilst *S. fluitans* III and *S. natans* VIII had similar epiphytic coverage (Fig. 5).

A comparison of the epiphytic community hosted by sargassum arriving in Barbados from the two sub-origins within the NERR indicated a slightly higher abundance of O. dichotoma and filamentous alga associated with sub-origin B (Supplementary Fig. 2 a,b). However, the apparent difference was not significant (Pseudo-F = 2.352, p = 0.081). The epiphytic community associated with incoming sargassum differed significantly based on host morphotype (Pseudo-F = 13.224, p = 0.001; Fig. 6). The bryozoan, M. tuberculata was the predominant species observed on S. fluitans III and S. natans I. The hydroid, A. latecarinata was the predominant species observed on S. natans VIII, but did not occur on the conspecific S. natans I; while, C. noliformis and O. dichotoma primarily occurred on S. fluitans III and S. natans I respectively (Fig. 6). S. spirorbis and the filamentous alga were observed on all three sargassum morphotypes with low percentage cover. S. natans VIII was the only morphotype to host all of the observed species but no epiphytic species was specific to a single sargassum morphotype (Fig. 6).

With the exception of *M. tuberculata*, epiphytes appear to have a preference for different regions of the sargassum thallus. Preliminary,

#### Table 1

Occurrence (% cover) of epiphyte species on pelagic sargassum morphotypes arriving in Barbados.

Group	Species	Family	Type of organism	Average epiphyte % cover ± SD
Fauna	Membranipora tuberculata	Membraniporidae	Bryozoan	$\textbf{33.4} \pm \textbf{16.9}$
	Aglaophenia latecarinata	Aglaopheniidae	Hydroid	$13.0\pm19.3$
	Clytia noliformis	Campanulariidae	Hydroid	$6.8 \pm 17.3$
	Spirorbis spirorbis	Serpulidae	Polychaete	$\textbf{5.0} \pm \textbf{4.9}$
	Obelia dichotoma	Campanulariidae	Hydroid	$\textbf{3.7} \pm \textbf{5.7}$
	Plumularia strictocarpa	Plumulariidae	Hydroid	$0.1\pm0.5$
Flora	Unid. filamentous alga	Chlorosarcinaceae	Algae	$\textbf{0.7}\pm\textbf{1.5}$

albeit qualitative, observations revealed that hydroids predominantly occupied the blades of sargassum with occasional growth on the aerocysts and axes (Fig. 7). *S. spirorbis* was mainly observed on the blades and epiphytic alga predominantly occupied the basal region of the axis. In contrast, *M. tuberculata* showed no preference for a particular region and as a result was observed on the axes, blades and aerocysts of sargassum thalli.

#### 4. Discussion

Pelagic sargassum arriving in Barbados during July and August 2021 (summer) and February and March 2022 (winter) was associated with six species of fauna and an unidentified filamentous alga. This first account of the epiphytic community associated with pelagic sargassum in the Eastern Caribbean found fewer species than reported by earlier studies in the North Atlantic (Weis, 1968:10 species). Specifically, our records of four hydroid species were considerably lower than those reported from the Sargasso Sea (Calder, 1995:10 hydroids), (Rackley, 1974: 29 hydroids). They were also lower than reported by Mendoza--Becerril et al. (2020) (9 hydroids) for pelagic sargassum arriving in Mexico from the NERR, via the Caribbean Sea. According to Kingsford (1992) species diversity increases with the amount of time a drifting structure, in this case pelagic sargassum, stays afloat. Thus, we postulate, that studies with ties to the well-established Sargasso Sea and those conducted in the countries further away from the NERR would have greater biodiversity than Barbados which is one of the first countries to receive sargassum from the Tropical Atlantic.

Within the present study, hydroids accounted for 4 of the 7 species associated with incoming sargassum. These colonial animals are substrate generalists (Calder, 1991) that attach to substrates after the build-up of bacteria (Sieburth and Conover, 1965; Coston-Clements et al., 1991). The ability of hydroids to travel great distances when attached to substrates (Calder, 1991) increases the likelihood that the observed hydroid species arrived from sub-origins within the NERR and/or along their transport pathways to Barbados. However, it is not possible to consider the observed species new to Barbados given the dearth of information, especially on floating substrates, of hydroid species for the island. Early studies of hydroids observed in Barbados recorded one athecate species, Ralpharia gorgoniae, (Calder and Kirkendale, 2005) and five thecate species, Dynamena quadridentata, Synthecium tubithecum, Thyroscyphus marginatus (reported as Obelia marginata), Thyroscyphus ramosus (Calder and Kirkendale, 2005) and Gymnangium speciosum (Calder, 2013); none of which were observed in this study.

Our results suggest that there is no significant difference in epiphyte percentage cover or the epiphytic community of sargassum between sub-origins A and B. However, epiphytic assessments of *S. fluitans* III, *S. natans* I and *S. natans* VIII revealed host preference among hydroid species. Although hydroids are capable of attaching to a range of sub-strate groups, they can occasionally exhibit fidelity for certain substrates (Calder, 1991). Variation in the spatial arrangement of blades and aerocysts as well as foliage density among the various sargassum morphotypes, therefore makes it plausible for some epiphytes to be more or less prone to settle on a given morphotype. Recent studies by Martin et al. (2021) linked differences in architectural complexity among sargassum morphotypes to their capacity to support various densities of motile epifauna. Moreover, the number of epiphytes on sargassum adds to the structural complexity and in turn, increases the occurrence and abundance of clinging organisms (Cunha et al., 2018).

Similar to Govindarajan et al. (2019), *A. latecarinata* hydroids were observed on *S. natans* VIII and *S. fluitans* III. Contrastingly, we observed a higher abundance of *A. latecarinata* on *S. natans* VIII compared to *S. fluitans* III with no occurrence of *A. latecarinata* on *S. natans* I. This differed from studies in the Sargasso Sea (Weis, 1968; Ryland, 1974; Niermann, 1986) that reported a dominance of *A. latecarinata* on *S. fluitans* III; albeit this difference may be due to the absence of *S. natans* 



Fig. 3. Epiphytes associated with Sargassum fluitans III, S. natans I and S. natans VIII arriving in Barbados. (A) Spirorbis spirorbis; (B) Membranipora tuberculata; (C) filamentous alga; (D) Aglaophenia latecarinata; (E) Clytia noliformis; (F–H) Obelia dichotoma; (I) Plumularia strictocarpa. Scale bars for (A), (B), (C) equal 10 mm, for (D), (E), (G) equal 0.2 mm and (F), (H), (I) equal 1 mm.



Fig. 4. Backtracks of pelagic sargassum collected from Conset Bay beach in Barbados. Panel (a) shows sample backtracks that originate close to the equator and travel along northeast Brazil before arriving in Barbados; origin/transport pathway A. Panel (b) shows backtracks that originate further north and traveled a relatively direct westerly route to Barbados; sub-origin/transport pathway B. Backtracks were run over a 365-day period using 100 particles. White dots indicate the origin of each backtrack particle (i.e., the backtrack location 365 days before arriving to Barbados) and the black square represents the origin of highest probability (mean of all backtrack particles).

VIII in the aforementioned studies. *A. latecarinata* forms feather-like colonies that can reach up to 20 mm in height (Rackley, 1974; Morris and Mogelberg, 1973). It is plausible that the densely clustered and broad-leafed *S. fluitans* III provides a more suitable structure for the attachment of *A. latecarinata* hydroids in the Sargasso Sea where the smaller fine-leafed *S. natans* I is the most abundant morphotype (Schell et al., 2015). Furthermore, Burkenroad (in Parr, 1939) concluded that the growth rate of sargassum, hydroids and competitive interactions between epiphytes will ultimately determine dominant hydroid species.

In the Sargasso Sea, *S. natans* I and *C. noliformis* both exhibit rapid growth rates and as a result, *C. noliformis* is almost always the dominant species on *S. natans* I; leaving the slower growing *A. latecarinata* to occupy *S. fluitans* III (Rackley, 1974). However, sargassum species exhibit different growth rates under optimal conditions (Hanisak and Samuel, 1987; Lapointe, 1995) and recent studies on pelagic sargassum originating from the NERR identify *S. fluitans* III as the fastest growing morphotype when compared to *S. natans* I and *S. natans* VIII (Corbin 2022: in press). Rapid growth rates of *S. fluitans* III when compared to its



**Fig. 5.** Percent cover of epiphytes on the three prevalent sargassum morphotypes (*Sargassum fluitans* III, *S. natans* I, *S. natans* VIII) arriving in Barbados from sub-origins within the NERR.

counterparts could explain why it is dominated by the fast-growing *C. noliformis*; and likewise, the dominance of *A. latecarinata* on the slower growing *S. natans* VIII. Mendoza-Becerril et al. (2020) in Mexico also reported a dominance of *C. noliformis* on *S. fluitans* III and *A. latecarinata* on *S. natans* VIII, but interestingly, found no occurrence of *A. latecarinata* on *S. fluitans* III. During our observations *O. dichotoma* was the predominant hydroid on *S. natans* I, albeit with a low percentage cover (4.2%). In addition to *O. dichotoma, S. natans* I was occupied by very small colonies of *C. noliformis* and *P. strictocarpa* but never with *A. latecarinata*.

Apart from hydroids, other epiphytes observed were the bryozoan *M. tuberculata*, the polycheate tube-worm *S. spirorbis* and a single filamentous epiphytic alga. *M. tuberculata* dominated *S. fluitans* III and *S. natans* I, with a percentage cover of 45.2 % and 35 % respectively. Investigations into the succession of epiphytes on pelagic sargassum revealed an abundance of hydroids on new growth areas, with bryozoans and tube-worms primarily occupying older regions of the thalli (Ryland, 1974). This suggests that samples collected within the present study were relatively mature. Consistent with our findings, Shadle et al. (2019) also reported a high abundance of bryozoans to outcompete rapidly colonizing but inefficient space competitors, such as hydroids (Calder, 1991), requires further research as it will likely influence the structure of the epiphytic community. Unlike hydroids, other epiphytes (bryozoans, brave) and the succession of the structure of the epiphytes (bryozoans).

tube-worms and filamentous alga) showed no obvious preference for host morphotype. Since *S. natans* I has narrower leaves, it provides less space for epiphytes to attach (Weis, 1968); however, *S. natans* I was capable of supporting just as many species (6) as the broader leafed *S. fluitans* III during our assessments. *S. natans* VIII was the only morphotype occupied by all of the identified epiphyte species.

The findings of this study contribute to the limited body of knowledge on the epiphytic community associated with pelagic sargassum influxes originating from the NERR. Further studies on this epiphytic community are necessary as sargassum originating from the NERR plays a major role in Caribbean beach inundations and therefore capable of transporting invasive species to local communities. Similar to Mendoza-Becerril et al. (2020), this study reported the presence of O. dichotoma which is considered an invasive species in Mexico (GBIF, 2019); however, its impacts (if any) in Barbados are unknown. Epiphytic assessments can also prove useful for guiding potential uses of sargassum biomass. As sargassum ages it gradually becomes heavily biofouled making it less suitable for valorization applications that require 'fresh' clean sargassum for use (e.g., applications that require a high phenolic content). Additionally, estimates of epiphytes can be used as factors for assessing variability in the associated motile community (Shadle et al., 2019) that can be used to guide in-water harvesting efforts.

This research provides the first quantification of the epiphytic community associated with pelagic sargassum in the Eastern Caribbean as it transitions from open Tropical Atlantic Ocean into the Caribbean Sea and will provide a useful baseline for monitoring potential change over time. All of the identified hydroids within this study were previously identified by the only other Caribbean study (Mendoza-Becerril et al., 2020) that assessed the hydroid community associated with influxes from the NERR. Similar to previous studies our results suggest distinct differences in the epiphytic communities hosted by different sargassum morphotypes. These findings suggest that sargassum morphology is likely a stronger determinant of epiphyte composition than any environmental differences encountered between sub-origins and their associated transport pathways. Earlier studies postulate that differences in hydroid species composition on S. fluitans III, S. natans I and S. natans VIII maybe associated with: (1) thallus morphology and/or the substances they produce (Nishihira in Mendoza-Becerril et al., 2020); (2) growth patterns of hydroid and morphotype species (Burkenroad in Parr, 1939) and; (3) location of host origins (Govindarajan et al., 2019). While our results support explanations 1 and 2, further studies on the epiphytic community associated with pelagic sargassum arriving from the NERR are warranted. Govindarajan et al. (2019) found significant



Fig. 6. Epiphytic percentage cover of Sargassum fluitans III (SFIII), S. natans I (SNI) and S. natans VIII (SNVIII) arriving in Barbados.



Fig. 7. In-water images of hydroid species associated with pelagic sargassum. Panel A: left shows *S. natans* VIII with *Aglaophenia latecarinata;* right shows close up of *A. latecarinata.* Panel B: left shows *S. fluitans* III with *Clytia noliformis;* right shows close up of *C. noliformis.* Underwater photographs provided by Makeda Corbin. Scale bars are equal to 0.2 mm.

population genetic structure in *A. latecarinata* hydroids, consistent with distributional patterns of sargassum morphotypes. These results suggest potential population-level connections between host origins and hydroid/epiphyte genetic identity. Thus, the use of morphological characteristics for taxonomic identification in the present study, limits our ability to determine potential differences in host origins. Future studies are needed to better assess differences in population genetics of the epiphytic community associated with sargassum originating from sub-origins within the NERR.

## CRediT authorship contribution statement

KA and HO conceptualized the work. KA conducted and analyzed the data. All authors contributed to the writing of the article and approved the submitted version.

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#### **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.

# Data Availability

Data will be made available on request.

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#### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2023.103635.

#### References

- Alleyne, K.S.T., Johnson, D., Neat, F., Oxenford, H.A., Vallès, H., 2023. Seasonal variation in morphotype composition of pelagic Sargassum influx events is linked to oceanic origin. Scientific Reports (In press).
- Amador-Castro, Fernando, García-Cayuela, Tomás, Alper, Hal S., Rodriguez-Martinez, Verónica, Carrillo-Nieves, Danay, 2021. Valorization of pelagic sargassum biomass into sustainable applications: current trends and challenges. J. Environ. Manag. 283 (April), 112013 https://doi.org/10.1016/j.jenvman.2021.112013.
- United Nations Environment Programme- Caribbean Environment Programme, 2021. Sargassum White Paper – Turning the crisis into an opportunity. Ninth Meeting of the Scientific and Technical Advisory Committee (STAC) to the Protocol Concerning Specially Protected Areas and Wildlife (SPAW) in the Wider Caribbean Region. Kingston, Jamaica.

Bartlett, Debbie, Elmer, Franziska, 2021. The impact of Sargassum inundations on the Turks and Caicos Islands. Phycology 1, 83–104. https://doi.org/10.3390/ phycology1020007.

- Butler, James N., Morris, Byron F., Cadwallader, Jill, Stoner, Allan W., 1983. Studies of Sargassum and the Sargassum Community. Special Publication 22. Bermuda Biological Station for Research, Inc, Bermuda.
- Calder, Dale R., 1991. Associations between hydroid species assemblages and substrate types in the Mangal at Twin Cays, Belize. Can. J. Zool. 69 (8), 2067–2074. https://doi.org/10.1139/z91-288.
- Calder, Dale R., 1995. Hydroid assemblages on holopelagic Sargassum from the Sargasso sea at Bermuda. Bull. Mar. Sci. 56 (2), 537–546.
- Calder, Dale R., 2013. Some shallow-water hydroids (Cnidaria: Hydrozoa) from the central East Coast of Florida, USA. Zootaxa 3648 (1), 1. https://doi.org/10.11646/zootaxa.3648.1.1.
- Calder, Dale R., Kirkendale, Lisa, 2005. Hydroids (Cnidaria, Hydrozoa) from shallowwater environments along the Caribbean Coast of Panama. vol. 41(no. 3), pp. 476–91.
- Chávez, Valeria, Uribe-Martínez, Abigail, Cuevas, Eduardo, Rodríguez-Martínez, Rosa E., van Tussenbroek, Brigitta I., Francisco, Vanessa, Estévez, Miriam, et al., 2020. Massive influx of pelagic Sargassum Spp. on the coasts of the Mexican Caribbean 2014–2020: challenges and opportunities. Water 12 (10), 2908. https://doi.org/ 10.3390/v12102908.
- Coston-Clements, L., Settle, L.R., Hoss, D.E., Cross, F.A., 1991. Utilization of the Sargassum habitat by marine invertebrates and vertebrates – a review. NOAA Tech. Memo. NMFS-SEFSC 296.
- Cunha, Amanda Ferreira, Maruyama, Pietro Kiyoshi, Giuliano, Buzá Jacobucci, 2018. Epiphytic hydroids (Cnidaria, Hydrozoa) contribute to a higher abundance of caprellid amphipods (Crustacea, Peracarida) on macroalgae. Hydrobiologia 808 (1), 251–264. https://doi.org/10.1007/s10750-017-3427-5.
- Desrochers, Anne, Cox, Shelly-Ann, Oxenford, Hazel A., van Tussenbroek, Brigitta I., 2020. Sargassum Uses Guide: A Resource for Caribbean Researchers, Entrepreneurs and Policy Makers (CERMES Technical Report 97). University of the West Indies, Cave Hill Campus. Centre for Resource Management and Environmental Studies, Barbados. (https://www.cavehill.uwi.edu/cermes/projects/sargassum/docs/des rochers\_et\_al\_2020\_sargassum\_uses\_guide\_advance.aspx).
- Dooley, James K., 1972. Fishes associated with the pelagic sargassum complex, with a discussion of the Sargassum community. Contrib. Mar. Sci. 16, 1–32.
- Franks, James S., Johnson, Donald R., Ko, Dong S., 2016. Pelagic Sargassum in the tropical North Atlantic. Gulf Caribb. Res. 27 (1) https://doi.org/10.18785/ gcr.2701.08.
- García-Sánchez, Marta, Graham, Caroline, Vera, Elisa, Escalante-Mancera, Edgar, Álvarez-Filip, Lorenzo, van Tussenbroek, Brigitta I., 2020. Temporal changes in the composition and biomass of beached pelagic Sargassum species in the Mexican Caribbean. Aquat. Bot. 167 (October), 103275 https://doi.org/10.1016/j. aquabot.2020.103275.
- Global Biodiversity Information Facility (GBIF), 2019. Obelia dichotoma (Linnaeus, 1758). Available at (https://www.gbif.org/species/5185976), (Accessed 14 December 2022).
- Goodwin, Deborah S., Siuda, Amy N.S., Schell, Jeffrey M., 2022. In situ observation of holopelagic Sargassum distribution and aggregation state across the Entire North Atlantic from 2011 to 2020. PeerJ 10 (September), e14079. https://doi.org/ 10.7717/peerj.14079.
- Govindarajan, Annette F., Cooney, Laura, Whittaker, Kerry, Bloch, Dana, Burdorf, Rachel M., Canning, Shalagh, Carter, Caroline, et al., 2019. The distribution and mitochondrial genotype of the hydroid Aglaophenia latecarinatais correlated with its pelagic Sargassum substrate type in the tropical and subtropical Western Atlantic Ocean. PeerJ 7, e7814. https://doi.org/10.7717/peerj.7814.
- Gower, J., Young, E., King, S., 2013. Satellite images suggest a new Sargassum source region in 2011. Remote Sens Lett 4, 764–773. https://doi.org/10.1080/ 2150704X.2013.796433.
- Hanisak, M.D., Samuel, M.A., 1987. Growth rates in culture of several species of Sargassum from Florida, USA. Hydrobiologia 151, 399–404. https://doi.org/ 10.1007/BF00046159.
- Johns, Elizabeth M., Lumpkin, Rick, Putman, Nathan F., Smith, Ryan H., Muller-Karger, Frank E., Rueda-Roa, Digna T., Hu, Chuanmin, et al., 2020. The establishment of a pelagic Sargassum population in the Tropical Atlantic: biological consequences of a basin-scale long distance dispersal event. Prog. Oceanogr. 182 (March), 102269 https://doi.org/10.1016/j.pocean.2020.102269.
- Johnson, Donald R., Franks, James S., Oxenford, Hazel A., Cox, Shelly-Ann L., 2020. Pelagic Sargassum prediction and marine connectivity in the Tropical Atlantic. Gulf Caribb. Res. 31, GCFI20–GCFI30. https://doi.org/10.18785/gcr.3101.15.
- Kingsford, Mj, 1992. Drift algae and small fish in coastal waters of Northeastern New Zealand. Mar. Ecol. Prog. Ser. 80, 41–55. https://doi.org/10.3354/meps080041.
- Lapointe, B.E., Brewton, R.A., Herren, L.W., Wang, M., Hu, C., McGillicuddy, D.J., Lindell, S., Hernandez, F.J., Morton, P.L., 2021. Nutrient content and stoichiometry of pelagic Sargassum reflects increasing nitrogen availability in the Atlantic Basin. Nat. Commun. 12 (1), 3060. https://doi.org/10.1038/s41467-021-23135-7.
- Lapointe, Brian E., 1995. A comparison of nutrient-limited productivity in Sargassum natans from neritic vs. oceanic waters of the Western North Atlantic Ocean. Limnol. Oceanogr. 40 (3), 625.
- Machado, Carla Botelho, Maddix, Gina-Marie, Francis, Patrice, Thomas, Shanna-Lee, Burton, Jodi-Ann, Langer, Swen, Larson, Tony R., Marsh, Robert, Webber, Mona, Tonon, Thierry, 2022. Pelagic Sargassum events in Jamaica: provenance, morphotype abundance, and influence of sample processing on biochemical composition of the biomass. Sci. Total Environ. 817 (April), 152761 https://doi.org/ 10.1016/j.scitotenv.2021.152761.

- Marsh, R., Oxenford, H.A., Cox, S-A.L., Johnson, D.R., Bellamy, J., 2022. Forecasting seasonal Sargassum events across the Tropical Atlantic: overview and challenges. Front Mar Sci 9, 914501. https://doi.org/10.3389/fmars.2022.914501.
- Martin, Lindsay M., Taylor, Madalyn, Huston, Grayson, Goodwin, Deborah S., Schell, Jeffrey M., Siuda, Amy N.S., 2021. Pelagic Sargassum morphotypes support different rafting motile epifauna communities. Mar. Biol. 168 (7), 115. https://doi. org/10.1007/s00227-021-03910-2.
- Mendoza-Becerril, María A., Serviere-Zaragoza, Elisa, Mazariegos-Villarreal, Alejandra, Rivera-Perez, Crisalejandra, Calder, Dale R., Vázquez-Delfín, Erika F., Freile-Pelegrín, Yolanda, Agüero, José, Robledo, Daniel, 2020. Epibiont hydroids on beachcast Sargassum in the Mexican Caribbean. PeerJ. https://doi.org/10.7717/ peerj.9795.
- Monroy-Velázquez, Luz Verónica, Rodríguez-Martínez, Rosa Elisa, van Tussenbroek, Brigitta I., Aguiar, Teresa, Solís-Weiss, Vivianne, Briones-Fourzán, Patricia, 2019. Motile macrofauna associated with pelagic Sargassum in a Mexican reef lagoon. J. Environ. Manag. 252. https://doi.org/10.1016/j. ienvman.2019.109650.
- Morris, Byron F., Mogelberg, Deborah D., 1973. Identification Manual to the Pelagic Sargassum Fauna (Special Publication 11). Bermuda Biological Station for Research, Bermuda.
- Niermann, U., 1986. Distribution of Sargassum natans and some of its epibionts in the Sargasso Sea. Helgol. Meeresunters. 40, 343–353.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., et al., 2018. vegan: community ecology package. R package version 2.5-3. (https:// CRAN.R-project.org/package=vegan).
- Oliveira, Otto Müller Patrão de, Marques, Antonio Carlos, Migotto, Alvaro Esteves, 2006. Chave de identificação dos hidróides (Cnidaria, Hydrozoa) epifíticos do Canal de São Sebastião (SE, Brasil). Biota Neotrop. 6 (2) https://doi.org/10.1590/S1676-06032006000200025.
- Oxenford, Hazel A., Johnson, Donald, Cox, Shelly-Ann, Franks, James, 2019. Report on the Relationships between Sargassum Events, Oceanic Variables, and Dolphinfish and Flyingfish Fisheries. Report prepared for the Climate Change Adaptation in the Eastern Caribbean Fisheries Sector (CC4FISH) Project of the Food and Agriculture Organization (FAO) and the Global Environment Facility (GEF). Centre for Resource Management and Environmental Studies, University of the West Indies, Cave Hill, Barbados. 32pp. (https://www.cavehill.uwi.edu/cermes/projects/sargassum/docs /cc4fish/d30 cc4fish report on the relationships between sa.aspx).
- Parr, Albert Eide, 1939. Quantitative Observations on the Pelagic Sasrgassum Vegetation of the Western North Atlantic. Vol. 6. Bulletin of the Bingham Oceanographic Collection. Bingham Oceanographic Laboratory, New Haven, Connecticut, USA.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. (https://www.R-project.org/
- Rackley, David, 1974. Hydroids of The Pelagic Sargassum Community of The Gulf Stream And Sargasso Sea. (https://doi.org/10.25773/V5-WAA7-4E36).
- Ramlogan, N.R., McConney, Patrick, Oxenford, Hazel A., 2017. Socio-Economic Impacts of Sargassum Influx Events on the Fishery Sector of Barbados (81. CERMES Technical Report). Centre for Resource Management and Environmental Studies, University of the West Indies, Cave Hill Campus, Bridgetown, Barbados.
- Resiere, Dabor, Hossein Mehdaoui, Rémi Nevière, Mégarbane, Bruno, 2019. Sargassum invasion in the Caribbean: the role of medical and scientific cooperation. Rev. Panam. De. Salud Pública 43, e52. https://doi.org/10.26633/RPSP.2019.52.
- Resiere, Dabor, Mehdaoui, Hossein, Florentin, Jonathan, Gueye, Papa, Lebrun, Thierry, Blateau, Alain, Viguier, Jerome, et al., 2021. Sargassum seaweed health menace in the Caribbean: clinical characteristics of a population exposed to hydrogen sulfide during the 2018 massive stranding. Clin. Toxicol. 59 (3), 215–223. https://doi.org/ 10.1080/15563650.2020.1789162.
- Ryland, J.S., 1974. Observations on some epibionts of gulf-weed, Sargassum natans (L.) Meyen. J. Exp. Mar. Biol. Ecol. 14 (1), 17–25. https://doi.org/10.1016/0022-0981 (74)90034-3.
- Schell, Jeffrey, Siuda, Amy N.S., Goodwin, Deborah S., 2016. Shipboard observation of pelagic Sargassum Spp. reveals proliferation of a rare form and differences in associated mobile fauna community structure. Proc. Gulf Caribb. Fish. Inst. 68, 421–423.
- Schell, Jeffrey, Goodwin, Deborah S., Siuda, Amy N.S., 2015. Recent sargassum inundation events in the caribbean: shipboard observations reveal dominance of a previously rare form. Oceanography, 2015.
- Schuchert, Peter, 2012. North-West European athecate hydroids and their medusae. In: Crothers, J.H., Hayward, P.J. (eds.), Synopses of the British Fauna, 59.
- Shadle, Sarah, Lestrade, Olivia, Elmer, Franziska, Hernandez Jr, Frank, 2019. Estimation and comparison of epiphyte loading on holopelagic Sargassum fluitans collected in the North Atlantic Ocean and the Gulf of Mexico. Gulf Caribb. Res. 30 (1) https:// doi.org/10.18785/gcr.3001.16.
- Sieburth, John, Conover, John, 1965. Sargassum Tannin, an antibiotic which retards fouling, vol. 208, pp. 52–3. (https://doi.org/10.1038/208052a0).
- Skliris, Nikolaos, Marsh, Robert, Appeaning Addo, Kwasi, Oxenford, Hazel, 2022. Physical drivers of pelagic Sargassum bloom interannual variability in the Central West Atlantic over 2010–2020. Ocean Dyn. 72, 383–404. https://doi.org/10.1007/ s10236-022-01511-1.
- van Tussenbroek, Brigitta I., Hernández-Arana, Héctor A., Rodríguez-Martínez, Rosa Elisa, Espinoza-Avalos, Julio, Canizales-Flores, Hazel M., González-Godoy, Carlos E., Guadalupe Barba-Santos, M., Vega-Zepeda, Alejandro, Collado-Vides, Ligia, 2017. Severe impacts of brown tides caused by Sargassum Spp. on near-shore Caribbean

seagrass communities. Mar. Pollut. Bull. 122, 272–281. https://doi.org/10.1016/j.marpolbul.2017.06.057 (1–2).
Wang, Mengqiu, Hu, Chuanmin, Barnes, Brian B., Mitchum, Gary, Lapointe, Brian, Montoya, Joseph P., 2019. The great Atlantic Sargassum belt. Science 365, 83–87.

Weis, Judith Shulman, 1968. Fauna associated with pelagic Sargassum in the Gulf Stream. Am. Midl. Nat. 80 (2), 554. https://doi.org/10.2307/2423550.