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Spatiotemporal analyses of pelagic Sargassum : biodiversity, morphotypes and arsenic content

Kristie Alleyne

SPATIOTEMPORAL ANALYSES OF PELAGIC SARGASSUM:

Biodiversity, morphotypes and arsenic content

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Spatiotemporal analyses of pelagic sargassum: biodiversity, morphotypes and arsenic content

Kristie Alleyne

Barbados

A dissertation submitted to the World Maritime University in partial fulfilment of the requirements for the award of the degree of

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Dedicated to my mother,
a strong woman who taught me that where you come from
is not as important as where you’re going.

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Acknowledgement

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Abstract

Pelagic sargassum blooming in the Tropical Atlantic has been linked to the mass shoreline inundations observed over the last decade in Caribbean and West African countries. Since the onset in 2011, affected countries have and continue to experience multiscale impacts across fisheries, tourism, nearshore coastal ecosystems, maritime transport and public health. Impacts associated with influx events have generated significant economic damage across the region. Moreover, clean-up efforts in response to mass shoreline strandings placed further strain on national economies and in some instances amplified the negative environmental effects caused by inundations. Evidence suggests that influx events are likely to continue into the foreseeable future leaving countries with no choice but to adapt to their new reality. In an attempt to 'turn the tide' against influx events, researchers and entrepreneurs are searching for innovative applications for the large quantities of sargassum arriving on their shores. Whilst valorisation of pelagic sargassum presents an opportunity to ameliorate some of the economic damage generated from influx events; commercialization efforts face key constraints that must be overcome in order to turn the current threats associated with influxes into opportunities. Constraints associated with sargassum valorisation can be grouped into five broad categories: (1) unpredictable supply (of sargassum and its different morphotypes); (2) insufficient knowledge of the biological and chemical properties including micro-pollutants; (3) harvesting, transport and storage; (4) governance; and (5) funding.

The main focus of this thesis is to understand the spatiotemporal variation in the biological and chemical composition of sargassum influx events. The research takes a compilation approach centring each of the five core papers on knowledge gaps relating to key valorisation constraints. Specifically, this research focussed on understanding: the biodiversity associated with sargassum influx events and identifying implications for in-water harvesting; the variation in the supply of sargassum morphotypes; and the arsenic levels and arsenic 'species' composition associated with influx events. Using a combination of quantitative research methods this thesis provides important baseline information on the sargassum community, its morphotypes and arsenic content. Biodiversity assessments indicate that there is a low species diversity associated with shore bound pelagic sargassum. Furthermore, raft size and distance from shore was positively correlated with species abundance. This suggests that in-water harvesting of smaller mats and those within the nearshore environment is unlikely to have any significant negative impacts on the associated community. Assessment of the morphotype composition over the course of one year reveals that variation in the predominant morphotype during influx events is linked to oceanic sub-origins within the Tropical Atlantic. Contrastingly, arsenic analyses suggest that arsenic contamination of pelagic sargassum arriving in Barbados was not affected by sub-origins, sample month or year. However, results indicate that the toxic inorganic arsenic species represents a substantial percentage of the total arsenic content of sargassum arriving in Barbados. Findings of this research contribute to the growing body of knowledge on pelagic sargassum influx events in the Caribbean and are relevant to the budding sargassum industry and ultimately to the adaptation of Caribbean people to this new hazard.

Abbreviations

AMM	Atlantic Meridional Mode
BAL	Brooks Applied Labs
BVI	Sanders Biological Value index
CANARI	Caribbean Natural Resources Institute
CENA	Central Equatorial North Atlantic
CERMES	Centre for Resource Management and Environmental Studies
CTNA	Central Tropical North Atlantic
eDNA	Environmental deoxyribonucleic acid
FAD	Fish Aggregating Device
GASB	Great Atlantic Sargassum Belt
GDP	Global Drifter Program
GOI	Global Ocean Institute
HAB	Harmful Algal Bloom
H_2S	Hydrogen Sulfide
ICP-QQQ-MS	Inductively Coupled Plasma Triple Quadrupole Mass Spectrometry
IC-ICP-CRC-MS	Ion Chromatography Inductively Coupled Plasma Collision Reaction Cell Mass Spectrometry
ITCZ	Intertropical Convergence Zone
MaxN	Maximum number of individuals
MANOVA	Multivariate Analysis of Variance
MSP	Marine Spatial Planning
NAO	North Atlantic Oscillation
NBC	North Brazil Current
NEC	North Equatorial Current
NECC	North Equatorial Counter Current
NERR	North Equatorial Recirculation Region
PERMANOVA	Permutational Multivariate Analysis of Variance
RDA	Redundancy Analysis
Sbt	Sargassum Brown Tide
SEC	South Equatorial Current
SST	Sea Surface Temperature
SVP	Surface Velocity Program
WCR	Wider Caribbean Region
WTNA	West Tropical North Atlantic

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Alleyne, K. S. (2022). How is pelagic sargassum-associated biodiversity assessed? Insights from the literature. *Gulf and Caribbean Research 33 (1)*, GCFI 14-GCFI 23. DOI: https://doi.org/10.18785/gcr.3301.08

Paper 2:

Alleyne, K. S. T., Neat, F., & Oxenford, H. A. (2023). A baseline assessment of the epiphytic community associated with pelagic sargassum in the Tropical Atlantic. *Aquatic Botany, 186*, 103635. https://doi.org/10.1016/j.aquabot.2023.103635

Paper 3:

Alleyne, K. S. T., Small, M., Corbin, M., Vallès, H., & Oxenford, H. A. (2023). Free-swimming fauna associated with influxes of pelagic sargassum: Implications for management and harvesting. *Frontiers in Marine Science, 10*, ISSN 2296-7745. https://www.frontiersin.org/articles/10.3389/fmars.2023.109074

Paper 4:

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, 13(1)*, 3753. https://doi.org/10.1038/s41598-023-30969-2

Paper 5:

Alleyne, K. S. T., Neat, F., & Oxenford, H. A. (2023). An analysis of arsenic concentrations associated with sargassum influx events in Barbados. *Marine Pollution Bulletin, 192*, 115064. https://doi.org/10.1016/j.marpolbul.2023.115064

1. Introduction

1.1. What is pelagic sargassum?

Named after the prominent Sargasso Sea, pelagic *Sargassum* is a brown macroalgae (seaweed) under the genus *Sargassum* (Godínez-Ortega et al., 2021; Parr, 1939). Within the *Sargassum* genus, there are over 350 species distributed throughout tropical and subtropical oceans (Butler et al., 1983; Desrochers et al., 2022; Guiry & Guiry, 2023; Martin et al., 2016). Species of *Sargassum* are often classified based on the degree of branching, blade morphology, margins of the blades and the structure of reproductive organs; however, misidentification can occur due to their polymorphic character and phenotypic plasticity (Godínez-Ortega et al., 2021; Mattio & Payri, 2010). Pelagic *Sargassum* however is quite different from its benthic counterparts. Whilst benthic species are attached to the seafloor, pelagic *Sargassum* spends its entire life cycle floating on the surface of the ocean (Butler et al., 1983; Parr, 1939). In the North Atlantic this aquatic biomass is composed of two species (*Sargassum natans* and *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) (Parr, 1939).

Within the North Atlantic Ocean, the Sargasso Sea is bounded by a quadruple of currents (the Gulf Stream on the west, the North Atlantic Current to the north, the Canary Current on the east and the North Atlantic Equatorial Current on the south) (Gower & King, 2011; Trott et al., 2011) that form an oceanic gyre entraining the sargassum as a self-sustained floating 'rainforest'. This golden oasis in the midst of oligotrophic waters provides essential habitat, refuge and nursery grounds to a diverse assemblage of endemic and associated fauna (Bortone et al., 1977; Butler et al., 1983; Dooley, 1972; Moser & Lee, 2012; Wells & Rooker, 2003; Witherington et al., 2012). Pelagic sargassum in the North Atlantic has great ecological value and as a result significant steps have been taken to protect it (Laffoley et al., 2011).

1.2. The arrival of pelagic sargassum in the Caribbean

Since the days of Columbus, the vast quantities of pelagic sargassum in the Sargasso Sea have been the subject of scientific curiosity (Butler et al., 1983; Godínez-Ortega et al., 2021; Niermann, 1986; Parr, 1939). For centuries sargassum in the North Atlantic was the single largest aggregation of pelagic sargassum ever observed. No one predicted the turn of events that resulted in the unprecedented blooming of pelagic sargassum beyond the 'boundaries' of the Sargasso Sea. During the summer of 2011 there was a significant increase in the presence of pelagic sargassum in the equatorial Atlantic (centred at about 7° N, 45° W), an area not previously associated with sargassum growth (Franks et al., 2012; Gower et al., 2013). This 'new' bloom region is loosely bounded by the South Equatorial Current (SEC) and the North Equatorial Counter Current (NECC) and is referred to as the North Equatorial Recirculation Region (NERR) (Figure 1a) (Franks et al., 2016; Gower et al., 2013; Wang et al., 2019).

Within this thesis, 'Tropical Atlantic' is used to refer to three areas of primary concern: the Central Equatorial North Atlantic (CENA), the Central Tropical North Atlantic (CTNA) and the West Tropical North Atlantic (WTNA) (Skliris et al., 2022) (Figure 1b). Circumstances surrounding the onset of the 2011 proliferation in the Tropical Atlantic involve several significant events that created what can only be described as the 'perfect storm'. Starting with major climate indices, the Atlantic Meridional Mode (AMM) is the dominant source of coupled ocean-atmosphere (i.e., Sea Surface Temperature (SST) and wind anomalies) variability in the Tropical Atlantic (Djakouré et al., 2017; Xia et al., 2023). During positive AMM phases the trade winds become weaker resulting in higher SST, and weaker vertical wind shear in the Tropical Atlantic (Djakouré et al., 2017; Skliris et al., 2022). Surface warming anomalies observed during 2010 to 2011 were consistent with a continuously positive AMM (Djakouré et al., 2017; Skliris et al., 2022). Interestingly, the observed positive AMM phase of 2010 to 2011 was also associated with a northward shift of the Atlantic Intertropical Convergence Zone (ITCZ) (Djakouré et al., 2017). To understand the significance of this shift, the relationship between the ITCZ and the NECC must be acknowledged.

The ITCZ is an area of convergence between the northeast and southeast trade winds. This area exhibits seasonal meridional migration from the equatorial area to the northern area of the Tropical Atlantic (Djakouré et al., 2017). The NECC is a major eastward flowing wind driven current within the Tropical Atlantic (Figure 1a).

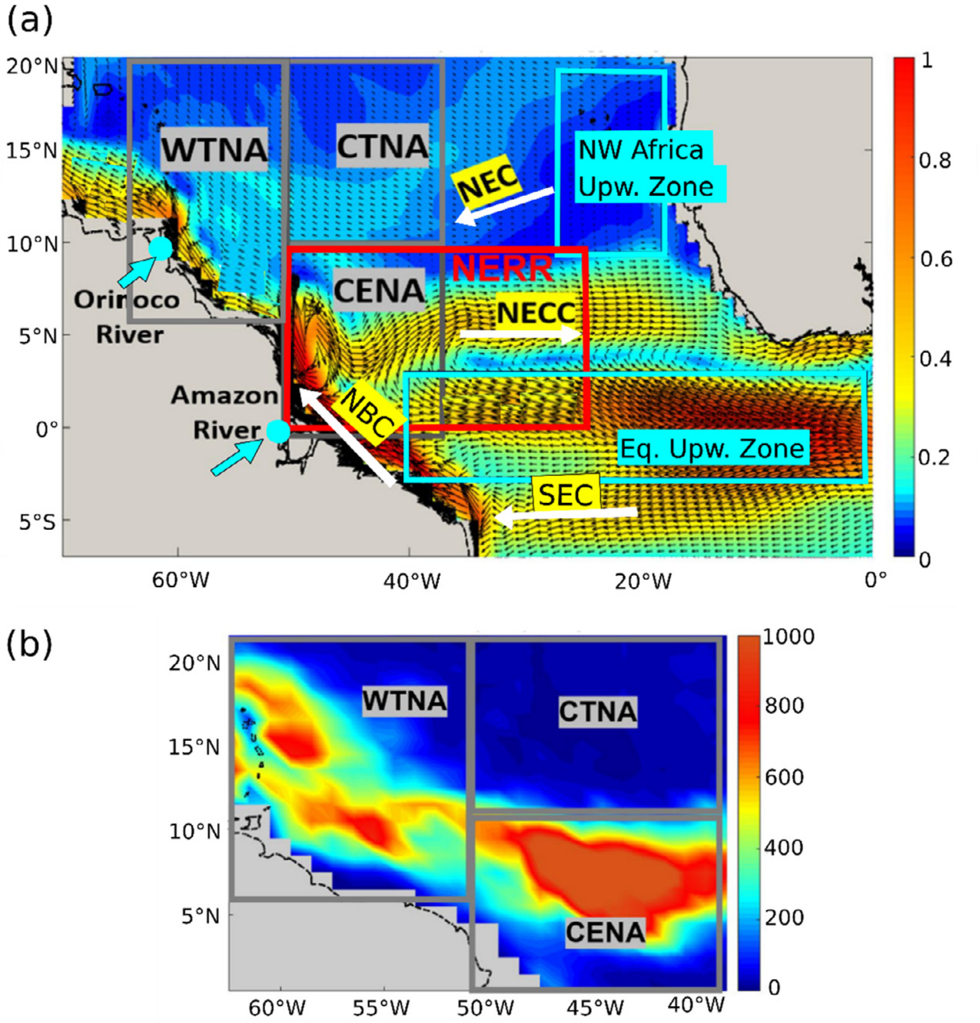

Figure 1: Major currents (based on climatological mean surface current velocity field (m/s)) and nutrient sources influencing sargassum proliferation in the Tropical Atlantic. In panel (a) the red box depicts the North Equatorial Recirculation Region (NERR, 25–50°W, 0–10°N). Light blue boxes depict areas encompassing the NW Africa coastal upwelling zone (20°W–30°W, 12°N–20°N) and equatorial upwelling zone, respectively. Main currents (NEC: North Equatorial Current; NBC: North Brazil Current; SEC: South Equatorial Current, NECC: North Equatorial Counter Current) are depicted in yellow. The approximate locations of the Amazon and Orinoco River mouths are depicted with light blue arrows. Panel (b) shows pelagic sargassum (based on climatological mean AFAI (2011–2020) areal fraction (km2) in July) in the areas of the Tropical Atlantic: Central equatorial North Atlantic (CENA: 38–50°W, 0–10°N), central tropical North Atlantic (CTNA: 38–50°W, 10–20°N), and west tropical North Atlantic (WTNA: 50–63°W, 6–22°N). Adapted from Skliris et al. (2022).

Formation of the NECC usually starts in Spring and strengthens in Summer preventing northward transport of nutrient rich waters from the equatorial upwelling zone (Skliris et al., 2022). During Autumn the NECC is pushed further north as the

ITCZ starts its upward migration. Northward movement of the NECC results in its gradual breakdown thus facilitating transport of nutrient-rich waters from the equatorial Atlantic (Skliris et al., 2022). Sargassum blooms are enhanced by high nutrient conditions (Lapointe, 1995; Lapointe et al., 2021), it is therefore plausible that the northward ITCZ shift during 2010 provided ideal nutrient conditions for the proliferation of sargassum. Despite ideal nutrient conditions, Johns et al. (2020) postulate that concurrent extreme SSTs in 2010 suppressed the growth of sargassum populations. Recent works by Magaña-Gallegos et al. (2023) and Corbin & Oxenford (2023) indicate that growth rates of pelagic S*argassum* spp. in the Tropical Atlantic decrease with increasing ambient temperatures; thus, supporting the hypothesis put forth by Johns et al. (2020). In the presence of a high nutrient environment, decreased SSTs in 2011 would have created ideal conditions for the proliferation of sargassum. However, even with favourable conditions, an important question remained, how did the 'seed' population arrive in the Tropical Atlantic? Using multiple lines of evidence Johns et al., (2020) conclude that during a record-breaking negative North Atlantic Oscillation (NAO) occurring from December 2009 through March 2010, sargassum from the Sargasso Sea was redistributed to the Tropical Atlantic via an extreme wind anomaly. With sargassum now 'transplanted' to the Tropical Atlantic surrounded by favourable nutrients and temperatures, the 'golden tides' of sargassum (Smetacek & Zingone, 2013) emerged and were transported into the Caribbean mainly via the North Equatorial Current (NEC) and the Guiana Current (Putman et al., 2018).

This broadscale complex event has resulted in several post-2011 blooms that have now developed into a vast band (5,500 miles in 2018) of sargassum commonly known as the Great Atlantic Sargassum Belt (GASB) (Wang et al., 2019). With the seed population now established, recurrent blooms have occurred under both positive and negative AMM phases fed by equatorial upwelling, Northwest Africa upwelling and inputs from the Amazon, Orinoco and Congo River (Djakouré et al., 2017; Oviatt et al., 2019; Skliris et al., 2022). Variations in the intensity of blooms from one year to another are primarily driven by patterns of regional winds and currents that control nutrient abundance and disperse sargassum biomass (Skliris et al., 2022).

1.3. Impacts associated with sargassum influx events

Across the globe there has been an increase in Harmful Algae Blooms (HABs) (Fidai et al., 2020; Joniver et al., 2021; Kraan, 2008; Smetacek & Zingone, 2013; Zhang et al., 2019). Although many of these blooms are not toxic, they have deleterious consequences for shore-based activities (Chávez et al., 2020; Cruz-

Rivera et al., 2015; McLawrence et al., 2017) and create a trophic collapse of nearshore coastal ecosystems (Hendy et al., 2021).

In most cases, sargassum transported on various currents from the bloom region ultimately makes landfall, blanketing the impacted area and builds up in the nearshore environment (Figure 2). These shoreline inundations are often referred to as ‘sargassum influx events’ (Chávez et al., 2020; Godínez-Ortega et al., 2021).

Figure 2: Sargassum inundation events along the east coast of Barbados. Panel (a) photo was taken by Gary Marshall. Panels (b) and (c) photos were taken by Hazel Oxenford.

During major influx events, beached sargassum starts to decay releasing a pungent odour, predominantly composed of hydrogen sulphide (H_2S) (Bartlett & Elmer, 2021; Chávez et al., 2020; Engel, 2018; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). Moreover, decaying sargassum within the nearshore environment results in the formation of Sargassum Brown Tides (Sbt). During a Sbt, decomposing sargassum releases leachates and organic material into the surrounding environment, turning usually clear waters into murky brown water (van Tussenbroek et al., 2017). Throughout the Caribbean region, coastal environments often consist of important seagrass and coral habitats (Chávez et al., 2020; Engel, 2018; Schuhmann et al., 2019; van Tussenbroek et al., 2017). Transformation of the nearshore environment during Sbts triggers a cascade of events that result in reduced sunlight and depleted oxygen levels (van Tussenbroek et al., 2017); severely impacting corals, seagrass communities and associated fauna (Chávez et al., 2020; Engel, 2018; van Tussenbroek et al., 2017).

Mass accumulation and decomposition of sargassum throughout the Caribbean, besiege key economic sectors (i.e., tourism, fisheries) on which the region depends (Caribbean Regional Fisheries Mechanism & Japanese International Cooperation Agency, 2019; Chávez et al., 2020; Cruz-Rivera et al., 2015; McLawrence et al., 2017; Ramlogan et al., 2017; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). The Caribbean is known for its sun, sand and emblematic beaches and many visitors base their decision to return on the quality of the marine environment (Schuhmann et al., 2019). Sargassum influx events and subsequent brown tides create conditions unconducive to coastal tourism. During peak sargassum periods (March-July), hotels along the coast experience decreased occupancy and incur high management costs associated with sargassum removal (Chávez et al., 2020; Godínez-Ortega et al., 2021). In most cases, operators offering tourist activities (i.e., boat trips, snorkelling/diving, surface water sports, shore leisure) experience greater impacts when compared to hoteliers and accommodation owners (Bartlett & Elmer, 2021).

Within the Caribbean, marine fisheries provide valuable economic opportunities, facilitate social networks and contribute to food security (Caribbean Natural Resources Institute (CANARI), 2020). The arrival of sargassum in the Caribbean resulted in physical and socio-economic impacts across the harvest and post-harvest sector with the harvest sector being particularly affected (Ramlogan et al., 2017). Fishers across the region reported challenges at landing sites and at sea that led to loss of fishing days and increased fishing effort (Speede et al., 2018). At landing sites, inundated harbours restricted access to and prevented fishers from launching vessels. On the other hand, extraordinary amounts of incoming sargassum encountered at sea resulted in blocked water intakes, overheating engines, damaged fishing gear, restricted visibility while driving and in some cases loss of steerage (McLawrence et al., 2017; Speede et al., 2018).

Behavioural traits of fish species and methods used by fishers to capture species, exacerbated impacts to the sector during mass sargassum influxes. Since the onset of influx events, the Barbados fisheries sector has reported a reduction in the catches of key fisheries species such as the adult dolphinfish (*Coryphaena hippurus*) and flyingfish (*Hirundicthys affinis*) (Oxenford et al., 2019). Prior to 2011, Barbadian fishers customarily caught high abundances of adult dolphinfish; however, there has been a decline in the landed weight since the arrival of sargassum. With very small dolphinfish now observed with peak summer sargassum influxes; Oxenford et al. (2019) postulates that the decline in landing weights is linked to the highly migratory behaviour of dolphinfish, with small juveniles now travelling into the region under sargassum rafts earlier in the fishing season than customary, and thus being caught at small sizes and not growing into larger individuals to be caught later. Contrastingly, decreased flyingfish landings appears to be attributed to their affinity to spawn on the available sargassum; thus, rendering floating Fish Aggregating Devices (FADs), traditionally used by fishers, ineffective (Oxenford et al., 2019).

Economic growth within the Caribbean is intrinsically linked to the marine environment (Maraj et al., 2011; Schuhmann et al., 2019; Scott et al., 2012); thus, negative impacts on fisheries, tourism and the environment are especially concerning. Given the unprecedented nature of sargassum influx events, responses to the large-scale blooms were reactive and somewhat haphazard (Hinds et al., 2016). Across the region inceptive management efforts focused on removing sargassum from affected beaches in hopes of minimising impacts to the tourism sector. Governments and hoteliers primarily utilised tractors and other heavy machinery to collect sargassum, inadvertently exacerbating coastal erosion through the removal of sand (Hinds et al., 2016; Kershaw & Hilal, 2017). Effective and sustainable management of influxes has proven to be a conundrum for managers. For example, mass inundations, blanket sea turtle nests with mounds of sargassum preventing hatchlings from reaching the ocean (Schiariti & Salmon, 2022). Yet attempts to alleviate these impacts, via shoreline harvesting, results in sand compaction exacerbating impacts to endangered sea turtle populations. Although commendable, clean-up efforts by government agencies and the private sector had severe, albeit unintentional, impacts on the environment and came at a considerable cost (hundreds of millions of US dollars per year) to national economies (Chávez et al., 2020; Liranzo-Gómez et al., 2021; Milledge & Harvey, 2016; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). In the end, a seemingly 'shoreline threat' is felt far beyond the ridges of Caribbean islands (United Nations Environment Programme - Caribbean Environment Programme et al., 2021).

1.4. Turning a threat into opportunities

It has now been over a decade since pelagic sargassum first arrived on the shores of Caribbean and West African countries; and like most uninvited guests, it does not appear to be leaving any time soon. The initial approach to influx events resembled that of crisis management and many countries declared states of national emergency (Chávez et al., 2020; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). Truckloads of sargassum were being transported from beaches directly to landfills (Milledge et al., 2020; Tonon et al., 2022). No one operated on the contingency that the current 'sargassum threat' could potentially lead to 'golden' opportunities. Today, there is a rapidly growing interest in utilising sargassum and turning it into valuable products (Amador-Castro et al., 2021; Desrochers et al., 2022; Robledo et al., 2021; Thompson et al., 2020) in an effort to ameliorate the economic damage generated in the region (Robledo et al., 2021).

1.4.1. Sargassum valorisation

Sargassum influxes affecting the Caribbean are widely recognised as comprising two species (three dominant morphotypes): *Sargassum natans* I, *S. natans* VIII and *S. fluitans* III (Schell et al., 2015). Observable differences among these three morphotypes include the lack of thorns/spines, the shape of the air bladders and the shape of the blades (Figure 3).

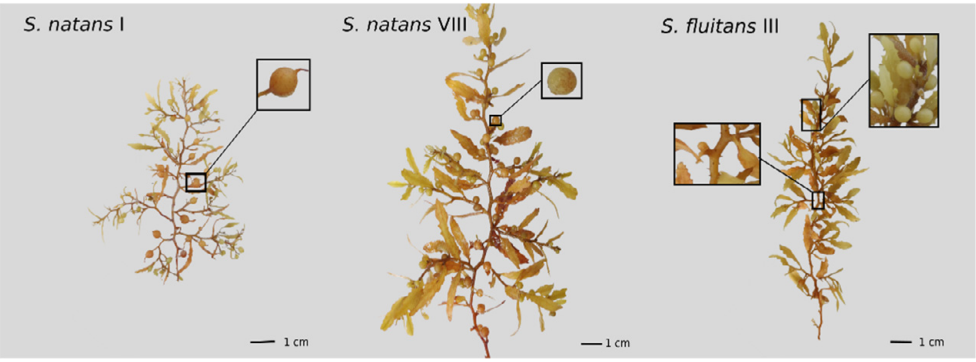

Figure 3: Three commonly occurring sargassum morphotypes in the Tropical Atlantic. Inset on *S. natans* I shows the presence of spines on the circular air bladders. Inset on *S. natans* VIII shows the absence of spines on the circular air bladders. The top right inset on *S. fluitans* III shows the absence of spines on the elongated air bladders and the bottom left inset shows the presence of spines along the stem. Image taken from (Alleyne, Neat, et al., 2023a).

Like most brown algae, pelagic sargassum contains carbohydrates, ash, fibre, proteins, lipids, vitamins, minerals and secondary metabolites making it potentially valuable in a large number of applications (Davis et al., 2020; Desrochers et al., 2022; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020; Tonon et al., 2022). Beyond their physical differences, pelagic sargassum morphotypes vary in the exact proportions of the constituent minerals and bioactive compounds (Davis et al., 2020; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020; Tonon et al., 2022). As a result, the composition of 'mixed pelagic sargassum' can often be substantially different from individual morphotypes (Milledge et al., 2020).

Based on the element and biochemical composition of pelagic sargassum and using previous examples of seaweed applications, potential uses within the Caribbean have been identified for 15 sectors: (1) Animal husbandry, (2) Crop production, (3) Antifouling, (4) Bioenergy, (5) Bioplastics, (6) Bioremediation and purification, (7) Clothing, footwear and accessories, (8) Construction materials, (9) Cosmetics, (10) Electrochemical industry, (11) Environmental restoration, (12) Food and beverages, (13) Lubricants, surfactants and adhesives, (14) Paper products, and (15) Pharmaceutical and biomedical (Desrochers et al., 2020, 2022). Presented with a wide range of options, researchers and entrepreneurs across the region are working arduously to find innovative businesses that can utilise large volumes of sargassum (Desrochers et al., 2020, 2022). Efforts to 'scale-up' potential sargassum uses indicate that one metric ton of fresh sargassum is capable of providing a wide range of valuable products (Desrochers et al., 2022) (Figure 4). To date sargassum-based products and/or businesses include: sargassum blocks 'Sargablocks', fertilizers, biodegradable plates, coasters and notebooks (Desrochers et al., 2022) with applications for bioenergy and composting being explored (Sembera et al., 2017; Thompson et al., 2020; Trench et al., 2022).

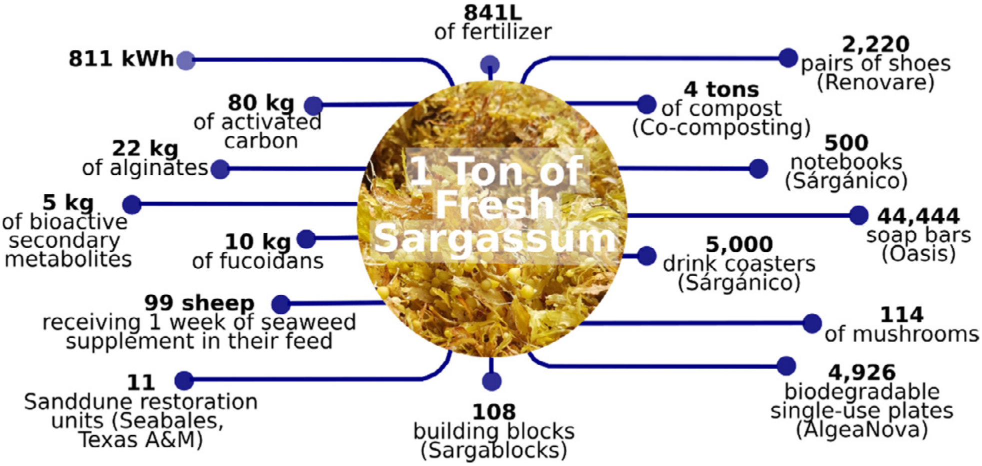

Figure 4: Relative product yields that could potentially be produced from one metric ton (1000 kg) of fresh sargassum. Taken from United Nations Environment Programme - Caribbean Environment Programme et al. (2021).

The use of sargassum for the production of bioenergy presents an opportunity to 'turn the tide' not only against the economically harmful influx events but also climate change. Anaerobic digestion is a well-established technique for energy recovery of organic residues (Ayala-Mercado et al., 2022) used to produce biogas. Research on the biogas potential of pelagic sargassum indicated that Tropical Atlantic blooms exhibit low methane productivity making them a poor feedstock for mono-digestion (Thompson et al., 2020). However, experiments using co-digestion and/or pre-treatments successfully increased methane yields and enhanced biogas production (Ayala-Mercado et al., 2022; Milledge et al., 2020; Nielsen et al., 2021; Oliveira et al., 2015; Thompson et al., 2020). In Barbados, innovative solutions to the escalating gas prices and the country's commitment to become fossil-fuel free, beach-cast sargassum is being utilised in combination with wastewater from the rum industry to produce biofuel (Sustainable Solution Development Network, 2022). Interestingly, the potential role of influx events on mitigating climate change does not stop with bioenergy. Research by Trench et al. (2022) indicates that sargassum has the potential to make ecologically meaningful contributions towards carbon storage, through the use of composting for mangrove restoration. Similarly, Gouvêa et al. (2020) suggest that the present high amounts of sargassum plays a critical role in CO_2 removal; although other research (Hu et al., 2021) indicate that carbon stock and carbon fixation may only be important within the GASB and not on a global scale. Nevertheless, it appears that the sargassum 'threat' thrust upon the Caribbean in some part due to climate change may very well provide mitigation opportunities; the irony is certainly not lost.

1.4.2. Challenges associated with sargassum valorisation

The valorisation of sargassum can render sargassum influx events into an economic opportunity for Caribbean islands. However, despite its potential, the development of sargassum-based products and businesses has met several challenges/constraints. To identify the challenges associated with sargassum valorisation, Desrochers et al. (2022) undertook 72 key informant (researchers and entrepreneurs) interviews across 24 countries/territories in the Wider Caribbean Region (WCR) and beyond (North America, United States of America, Europe, Asia). Results indicate that challenges associated with sargassum valorisation can be grouped into five broad categories: (1) unpredictable supply (of sargassum and its different morphotypes); (2) insufficient knowledge of the chemical components including micro-pollutants; (3) harvesting, transport and storage; (4) governance; and (5) funding (Desrochers et al., 2022; Oxenford et al., 2021).

Since the initial influx in 2011, the intensity of Tropical Atlantic blooms has varied greatly. Some years produced extraordinary amounts (over 20 million metric tons in June 2018 alone) of sargassum biomass and other years (e.g., 2013) there was little to no influx (United Nations Environment Programme, 2018; United Nations Environment Programme - Caribbean Environment Programme et al., 2021; Wang et al., 2019). Moreover, there is evidence of substantial interannual and/or intra-annual variation in the morphotype composition of Tropical Atlantic blooms (Botelho Machado et al., 2022; García-Sánchez et al., 2020; Schell et al., 2015) which may ultimately result in variation in the chemical composition and what that sargassum can be used for. Given that businesses need a reliable supply of raw material to support sustainable production, not knowing when or how much sargassum will arrive in any given year makes it very difficult to fully commercialise the bioresource (Oxenford et al., 2021). To date, significant strides are being made to detect, monitor and predict influx events (Johnson et al., 2018, 2020; Marsh et al., 2021, 2022); however, there is low precision in long term forecasting and estimating exactly how much biomass will reach the shore (Oxenford et al., 2021; Rodríguez-Martínez et al., 2022; United Nations Environment Programme, 2018).

Research on biochemical and elemental characteristics of sargassum blooming in the Tropical Atlantic (Cipolloni et al., 2022; Davis et al., 2020; Devault et al., 2020, 2022; Gobert et al., 2022; Machado et al., 2022; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020) has been undertaken to help identify potential valorisation pathways. Reports on the chemical composition show high spatial and temporal variation, likely resulting from biotic (e.g., age, morphotype) and abiotic (e.g., temperature, nutrients, pollutants) factors encountered along the various transport pathways (Beron-Vera et al., 2022; Putman et al., 2018; Skliris et al., 2022). More importantly, sargassum has the capacity to bioaccumulate toxic trace metals and metalloids from their surroundings (Barquilha et al., 2019; Devault et al., 2022; Saldarriaga-Hernandez et al., 2020). Among the different trace metals, arsenic is of particular concern due to its notorious toxicity (Devault et al., 2020, 2021, 2022) and has been reported in elevated concentrations in pelagic sargassum across the Tropical Atlantic (Bam et al., 2022; Cipolloni et al., 2022; Davis et al., 2020; Devault et al., 2022; Gobert et al., 2022; Milledge et al., 2020; Nielsen et al., 2021). Arsenic contamination in pelagic sargassum is further complicated by the fact that uptake of the toxic inorganic pentavalent form (AsO_4^{3-}), is negatively correlated with the availability of nutrients; in particular phosphates (Gobert et al., 2022). Due to similarities in size and geometry with the arsenate (AsO_4^{3-}) and phosphate (PO_4^{3-}) ions, sargassum growing in phosphorus-limited waters actively uptake and accumulates arsenic within the cell walls and cell membranes (Gobert et al., 2022). Arsenic contamination presents significant barriers for valorisation, especially when considering applications involving the direct consumption of lightly or unprocessed biomass (Tonon et al., 2022). To better understand the threat posed by arsenic contamination, further research is needed on: seasonal variation; linkages between environmental factors and arsenic uptake; arsenic speciation (organic vs inorganic); and methods that can potentially reduce arsenic concentrations (Oxenford et al., 2021; Sembera et al., 2017; United Nations Environment Programme - Caribbean Environment Programme et al., 2021; Wang et al., 2022).

A lack of norms and/or regulations for the harvest of pelagic sargassum (López Miranda et al., 2021; Oxenford et al., 2021) has also presented substantial challenges for commercial valorisation. Initial responses to inundations predominantly involved onshore harvesting (Milledge & Harvey, 2016; Oxenford et al., 2021) with a myriad of negative environmental impacts (Chávez et al., 2020; Kershaw & Hilal, 2017; Schiariti & Salmon, 2022; van Tussenbroek et al., 2017). Moreover, sargassum harvested from the shore would inevitably be sand filled and in some cases partially decayed (Oxenford et al., 2021). To reduce the impacts associated with onshore harvesting and provide large quantities of fresh ‘clean’ sargassum for valorisation, in-water harvesting is currently being developed (Liranzo-Gómez et al., 2021; Oxenford et al., 2021; Webber & Maddix, 2021). However, the ecological function of sargassum at sea (Butler et al., 1983; Dooley, 1972) presents management concerns with regards to the impacts to and/or the destruction of the ecosystem (Oxenford et al., 2021; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). Research by Monroy-Velázquez et al. (2019) indicates that once pelagic sargassum is close to shore, the quantity and diversity of associated fauna is diminished; thus, rendering in-water harvesting nearshore a viable option for collecting sargassum that would otherwise be stranded (Chávez et al., 2020; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). It should be noted however that whilst in-water harvesting has several advantages over harvesting on the shore; specialised machinery and customisation to local sea conditions will be required (Oxenford et al., 2021).

Successful valorisation of pelagic sargassum requires a sustainable, comprehensive and economically efficient approach (López Miranda et al., 2021; Robledo et al., 2021). To date, large-scale commercialisation of sargassum is constrained by a lack of regulations, and of national and regional policies (Desrochers et al., 2022; López Miranda et al., 2021; Oxenford et al., 2021). Some eastern Caribbean countries have begun drafting sargassum management plans/strategies but implementation is yet to occur (Cox et al., 2019). In the absence of local and regional harvesting regulations, and due to the uncertainties surrounding supply, entrepreneurs continue to experience funding barriers (Oxenford et al. 2021). Funding (predominantly for clean-up efforts) has largely been undertaken by governments and private sectors with competitive grants to support monitoring, prediction and education becoming available in recent years (Oxenford et al., 2021). A confounding issue however lies in the difficulty of accessing funding opportunities (Desrochers et al., 2022; Oxenford et al., 2021).

1.5. Research aim, objectives and questions

Given that sargassum influx events are expected to be the new ‘normal’ for the region (Desrochers et al., 2022; Wang et al., 2019), coping can no longer be seen as a management strategy for the long-term. Increased adaptive capacity, learning to live with sargassum, is essential for the Caribbean nations in order to overcome the current challenges associated with influx events and build sustainable industries that create jobs and address sargassum removal (Oxenford et al., 2021). The scale and complexity surrounding influx events requires collaborative applied research efforts across a range of disciplines to guide management initiatives and address the identified constraints (Robledo et al., 2021). The evidence suggests that although a wide range of potential valorisation opportunities exist, sargassum influxes will remain more of a hazard than an opportunity, unless current constraints are adequately addressed (Oxenford et al., 2021).

This research aims to understand the spatiotemporal variation in the biological and arsenic composition of sargassum influx events while providing knowledge on three of the five valorisation challenges identified by Desrochers et al., (2022) and Oxenford et al., (2021). Specifically, it aims to address knowledge gaps on: (1) in-water harvesting and sargassum-associated biodiversity, (2) uncertainties surrounding the supply of the three commonly occurring morphotypes and (3) arsenic levels associated with incoming sargassum (Figure 5). Objectives of this thesis are addressed through the four main research questions:

1. Are there standard methods for collecting, identifying and analysing the biodiversity associated with pelagic sargassum?
2. What is the biodiversity associated with pelagic sargassum originating from the Tropical Atlantic and what factors drive changes in the community composition?
3. Why does sargassum morphotype composition in the Tropical Atlantic vary over space and time?
4. How does arsenic species composition (% inorganic vs organic) and abundance (concentration levels) within pelagic sargassum vary among influx events; are levels and/or composition influenced by sub-origins?

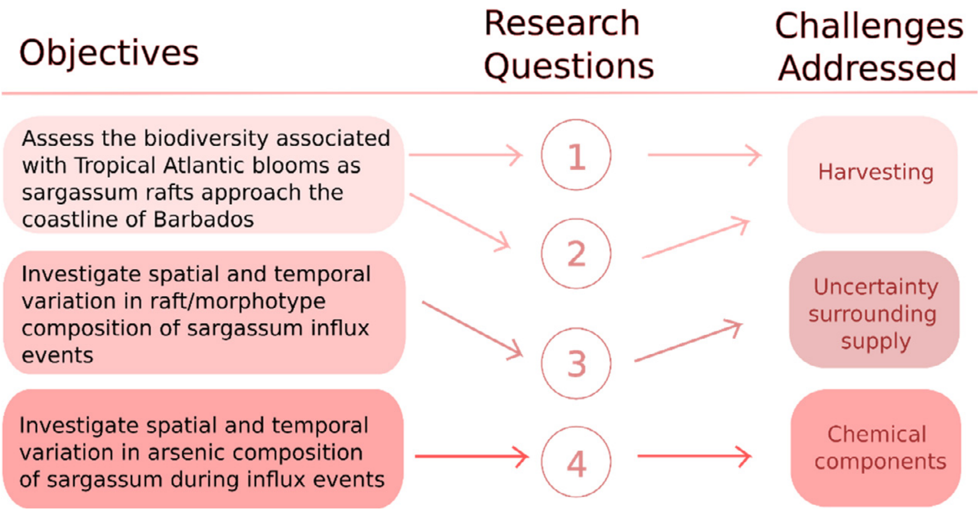

Figure 5: Schematic showing the linkages between research objectives, research questions and valorisation challenges that are addressed by this research.

Chapter 2 provides an overview of the research methodology. Chapter 3, draws on the core publications that have been written alongside this Kappa and provides answers to the posed research questions. The thesis then closes with a section on conclusions, limitations and future perspectives.

2. Methodology

This section describes the study sites and methods used to collect and analyse data during the course of study. This study utilised three main methods; 1) systematic literature review; 2) quantitative multivariate statistical testing; and 3) oceanic backtracking. Objectives under this research were achieved through the creation of hypotheses, study design, data collection and statistical analyses of data arising.

2.1. Study sites

This research took place on the island of Barbados (Figure 6), located in the Eastern Caribbean region, during 2021 and 2022. Barbados is uniquely positioned as a study site for sargassum influx events as it is one of the first islands to receive sargassum from the Tropical Atlantic. Positioned east of the Lesser Antilles Island Chain it receives sargassum directly from the open ocean making it an ideal place to examine: the biodiversity associated with Tropical Atlantic blooms; changes in morphotype composition; explore oceanic sub-origins; and assess arsenic concentrations.

During the one-year field data collection period, Conset Bay (13°10’47"N 59°27’57"W), Morgan Lewis beach (13°16'4.86"N 59°33'48.41"W) and Carlisle Bay (13° 5'14.13"N 59°36'50.84"W) were used as study sites (Figure 6). Sites were selected based on the objectives of each research component. Conset Bay and Carlisle Bay were selected as focal areas for biodiversity assessments which involved the collection of sargassum samples via handheld nets and deployment of underwater cameras to collect videos below floating sargassum rafts. The exposed, windward, East coast locations (Morgan Lewis and Conset Bay) are the first to receive sargassum arriving in Barbados and were thus selected as ideal sites to better understand patterns in morphotype composition and arsenic concentration for pelagic sargassum arriving in Barbados directly from the open ocean (Tropical Atlantic).

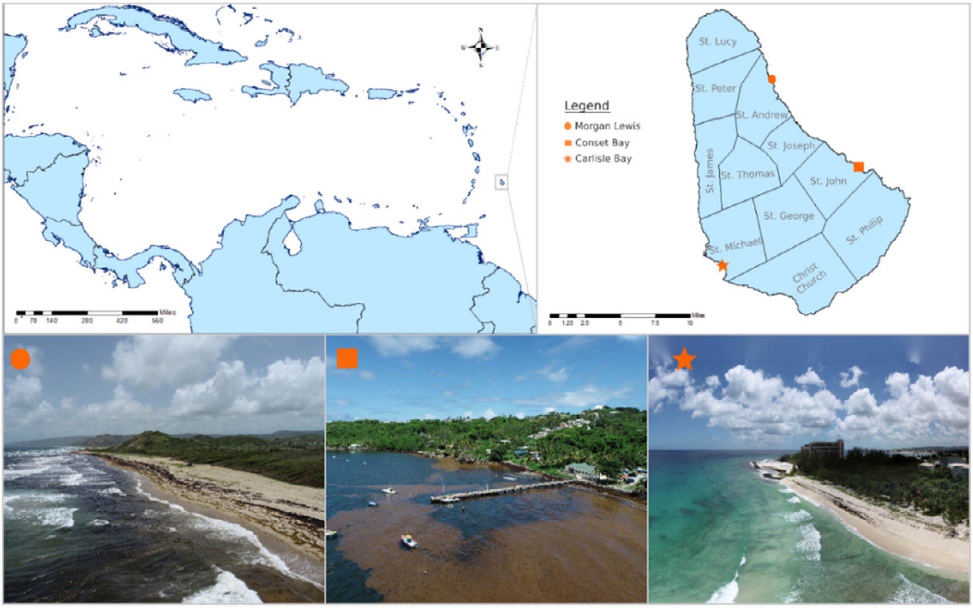

Figure 6: Map depicting the three study sites (Morgan Lewis beach, Conset Bay and Carlisle Bay) in Barbados. Shapes in the upper left corner of each photo correspond to the sampling sites shown on the map. Circle represents Morgan Lewis beach, square represents Conset Bay and star represents Carlisle Bay. Photos in the above are courtesy of Joseph Weekes from the Centre for Resource Management and Environmental Studies (CERMES).

2.2. Systematic literature review

To identify the most relevant literature, 22 scientific and environmental databases as well as the Sargassum Reference Repository hosted by the Centre for Resource Management and Environmental Studies (CERMES), were searched to identify primary studies focused on the biodiversity associated with pelagic sargassum. Using ‘Sargassum AND Biodiversity’, ‘Sargassum AND Faunal Communities’, ‘Sargasso Sea AND Faunal Communities’, ‘Sargassum AND Fauna’ and ‘Sargasso Sea AND Biodiversity’ as key search terms; relevant journal articles, M.S. theses and Ph.D. dissertations were identified. Following the initial selection, a snowballing exercise was conducted whereby the reference lists of all relevant papers were reviewed to broaden the scope of the study.

Articles selected for the assessment process focused only on the assessment of biodiversity associated with pelagic sargassum. No limitations were placed on the year of publication and, as a result, articles included in the review dated from 1968 to 2022. Selected articles were reviewed carefully to answer 5 research queries covering aspects relating to the collection, identification and assessment of pelagic sargassum-associated species, sample method and post-collection handling:

1. What type of sargassum-associated biodiversity is identified?
2. What method(s) are used to collect pelagic sargassum-associated biodiversity?
3. How are the samples sorted and preserved?
4. How are the species identified?
5. How are the data analysed?

A full description of the methods used during the systematic review can be found in (Alleyne, 2022).

2.3. Field collections and data analyses

2.3.1. Biodiversity assessments

The epiphytic and free-swimming community associated with pelagic sargassum arriving in Barbados were assessed using two distinct procedures.

Assessment of the epiphytic community

For epiphytic assessments, newly beach 'fresh-gold' sargassum was collected within the nearshore environment. Using gross morphological features, collected sargassum was then separated into *Sargassum natans* I, *S. natans* VIII and *S. fluitans* III following Parr (1939) and Schell et al. (2015).

On each sampling occasion, ten thalli of each sargassum morphotype were selected and placed between two acrylic plates each marked with a 1 x 1 cm square grid and epiphytic cover was estimated following Mendoza-Becerril et al. (2020) (Figure 7).

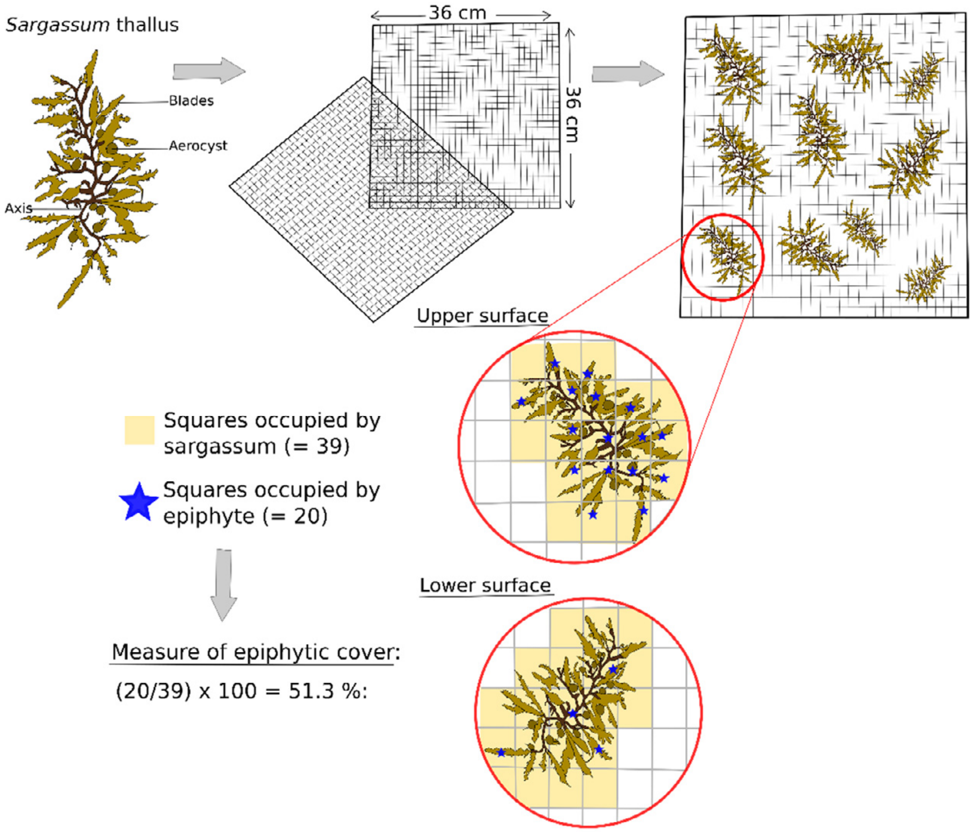

Figure 7: Schematic of the method used to measure epiphytic cover on pelagic sargassum samples. Taken from (Alleyne, Neat, et al., 2023a).

Epiphyte cover was first estimated by counting the number of grid squares occupied by sargassum with and without epiphytes on both sides of the acrylic plate. This was followed by counting the number of squares occupied by each of the observed epiphyte species on both sides of the acrylic plate. To calculate epiphyte percentage cover, the number of squares occupied by epiphytes was divided by the total number of squares occupied by sargassum (Figure 7). This was initially done for all epiphytes (regardless of species) and then again for each individual epiphyte species. Epiphytic fauna were identified to species-level with the use of dissecting (x 10 magnification) and compound (x 40 magnification) microscopes using morphological descriptions provided in (Morris & Mogelberg, 1973; Oliveira et al., 2015; Rackley, 1974; Schuchert, 2012). Contrastingly, epiphytic flora was simply recorded as filamentous alga.

To determine if the observed epiphytic fauna and flora were linked to sargassum sub-origins within the NERR, each collection date was backtracked following the procedure outlined in section 2.4 of this thesis. The exact steps taken to collect and assess the epiphytic community associated with pelagic sargassum can be found in Alleyne, Neat, et al. (2023a) and Alleyne, Irvine, Corbin, et al. (2022).

Assessment of the free-swimming community

To assess the free-swimming community associated with pelagic sargassum, 35 underwater surveys were conducted off the eastern (Conset Bay) and southern (Carlisle Bay) coastline of Barbados. Surveys were conducted using a free-floating underwater device consisting of a U-shape aluminium frame on which a GoPro camera HERO 8 (1920 x 1080 pixels with 30 frames per second) or HERO 9 (1920 x 1080 pixels with 60 frames per second) was mounted (Figure 8). Cameras were set to 'wide-angle' view and suspended below the water surface from a small open boat (length 5 m) with an outboard engine.

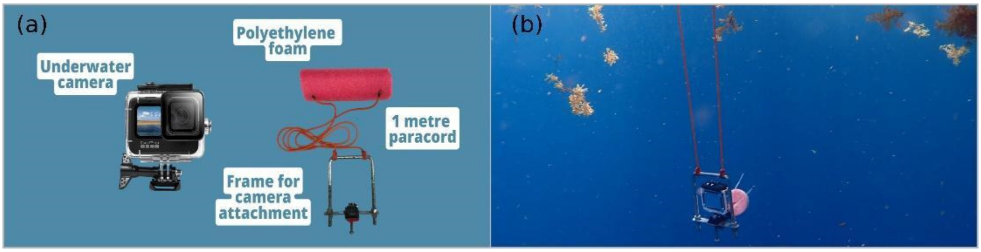

Figure 8: Materials used to construct underwater recording device (A) and a still image of the device deployed underwater (B). Taken from (Alleyne, Small, et al., 2023).

Cameras were deployed under two types of pelagic sargassum rafts (mats and windrows) (Figure 9), following descriptions provided in (Goodwin et al., 2022; Marmorino et al., 2011). Targeted rafts were sampled with one to three cameras based on size. Rafts ranging between 5-25 m in length were sampled with one camera. Alternatively, larger rafts (greater than 40 m) were sampled with two to three cameras spanning the extent of the raft. During deployment of multiple cameras, a minimum of 30 m apart was maintained to reduce overlap. To limit interference a minimal distance of 10 m was maintained between the vessel and deployed cameras.

Figure 9: Pelagic sargassum aggregation states sampled off the coast of Barbados. (A) Large raft (>100 m in diameter), (B) small raft (10 m in diameter) and (C) small raft (7 m in diameter). Taken from Alleyne, Small, et al. (2023).

In addition to video footage, the length of the sargassum raft, the diameter of the sargassum raft, the thickness of the sargassum raft, the depth of the water and the distance from shore were also recorded. Length and diameter of sargassum rafts were estimated using the boat length as a reference. The thickness of sargassum rafts was determined with the use of a graduated pole. The water depth of each sargassum raft was recorded using a handheld depth sounder. To estimate distance from shore, GPS coordinates were recorded with a handheld Garmin GPS device and subsequently uploaded to Google Earth.

During analysis, 15-minute videos were reduced to 10-minute clips by removing 2.5 minutes from the beginning and ending of each recording as interference may have occurred during camera deployment and/or retrieval. Collected videos were assessed using the maximum number of individuals sighted in any one field of view (referred to as MaxN) as a conservative measure of abundance. For each observed species, relative abundance was determined by dividing the MaxN of an individual species by the sum of MaxN values across all species. In addition to the relative abundance, species richness (total number of species observed) and species frequency (number of surveys in which a species occurred) were also recorded. Similar to relative abundance, the relative frequency of each species was calculated by dividing its frequency by the sum of frequencies across all species. Dominance and spatio-temporal consistency of dominant species within the free-swimming community associated with pelagic sargassum were assessed using Sanders Biological Value Index (BVI) following (Loya-Salinas & Escofet, 1990).

The exact steps taken to collect and assess the free-swimming community can be found in Alleyne, Small, et al. (2023) and Alleyne, Irvine, Corbin, et al. (2022).

2.3.2. Morphotype assessments

To assess the morphotype composition of pelagic sargassum arriving in Barbados, three clumps (~0.27 kg each) of newly beached, wet, ‘fresh gold’ sargassum were collected during each sampling effort. Clumps were separated into prevalent sargassum morphotypes (*Sargassum natans* I, *S. natans* VIII and *S. fluitans* III) using gross morphological features. A volume displacement method was then used to obtain estimated volumes for each of the three morphotypes from each clump.

To determine if the observed changes in morphotype composition were driven by oceanic origins, each collection date was backtracked following the procedure outlined in section 2.4 of this thesis. A comprehensive description of the methods used during morphotype assessments can be found in Alleyne, Irvine, & Oxenford (2022) and Alleyne, Johnson, et al. (2023).

2.3.3. Arsenic assessments

Wet ‘fresh gold’ pelagic sargassum was collected from Consett Bay (13°10'47"N 59°27'57"W) and Morgan Lewis beach (13°16'4.86"N 59°33'48.41"W) Barbados during 2021 and 2022. Mixed samples (*Sargassum natans I, S. natans VIII and S. fluitans III*) of sargassum were collected in-water, within 40 m of the shoreline. Immediately after collection, sargassum was placed on ice and transported to the laboratory where it was rinsed with tap water, packaged into polypropylene vials (of similar weight (~ 30g)) and frozen at -80 °C. A total of 23 frozen samples were subsequently shipped (on ice) to Brooks Applied Labs (BAL) in Washington for the analyses of total recoverable Arsenic (As_t) and Inorganic Arsenic (As_i) (the sum of AsIII and AsV).

Fresh samples sent for analyses were assessed ‘as received’ resulting in arsenic concentration per wet weight (ww). Estimates of arsenic concentration per dry weight (dw) were obtained following Warburton & Seagarst (1993) and Agriculture & food Systems Institute (2023). An average moisture percentage value of 82%, reported in previous analyses (Milledge et al., 2020; Tonon et al., 2022) for mixed pelagic sargassum species samples, was applied to the below equation.

$$Dry\ weight\ conc. = \frac{wet\ weight\ conc.}{1 - (\frac{moisture\ \%}{100})}$$

Total Arsenic Quantitation by ICP-QQQ-MS

Once thawed, the samples were homogenised using pre-cleaned commercial grade homogenization equipment. A known mass of each sample homogenate was weighed into a microwave digestion vessel, and then aliquots of concentrated hydrogen peroxide and nitric acid were added to all samples and prepared for quality control. All vessels were sealed and then digested at elevated temperature and pressure in a laboratory microwave system. All resulting digests were diluted to a known final volume and then analysed for As_t content via Inductively Coupled

Plasma Triple Quadrupole Mass Spectrometry (ICP-QQQ-MS). The ICP-QQQ-MS uses advanced interference removal techniques, including multiple collision/reaction gases, to ensure accuracy of the sample results.

Arsenic Speciation by IC-ICP-CRC-MS

Each sample for As_i quantitation was prepared via a modified ISO EN 16802:2016. In summary, a known mass of each sample homogenate was extracted using dilute nitric acid and hydrogen peroxide on a hot block apparatus. All resulting extracts were then analysed for arsenic species using Ion Chromatography Inductively Coupled Plasma Collision Reaction Cell Mass Spectrometry (IC-ICP-CRC-MS).

To determine if the observed changes in arsenic content were linked to sub-origins within the NERR collection dates were backtracked following the procedure outlined in section 2.4 this thesis.

2.4. Backtracking (tracing origin)

Sample backtracking was an integral part of morphotype, epiphyte and chemical analyses. This research used a compiled file of the Global Drifter Program (GDP) data set consisting of: year, day, hour, longitude, latitude, east-current, west-current and drogue-on/drogue-off flag from 1979 to 2020. Data from the GDP are derived from satellite tracked mix-layer drifters (drogue element at 15 m) (Lumpkin & Pazos, 2007) that have been deployed around the globe since ~1979. These drifters track water particles at drogue depth and are equipped with batteries that are capable of lasting over 450 days. Using a Surface Velocity Program (SVP), data are provided on position, temperature and drogue on/off (Johnson et al., 2018). Current vector components are calculated at 6-hour intervals from sequential positions and can be retrieved from https://www.aoml.noaa.gov/phod/gdp/. For tracking, the data were interpolated to a 1/12th degree resolution grid at 365 year-day intervals following Johnson et al. (2020).

To determine potential origins of the sampled sargassum, collection days were backtracked with IDL 8.8.1 programming software (https://www.l3harris.com/all-capabilities/idl). Using a simple backtracking algorithm based on the drifter data set and 0.5% windage, sargassum was tracked back 365 days from collection points at respective study sites to determine the origin of each sample within the Tropical Atlantic. Backtracks were simulated using 100 particles launched simultaneously from the collection locations at Morgan Lewis beach and Conset Bay, applying subgrid-scale turbulent motions (Lagrangian Stochastic Model (Griffa, 1996)) to each particle's current component:

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

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. The addition of this simple turbulence to each of the east-west (u) and north-south (v) current components acknowledges that the gridded current database is smoother than reality. End points of each particle’s back-trajectory were obtained by centre-of-mass calculations of the 100 ending locations.

The tracking methodology used during the course of this research was developed by Johnson et al. (2020) and is currently used to obtain 3-month sargassum forecasts for the Lesser Antilles, published in the Sargassum Sub-Regional Outlook Bulletin. According to the recent works of Marsh et al. (2022), forecasts from the Outlook Bulletin are well suited for monitoring sargassum influx events within the Lesser Antilles and are in close agreement with observed influxes.

Descriptions of the backtracking used in this research are detailed in Alleyne, Johnson, et al. (2023) and Alleyne, Neat, et al. (2023a).

2.5. Statistical analysis

Within this research, all statistical analyses were conducted using various packages in R software (R Core Team, 2022). Here a summary of the analyses is provided for each paper. For specific details the reader is referred to the material and methods sections of papers 2, 3, 4 and 5.

For paper 2 (epiphyte assessment), the data were Hellinger-transformed using the decostand function of the “vegan” package (Oksanen et al., 2018) and a Multivariate Analysis of Variance (MANOVA) was used to assess differences in epiphyte composition between oceanic sub-origins. To determine if the observed effect was attributed to sub-origin and/or morphotype composition, the MANOVA was followed by a Permutational Multivariate Analysis of Variance (PERMANOVA) using the adonis function of the vegan package. Within the PERMANOVA epiphytic counts were used as response matrix data and sub-origins and morphotypes as independent factors.

For paper 3 (the free-swimming community assessment), species richness was standardised across surveys using rarefaction curves to facilitate cross-survey comparisons. Rarefied species richness was produced using the rarefy function in the vegan package. Spearman rank correlations were then used to determine the associations between the rarefied species richness estimates and raft characteristics; namely, raft volume, water depth and distance from shore. To test the effect(s) of the three aforementioned raft characteristics on community assemblage composition, a redundancy analysis (RDA) was performed on Hellinger-transformed species data using the vegan package. Independent and shared effects of raft volume, water depth and distance from shore were assessed using varpart command under the vegan package which conducts variance partitioning. Finally, to assess: (1) whether changes in community assemblage composition across surveys were being driven by species leaving the rafts (i.e., species loss) or by species replacement and; (2) which raft characteristic(s) were driving such changes, the beta.div.comp function in the "adespatial" package (Dray et al. 2022) was used.

For paper 4 (morphotype assessment) statistical analyses were conducted to: (1) understand monthly variations in the relative abundance of the three sargassum morphotypes and; (2) determine if the observed variation was attributed to oceanic sub-origins. Monthly changes in the relative abundance (volume of morphotype/total volume of Sargassum sample) of *Sargassum natans* I, *S. natans* VIII and *S. fluitans* III were calculated by averaging compositional sample data first by date (if multiple sargassum samples were collected the same date) and then by month (if multiple dates were sampled within the same month). Differences in relative abundance of sargassum morphotypes between identified sub-origins were tested with PERMANOVA analyses; conducted using the adonis function of the vegan package. In the PERMANOVA, sample compositional data (transformed into a bivariate matrix) were used as the response matrix, sub-origin represented the independent factor and sample dates served as independent statistical replicates for each sub-origin. Ternary plots, produced using the "ggplot2", "ggtern", "ggpubr", and "lattice" packages (Hamilton & Ferry, 2018; Kassambara, 2020; Sarkar, 2008; Wickham, 2016), were used to visualised the composition of samples.

For paper 5 (arsenic assessment), differences in arsenic content between sample years (2021 vs 2022) and identified sub-origins were tested with PERMANOVA analyses using the adonis function of the vegan package. In the PERMANOVA, total arsenic concentrations and inorganic arsenic concentrations were used as response bivariate matrix data and sub-origin location, year and month served as independent factors.

3. Findings and discussion

This Kappa embodies a chain of publications consisting of five core papers produced within the timeframe of this research.

In order to understand the evolution of this research, Figure 10 outlines the steps taken from conception to project completion. Research under the scope of this thesis took place within the boundaries of a broader project, entitled "Closing the Circle", that focused on exploring challenges and potential solutions to marine debris, sargassum threats and marine spatial planning (MSP) in the Eastern Caribbean region. Sargassum was chosen as the area of focus and objectives and research questions were formulated based on the valorisation challenges outlined in section 1.4.2 (Figure 10).

Results produced in this section represents a comprehensive overview of the key findings and makes linkages to research questions. Each of the four posed research questions are presented as subheadings within this section.

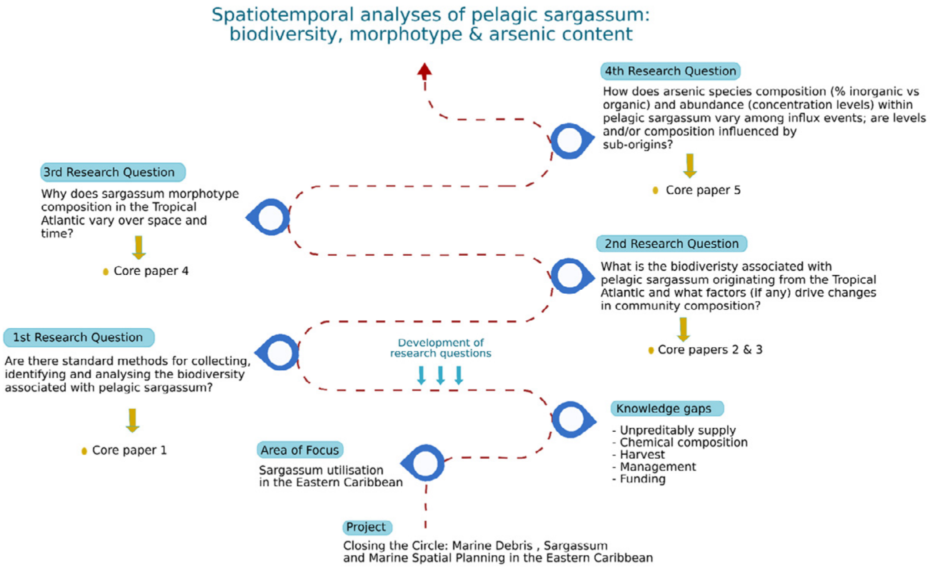

Figure 10: Schematic representation of the research evolution. Adapted from (Polejack, 2022).

3.1. Are there standard methods for collecting, identifying and analysing the biodiversity associated with pelagic sargassum?

It has long been known that pelagic sargassum in the North Atlantic provides essential habitat, refuge, nursery ground and foraging habitat for a wide variety of associated and endemic species (Butler et al., 1983; Dooley, 1972; Weis, 1968). However, much less is known about the ecological value of the recent Tropical Atlantic blooms. In light of the considerable efforts being made towards valorisation (Desrochers et al., 2022; Oxenford et al., 2021); in-water harvesting will likely be the optimal method for collecting large amounts of fresh 'clean' sargassum for applications whilst minimising the negative impacts associated with beach harvesting. Consequences of in-water harvesting on sargassum associated biodiversity need to be better understood in order to help guide best harvest practices. Site-specific biodiversity assessments across the region are therefore needed to fill knowledge gaps.

The first objective of this research was to assess the biodiversity associated with Tropical Atlantic blooms as sargassum approached the coastline of Barbados. To do this, an assessment of appropriate methods was first required. In Alleyne (2022), presented in the appendix as Paper 1, a systematic literature review was used to gather information on the methods used to collect, identify and analyse the biodiversity associated with pelagic sargassum that have been documented in the published literature.

From the review, biodiversity associated with pelagic sargassum can largely be grouped into three categories: epiphytic fauna, clinging fauna and free-swimming fauna (Figure 11). Epiphytic fauna are sessile organisms that grow on the sargassum; these include hydroids, tube worms and encrusting bryozoans. The clinging and free-swimming community both consists of motile organisms; however, their degree of motility is quite different. Clinging organisms exhibit a very limited range of movement and spend their time clinging to or climbing around the sargassum (e.g., crustaceans, worms, molluscs, turtle hatchlings, sargassum frogfish). Contrastingly, free-swimming organisms are more vagile and often found swimming inside or beneath the sargassum (e.g., juvenile and adult turtles, vertical migrating fishes and pelagic fishes).

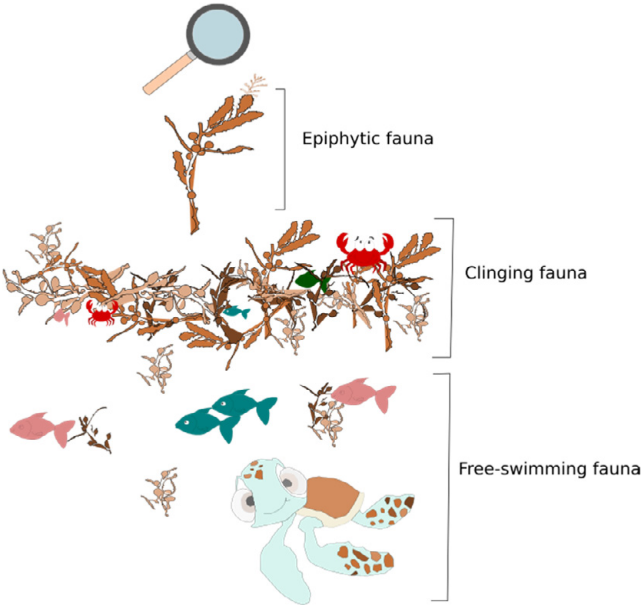

Figure 11: Schematic representation of the biodiversity groups associated with pelagic sargassum. Taken from (Alleyne, Irvine, Corbin, et al., 2022).

There was no standard method(s) for the collection, identification and/or analysis of species associated with pelagic sargassum. Methods used to collect/record biodiversity across the three groups include: encircling, towed and hand operated nets, hook and line, video recording, bare-handed collections and plastic bag collections (observed in a single occurrence). Furthermore, a wide range of net types, sizes, mesh sizes, sampling depths and preservation techniques were used. Overall, hand-operated nets (i.e., dipnets, landing nets) were the predominant tool utilised to collect organisms across the three biodiversity groups. Notwithstanding their wide application, dipnets may not be the most appropriate method for collecting information on the free-swimming community since large vagile species are likely to escape. This simple fact implies that there is no one size fits all. Selecting the most appropriate method(s) to collect information on sargassum associated biodiversity will first require researchers to consider their target biodiversity. With nets being the most variable and utilised method, Paper 1 provides a list of recommended net types, sizes and mesh sizes which can be used to collect organisms across the three biodiversity groups (Table 1).

Table 1: List of recommended net specifications to be used to collect epiphytic, clinging and free-swimming fauna from pelagic sargassum. Recommendations are based on the findings of 30 reviewed articles and serve as a starting point for future biodiversity assessments. Taken from Alleyne (2022).

Biodiversity group	Recommended net types(s)	Recommended frame opening (m^2)/ net length (m)	Recommended mesh size
Epiphytic fauna	Hand operated nets	0.07-0.25 m^2 (No optimal size was identified)	0.5 mm
Clinging fauna	Hand operated nets	0.28-2.64 m^2 (No optimal size was identified)	0.5 mm
Free-swimming fauna	Towed nets	0.28-2.64 m^2 (No optimal size was identified)	3-25 mmm (No optimal size was identified)
Free-swimming fauna	Encircling nets	30.5 m by 5.2 m (Based on a single study. No optimal size was identified)	12.5 mm (Based on a single study. No optimal size was identified)

Given that epiphytic and clinging fauna spend their lives attached to or climbing around the sargassum (Weis, 1968) net sampling will likely be the most appropriate method for collection. Contrastingly, vagile free-swimming species may require a combination of net and video sampling for a thorough assessment. Alternative sampling strategies that can be used to aid in species identification of and provide estimates for species abundances/biomass include Environmental DNA (eDNA) (Lacoursière-Roussel et al., 2016). However, while it is widely acknowledged that eDNA sampling effectively overcomes difficulties associated with conventional morphological identification (Zaiko et al., 2018), its use in fisheries management (Lacoursière-Roussel et al., 2016) and sargassum research remains limited. Integration of eDNA sampling within sargassum management reduces the need for the labour-intensive approaches identified in the reviewed literature; however, there is little capacity within the Caribbean region to process eDNA samples due to the associated costs and required equipment. Beyond the financial barriers, preliminary investigations to determine how collection methods as well as abiotic and biotic factors influence the eDNA abundance/biomass relationship (Lacoursière-Roussel et al., 2016; Rourke et al., 2022) will be necessary to ascertain a thorough understanding of the sargassum community.

Recommendations provided in Paper 1 guided the data collection process in Papers 2 and 3. Moreover, these findings were used to develop a simple, easy to follow, low-cost protocol (Alleyne, Irvine, Corbin, et al., 2022) for the collection and assessment of pelagic sargassum-associated biodiversity. Whilst the aforementioned recommendations cannot directly inform managers of the impact(s) of large-scale in-water harvesting, they can improve conservation efforts by clarifying the ecological value of sargassum to the broader pelagic ecosystems of the Tropical Atlantic and the Caribbean Sea.

3.2. What is the biodiversity associated with pelagic sargassum originating from the Tropical Atlantic and what factors (if any) drive changes in the community composition?

Papers 2 and 3 focused on the epiphytic and free-swimming community respectively.

3.2.1 The epiphytic community

Floating items on the surface of the ocean such as marine debris, tree branches and pelagic sargassum provide rafting opportunities (Thiel and Gutow, 2005) and facilitates connectivity between seascapes (Tabor et al., 2019). These drifting substrates provide attachment surfaces for many organisms including bryozoans, crustaceans, gastropods, hydroids and algae (Thiel and Gutow, 2005). Species composition and abundance of rafting communities therefore depends on the available substratum but can also vary due to conditions encountered along rafting trajectories. Pelagic sargassum blooming in the Tropical Atlantic presents an ideal opportunity to assess rafting communities among the structurally different morphotypes that may be originating from different sub-origins.

To date, very few studies (Govindarajan et al., 2019; Mendoza-Becerril et al., 2020) have focused on the rafting epiphytic community associated with Tropical Atlantic blooms. Paper 2 aimed to address knowledge gaps by: (1) identifying what epiphytic species are associated with sargassum influx events; (2) investigating the occurrence and percent coverage of epiphytes; (3) understanding differences in composition of epiphytes among sargassum morphotypes; and (4) investigating whether or not epiphytic assemblages are linked to sub-origins within the Tropical Atlantic. This research was based on two hypotheses. The first hypothesis draws from the recent findings of Martin et al. (2021) that pelagic sargassum morphotypes support different motile organisms. In light of this, it was hypothesised that the structural differences of morphotypes and the ability to attract different motile species would also influence their epiphytic assemblage. Acknowledging the heterogeneous surface environment of the Tropical Atlantic (Oviatt et al., 2019) the holopelagic nature of blooms and the influence of environmental parameters on metabolic performance (Robledo et al., 2021) and growth (Magaña-Gallegos et al., 2023). The study further hypothesised that differences in epiphytic assemblage on a given morphotype will occur as a result of their sub-origins and associated transport pathways.

The epiphytic community associated with sargassum arriving in Barbados had a relatively low species richness consisting of six species of fauna (*Membranipora tuberculata*, *Aglaophenia latecarinata*, *Clytia noliformis*, *Obelia dichotoma*, *Plumularia strictocarpa*, *Spirorbis spirorbis*) and an unidentified filamentous alga belonging to the family Chlorosarcinaceae (Figure 12).

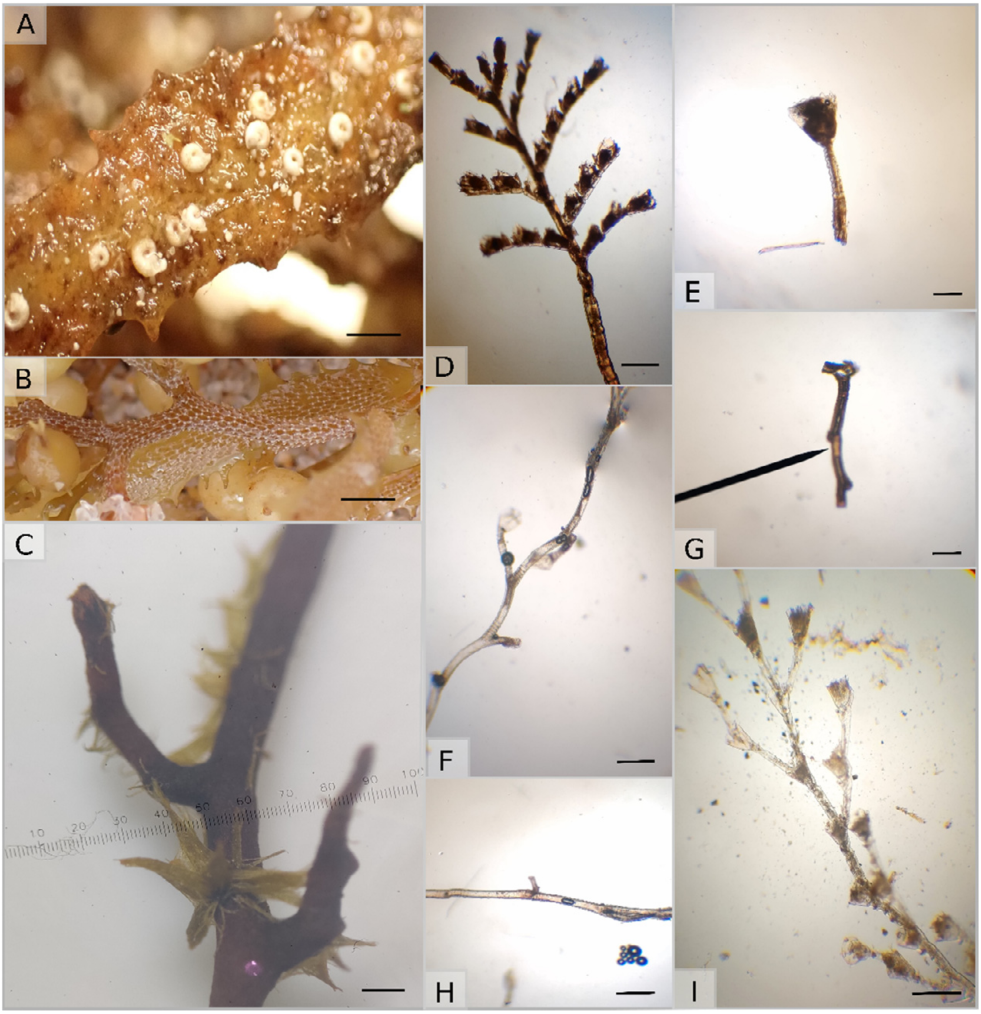

Figure 12: Epiphytes associated with *Sargassum fluitans* III, *S. natans* I and *S. natans* VIII arriving in Barbados. (A) *Spirorbis spirorbis*; (B) *Membranipora tuberculata*; (C) filamentous alga; (D) *Aglaophenia latecarinata*; (E) *Clytia noliformis*; (F–H) *Obelia dichotoma*; (I) *Plumularia strictocarpa*. Scale bars for (A), (B), (C) equal 10 mm, for (D), (E), (G) equal 0.2 mm and (F), (H), (I) equal 1 mm. Taken from (Alleyne, Neat, et al., 2023a).

This account of the epiphytic community associated with Tropical Atlantic blooms found fewer species than earlier reports from the North Atlantic (Calder, 1995; Rackley, 1974; Weis, 1968) and the Mexican Caribbean (Mendoza-Becerril et al., 2020). Overall, hydroids made up the majority (~ 67%) of epiphytic species and the bryozoan *M. tuberculata* was the predominant species observed and covered approximately one third of all sargassum thalli.

Backtracking efforts were undertaken to assess whether or not the observed epiphytic community and/or epiphyte composition were linked to sub-origins. Results suggest that there is no significant difference in epiphyte percentage cover or the epiphytic community of sargassum between identified sub-origins in the Tropical Atlantic. However, epiphytic assessments of individual morphotypes revealed host preference among hydroid species with *A. latecarinata* and *C. noliformis* predominantly found on *S. natans* VIII and *S. fluitans* III respectively. The study concludes that sargassum morphology is likely a stronger determinant of epiphyte composition than any environmental differences encountered between sub-origins and their associated transport pathways.

3.2.2 The free-swimming community

The third paper in this compilation set out to characterise the free-swimming community associated with pelagic sargassum arriving in Barbados and identify what factors (if any) drive changes in community assemblage. Drawing from ecological theory, the study hypothesised that larger rafts would host greater species richness (Lomolino, 2000; Simberloff, 1976).

The free-swimming community associated with pelagic sargassum arriving in Barbados consisted of 13 species (12 fishes and one comb jelly) (Figure 13). Similar to the findings of the epiphytic study, the account of free-swimming fauna associated with pelagic sargassum in Barbados was considerably lower than that reported by earlier studies (36-110 species) conducted across the Gulf of Mexico, the Gulf Stream, and various parts of the North Atlantic (Bortone et al., 1977; Dooley, 1972; Hoffmayer et al., 2005; Moser et al., 1998; Settle, 1993; Wells & Rooker, 2003).

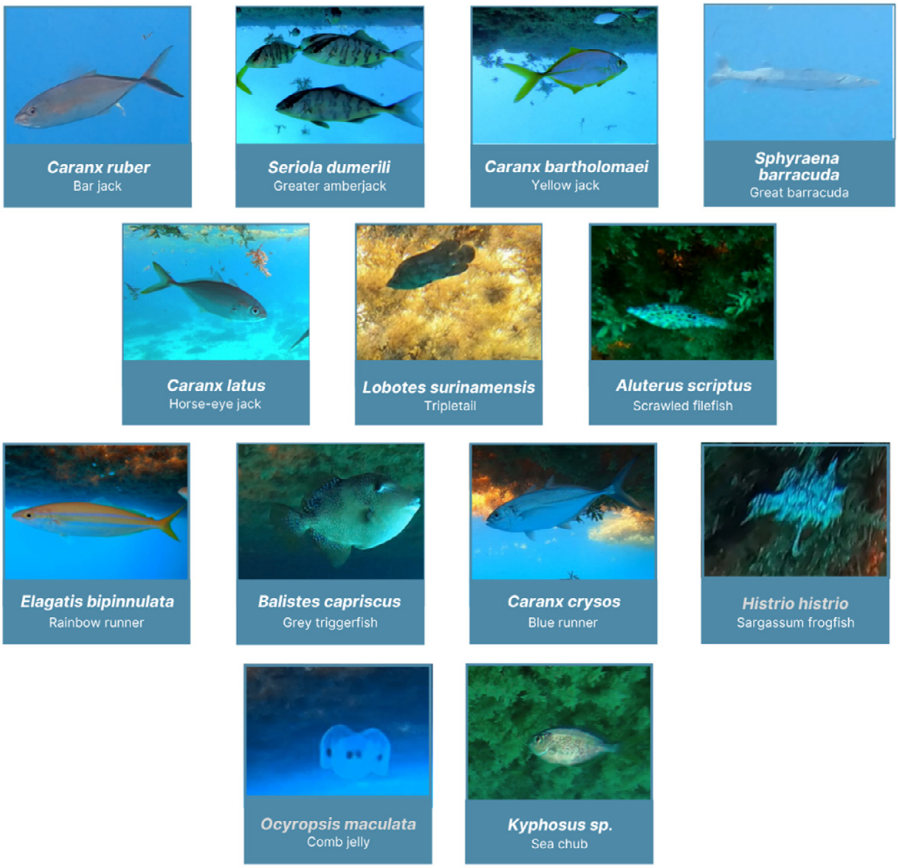

Figure 13: Still images collected from underwater videos of the 13 species found associated with pelagic sargassum arriving in Barbados. Taken from (Alleyne, Small, et al., 2023).

There was extensive variation in species assemblages and abundances (0-250 individuals) across the 35 surveys conducted; some sargassum rafts were teeming with life while 6% of rafts were unoccupied (Figure 14). In an effort to understand what factor(s) were influencing the observed variation, the study investigates the effect of raft volume, distance from shore and water depth on species assemblages and abundances.

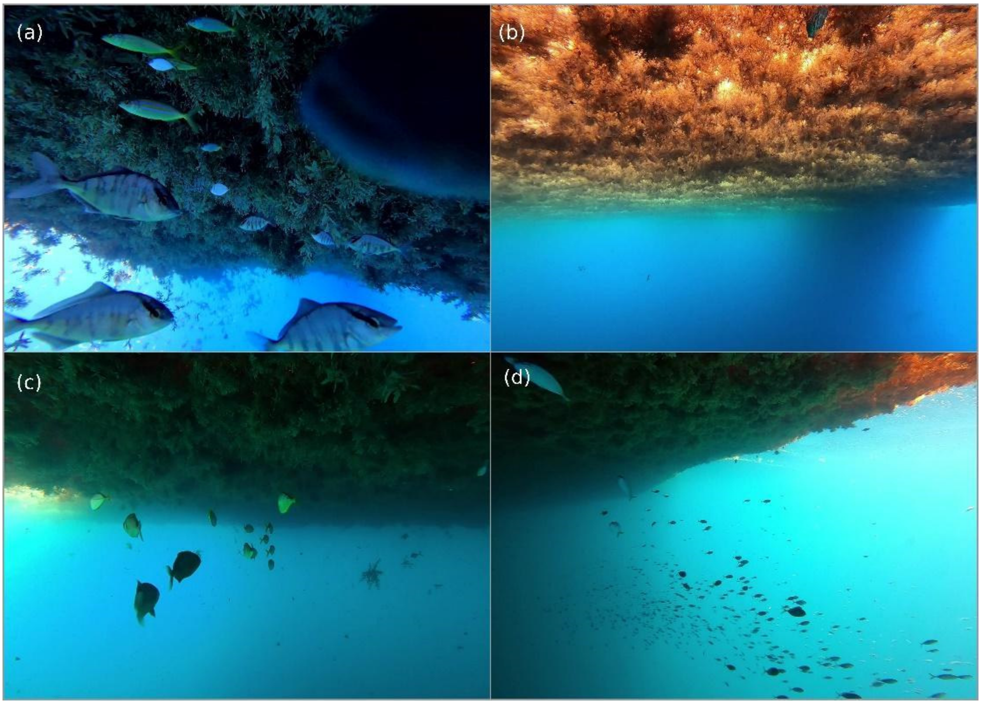

Figure 14: Still images collected from underwater videos of pelagic sargassum rafts. Smaller rafts (A) (5 m in diameter) and (B) (7 m in diameter). Larger rafts (C) (20 m in diameter) and (D) (100 m in diameter). Taken from (Alleyne, Small, et al., 2023).

Results indicate that among the three environmental variables, raft volume (a proxy for raft size) was the major structuring factor of the free-swimming community associated with pelagic sargassum in Barbados. As raft size decreased, individual abundance and species richness also decreased, as hypothesised. Moreover, beta-diversity analysis revealed that loss in species richness was significantly linked to raft volume (Pseudo-F= 1.97, p= 0.011) but not to water depth or distance from shore (Pseudo-F $\leq$ 0.79, p $\geq$ 0.809). This implies that species were being lost from the original species assemblage as the rafts got smaller. The findings of this study are consistent with earlier studies (Casazza & Ross, 2008; Goodwin et al., 2022; Martin et al., 2021; Moser et al., 1998; Settle, 1993) that report on the relationship between raft size and species richness. Interestingly, this study also reports a positive correlation between distance and abundance. This report of decreased macrofaunal abundances within nearshore environments supports the findings of Monroy-Velázquez et al. (2019), who reported on the biodiversity associated with pelagic sargassum in the Mexican Caribbean.

3.3. Why does sargassum morphotype composition in the Tropical Atlantic vary over space and time?

Understanding the distribution and geographic variation of species across the Earth's surface is a key aspect of Biogeography. To date, studies within the field of Biogeography highlight the important influence of climate, biotic interactions and dispersal abilities of species in shaping species composition within an area (Schickhoff et al., 2014). Drawing on this knowledge, this section seeks to understand how and why sargassum morphotype composition in the Tropical Atlantic varies over space and time.

Since the initial bloom in 2011, reports on morphotype composition has shown substantial intra- and inter-annual variation in predominant morphotype species (Botelho Machado et al., 2022; García-Sánchez et al., 2020; Schell et al., 2015). Early reports on morphotype composition identified *S. fluitans* III and *S. natans* VIII as the predominant forms, with a noticeable peak in *S. natans* VIII abundance during 2014-2015 (García-Sánchez et al., 2020; Oxenford et al., 2021; Schell et al., 2015). However, more recent observations (Botelho Machado et al., 2022) report a dominance of *S. fluitans* III. Acknowledging the influence of morphotype composition on both the chemical composition (Davis et al., 2020; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020; Tonon et al., 2022) and the associated biodiversity; Paper 4 sets out to assess variation in the relative abundance of *S. natans* I, *S. natans* VIII and *S. fluitans* III in sargassum strandings during 2021–2022 and analyse the origins of influx events with the use of backtracking. The study hypothesised that the morphotype composition of sargassum influx events varies seasonally and that this variation is linked to oceanic origins and transport pathways within the Tropical Atlantic.

3.3.1 Species composition of Tropical Atlantic blooms

In agreement with Botelho Machado et al. (2022), results indicate that *S. fluitans* III was the predominant morphotype observed overall. However, there were temporal variations in the predominant morphotype species. Specifically, samples collected in November, January and February were dominated by the previously rare *S. natans* VIII (Figure 15).

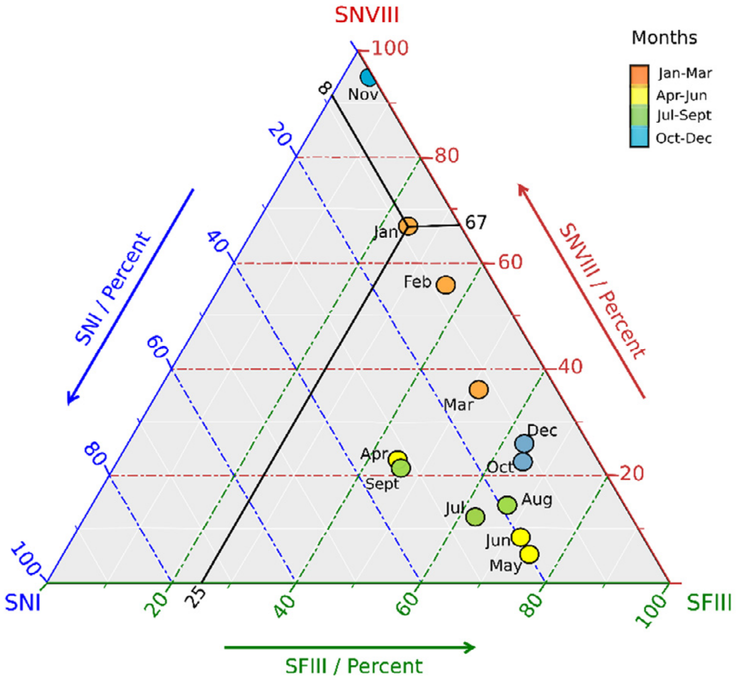

Figure 15: Ternary plot illustrating monthly variation in morphotype composition of sargassum stranding in Barbados over a 12-month period. *Sargassum natans* I (SNI), *S. natans* VIII (SNVIII) and *S. fluitans* III (SFIII). Black lines indicate the average percent contribution of each morphotype in the January samples (67% SNVIII, 25% SFIII, 8% SNI). Quarterly periods are represented by orange (Jan-Mar), yellow (April–Jun), green (Jul–Sept) and blue (Oct–Dec) dots. Taken from (Alleyne, Johnson, et al., 2023).

3.3.2 Linking morphotype composition to sub-origins

Ecological biogeography suggests that both biotic and abiotic factors influence species distribution and composition (Schickhoff et al., 2014). The Equatorial Atlantic has a heterogeneous surface environment with elevated temperatures and nutrient-rich water masses originating from various sources (Oviatt et al., 2019). It is therefore plausible that sargassum rafts exposed to differing conditions along their transport pathways, give rise to different morphotype compositions. To test the hypothesis that variation in morphotype composition was linked to sub-origins/transport pathways, sample backtracking for 365 days from the date of stranding was conducted. Backtracks reveal two putative sub-origins/transport pathways within the Tropical Atlantic. Sub-origin/transport pathway A, observed between March to early August, originates close to the equator (0–7° N) and follows a convoluted trajectory along the northeast coast of Brazil to Barbados. Sub-origins/transport pathway B, observed between late August to February, originates further north (9–18° N) and travels a direct westerly route to Barbados (Figure 16). Pathways identified in this study align with the findings of previous studies (Beron-Vera et al., 2022; Skliris et al., 2022).

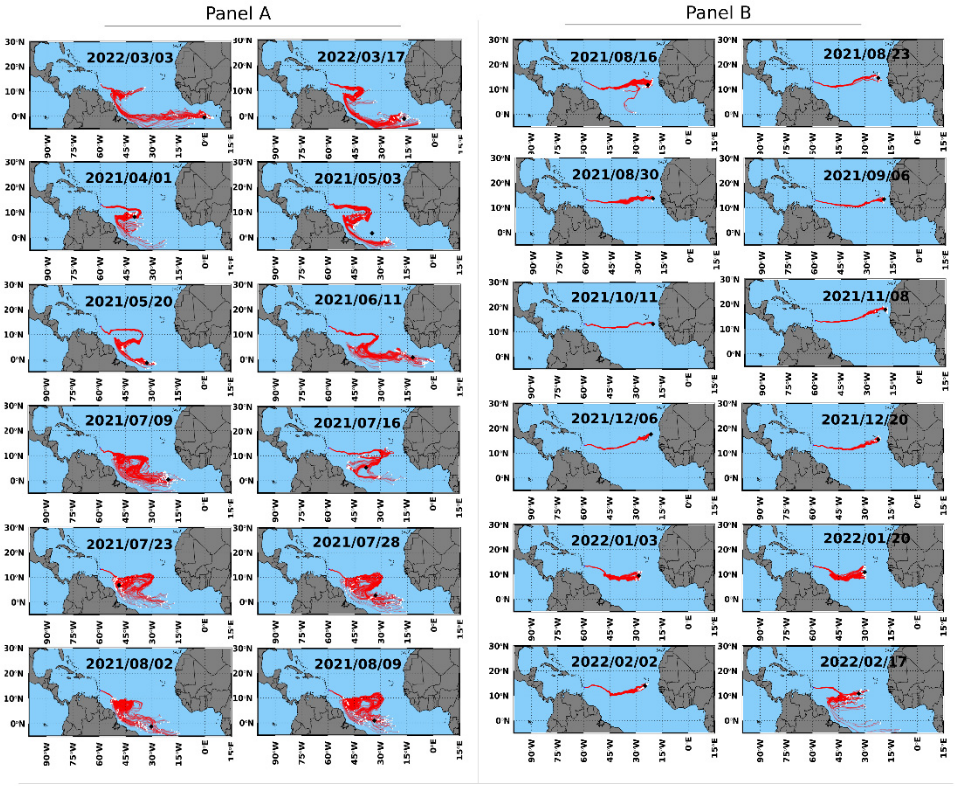

Figure 16: Backtracks of sargassum (mixed-morphotype samples) collected from Morgan Lewis beach in Barbados over the period of 1 year (2021–2022). Panel (a) shows sample backtracks from early March to early August and panel (b) shows backtracks from late August through February. All backtracks were run 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). Dates are presented in year/month/day format. Taken from (Alleyne, Johnson, et al., 2023).

As hypothesised, observed variation in morphotype composition during the 2021-2022 period was linked to sub-origins/transport pathways. In this study, *S. fluitans* III was the predominant morphotype observed in sargassum rafts originating from sub-origin/transport pathway A. In contrast, rafts originating from sub-origin/transport pathway B showed higher levels of *S. natans* VIII, with reduced quantities of *S. fluitans* III (Figure 17).

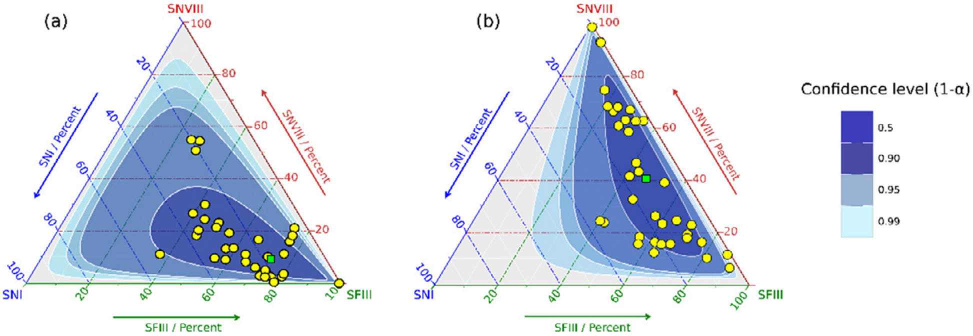

Figure 17: Ternary plots showing morphotype composition of sargassum samples stranding in Barbados over a 12-month period. Part (a) shows sargassum samples from sub-origin/transport pathway A (March–early August). Part (b) shows sargassum samples from sub-origin/transport pathway B (late August–February). *Sargassum natans* I (SNI), *S. natans* VIII (SNVIII) and *S. fluitans* III (SFIII). Samples are represented by yellow dots and the mean value is represented by a green square. Taken from (Alleyne, Johnson, et al., 2023).

Interestingly, the formation of sub-origin/transport pathway B aligns with the understanding of sargassum movement provided by John et al., (2020) and Skliris et al., (2022). According to their findings, the bulk of sargassum in the Tropical Atlantic is transported northward, in response to the ITCZ migration, during September to December. With movement of the ITCZ the strong zonal eastward flow (NECC) that blocks northward nutrient transport during summer months gradually breaks down (Skliris et al., 2022). This facilitates the transport of nutrient rich waters from the equatorial region to sub-origin/transport pathway B. Considering that the equatorial region is associated with elevated temperatures and high nutrient inputs (Djakouré et al., 2017; Oviatt et al., 2019; Skliris et al., 2022); differences in oceanographic conditions between the two sub-origins/transport pathway may be the proximal cause for the observed morphotype compositions. Studies by Magaña-Gallegos et al. (2023) indicate that *S. natans* VIII requires lower temperatures for optimal growth when compared to *S. fluitans* III. With movement from the equatorial region, *S. natans* VIII dominated blooms in sub-origin B are exposed to lower nutrients (Johns et al., 2020; Skliris et al., 2022) and possibly lower temperatures. In contrast, *S. fluitans* III dominated blooms in sub-origin/transport pathway A are concentrated under the ITCZ where they're exposed to high temperatures, equatorial upwelling and peak outflows from the Amazon River during summer months (Skliris et al., 2022; Wang et al., 2019).

The influence of sub-origins/transport pathways on morphotype composition helps to explain some of the variation reported by previous studies (Botelho Machado et al., 2022; García-Sánchez et al., 2020; Schell et al., 2015). From this study, it is likely that reports of *S. natans* VIII dominated influxes reported during 2015 (García-Sánchez et al., 2020; Schell et al., 2015) originated in sub-origin/transport pathway B whilst the recently reported *S. fluitans* III dominated rafts observed in

Jamaica during the summer of 2020 originated in sub-origin/transport pathway A. In Paper 4, understanding the distribution of sargassum morphotypes within the Tropical Atlantic was used as a first step in unravelling the complex problems of blooms; why now, why here, what are the dominant drivers controlling distribution and abundance? However, future studies examining the factors influencing population dynamics, especially those concerning growth and temperature-nutrient interactions, are needed.

3.4. How does arsenic species composition (% inorganic vs organic) and abundance (concentration levels) within pelagic sargassum vary among influx events; are levels and/or composition influenced by sub-origins?

Pelagic sargassum transported on the ocean's surface is exposed to contrasting environments with different nutrient levels, temperatures and trace metal pollution (Robledo et al., 2021). Identification of the different sub-origins/transport pathways in Paper 4, presented an opportunity to assess differences (if any) in arsenic concentrations between sargassum rafts originating from sub-origin/transport pathway A and those originating from sub-origin/transport pathway B. Acknowledging that commercial exploitation and definition of valorisation pathways will require a better understanding of arsenic speciation in pelagic sargassum (Davis et al., 2020; Desrochers et al., 2022; Oxenford et al., 2021; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). Paper 5 assessed the temporal variability of total arsenic and inorganic arsenic in pelagic sargassum arriving in Barbados; and tested whether arsenic concentrations are linked to identified sub-origins. The study hypothesised that arsenic variation will be linked to sub-origins/transport pathways within the Tropical Atlantic.

Across the 23 sargassum samples, considerable variation was observed in total arsenic (2.3-17.8 μg g^{-1} wet weight) and inorganic arsenic (0.3-11.3 μg g^{-1} wet weight) concentrations (Table 2). Despite the observed variation, there was no significant difference in the total arsenic or inorganic arsenic concentrations of pelagic sargassum collected across sample years (2021 and 2022) (Pseudo-F= 1.248, p = 0.265) or months (February to August) (Pseudo-F= 1.332, p = 0.316).

Table 2: Arsenic concentrations (mean ± SD) in mixed samples of pelagic sargassum. Concentrations are expressed as µg g-1 for wet weights (ww) and dry weights (dw). The symbol (*) indicates that only a single collection occurred. Taken from Alleyne, Neat, et al. (2023b).

Month	Number of samples	Year	Total arsenic (ww)	Inorganic arsenic (ww)	Total arsenic (estimated dw)	Inorganic arsenic (estimated dw)	% of inorganic arsenic
Feb	3	2022	8.66 ± 4.56	5.40 ± 3.19	48.11 ± 25.34	30.0 ± 17.75	62.4
March	4	2022	10.47 ± 4.36	5.78 ± 3.19	58.14 ± 24.24	32.1 ± 17.1	55.2
April	4	2022	8.27 ± 2.17	4.63 ± 1.58	45.96 ± 12.07	25.7 ± 8.76	56.0
May	2	2022	8.04 ± 0.45	4.90 ± 0.66	44.67 ± 2.51	27.2 ± 3.65	60.9
May	1	2021	12.30 *	7.22 *	68.33*	40.1*	58.7*
June	3	2022	11.61 ± 5.46	6.77 ± 4.05	64.50 ± 30.33	37.6 ± 22.48	58.3
July	2	2021	3.30 ± 1.46	1.41 ± 0.73	18.31 ± 8.13	7.8 ± 4.05	42.6
August	4	2021	8.85 ± 3.28	4.42 ± 2.88	49.17 ± 18.21	24.6 ± 16.00	50.0

Average total arsenic concentrations (49.8 ± 21.1 µg g^{-1} dry weight: mean ± standard deviation) reported in this study were at the low end of the general range (31-170 µg g^{-1} dry weight) reported in the literature (Alzate-Gaviria et al., 2021; Bam et al., 2022; Davis et al., 2020; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020; Tonon et al., 2022). Nevertheless, results indicate that inorganic arsenic represents a substantial percentage (up to 62.4%) of the total arsenic in pelagic sargassum.

To test the hypothesis that variation in arsenic concentration was linked to sub-origins/transport pathways, sample backtracking was done for each of the 23 samples. Samples collected between March and early August (n=16) originated from sub-origin/transport pathway A; whilst those collected between late August and February (n=7) originated from sub-origin/transport pathway B. Satellite imagery maps of average phosphate concentrations for March-early August (2021/03/01-2021/08/09) and late August-February (2021/08/10-2022/02/28) were used to visualise phosphate conditions between the two sub-origins/transport pathways (Figure 18).

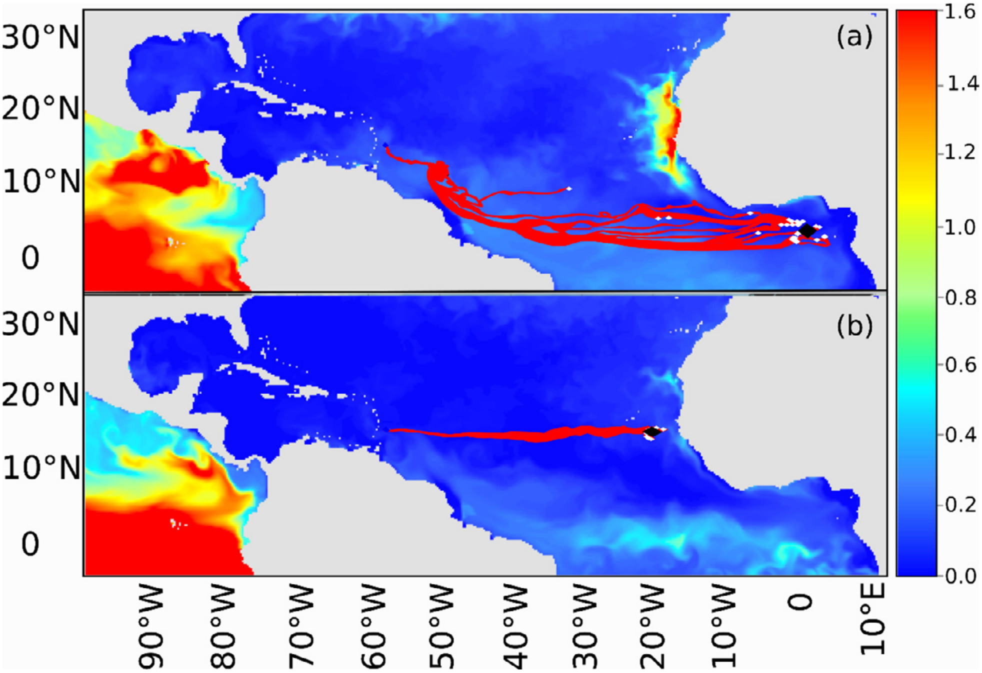

Figure 18: Backtracks of pelagic sargassum collected in Barbados overlayed on phosphate (mmol/m3) maps retrieved from Copernicus Marine Service (CMS) (https://doi.org/10.48670/moi-00015). Panel A represents sample backtracks that originate close to the equator and travel along northeast Brazil before arriving in Barbados; sub-origin/transport pathway A. Panel B represents backtracks that originate further north and travelled 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 in Barbados) and the black square represents the origin of highest probability (mean of all backtrack particles). Image taken from (Alleyne, Neat, et al., 2023b).

Overlays of backtracks on phosphate maps show that sargassum originating in sub-origin A is likely to have been exposed to slightly higher concentrations of phosphate across its transport pathway compared to sargassum originating from sub-origin B. However, there was no significant difference (Pseudo-F= 0.121, p = 0.754) in arsenic concentrations between the two sub-origins/transport pathways. Whilst these findings ultimately reject the hypothesis, it is clear from the visualised phosphate maps that high nutrient concentrations observed in the upwelling areas of West Africa (Figure 18a) and the equator (Figure 18b) did not coincide with either of the two sub-origins/transport pathways. This temporal difference in nutrient concentrations resulted in both sub-origins/transport pathways being exposed to relatively similar phosphate concentrations albeit slightly higher for sub-origin/transport pathway A. It is therefore not surprising that no apparent effect of phosphate concentrations on arsenic levels was observed between the two sub-origins/transport pathways.

The findings of Paper 5 contribute to the growing body of knowledge regarding trace metal contamination of pelagic sargassum and confirm the uncertainties surrounding the variation in arsenic concentrations over time.

4. Conclusions, limitations and future perspectives

Valorisation of pelagic sargassum will be integral to the Caribbean region's ability to adapt to the continuing mass influxes (Amador-Castro et al., 2021; Chávez et al., 2020; Oxenford et al., 2021; Robledo et al., 2021; United Nations Environment Programme - Caribbean Environment Programme et al., 2021). Research by Desrochers et al. (2022) indicates that there is potential for a wide variety of applications using pelagic sargassum as a raw material. However, constraints relating to supply, harvesting, arsenic, governance and funding must be adequately addressed in order to achieve the full commercial potential of this bioresource (López Miranda et al., 2021; Oxenford et al., 2021; Robledo et al., 2021). Against this backdrop, this thesis provides important baseline information on the associated biodiversity, morphotype composition and arsenic content of pelagic sargassum in the eastern Caribbean.

The biodiversity associated with pelagic sargassum arriving in Barbados was relatively low in species richness (Alleyne, Neat, et al., 2023a; Alleyne, Small, et al., 2023) compared to studies conducted in the North Atlantic (Butler et al., 1983; Calder, 1995; Dooley, 1972; Weis, 1968). Given the fact that species diversity increases with the amount of time a habitat is available (Kingsford, 1992) and Tropical Atlantic blooms are notably 'younger' compared to the well-established Sargasso Sea, the observed lower species richness was perhaps not surprising. Of greater interest are the observed correlations between: (1) raft size and species abundance; and (2) distance from shore and species abundance, identified in Paper 3. As raft size and distance from shore decrease, free-swimming fauna associated with pelagic sargassum appears to abandon rafts. These findings suggest that the removal of pelagic sargassum within the nearshore environment would unlikely result in significant negative effects on the free-swimming community. Whilst there are many benefits of nearshore harvesting compared to shoreline harvesting, it is important to recognise that not all fauna within the sargassum community will be affected the same way. According to Alleyne (2022), important clinging fauna such as sea turtle hatchlings and deposited flyingfish eggs are more likely to be captured during harvesting and special efforts will be required to reduce the impacts to these species. Biodiversity assessments conducted under the scope of this thesis were limited in geographic range (all sampling conducted in Barbados) and time frame (4 months). To better understand where or when in-water harvesting should occur, future studies assessing the relationship between clinging fauna and free-swimming fauna within the nearshore environment should be conducted over a greater number of sampling sites and over a longer time period than permitted in this thesis. Furthermore, acknowledging that local currents and winds may hinder the nearshore collection of sargassum before it reaches the coastline, sampling should also occur in oceanic waters to assess applicability of industrial-scale harvesting.

The findings of Paper 4 provide important baseline information on the morphotype composition arriving in Barbados over the course of an entire year and contribute towards the region's understanding of variability surrounding the three prevalent morphotypes. Morphotype assessments indicate that there is significant seasonal variation in the relative abundance of *S. natans* I, *S. natans* VIII and *S. fluitans* III; and this variation is linked to two distinct sub-origins and/or transport pathways within the Tropical Atlantic. Since morphotypes have different properties (Davis et al., 2020; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020; Tonon et al., 2022) that make them more or less suited for certain applications; the influence of oceanic sub-origins on variation in morphotype composition has relevance for the developing sargassum industry. Beyond the changing chemical compositions, variation in morphotype compositions may also have implications for in-water harvesting given that morphotype composition has the potential to influence the biodiversity associated with pelagic sargassum (Alleyne, Neat, et al., 2023a; Martin et al., 2021). Whilst the morphotype assessments within this thesis point to resolvability surrounding variation in the morphotype composition of influx events, generalisations within or across countries or years should not be made with only one year of data. Further studies on morphotype composition, across the region, are needed to better understand seasonality of the three prevalent sargassum forms. Ideally, these studies should incorporate the use of backtracking to determine sub-origins and assess growth and mortality of the different morphotypes as they encounter different nutrient and temperature environments.

Arsenic contamination remains a primary concern for the valorisation of pelagic sargassum (Oxenford et al., 2021; Tonon et al., 2022). Arsenic analyses conducted under the scope of this thesis indicate that the toxic inorganic arsenic represents a substantial percentage of the total arsenic content of sargassum arriving in Barbados. Even so, only 17% of samples (n=23) exceeded regulations set by the EU for the allowable level of inorganic arsenic (40 $\mu g\ g^{-1}$ dw) in organic fertilizers (European Union, 2019). Providing that future arsenic contamination reflects that observed under this research, arsenic levels of pelagic sargassum in Barbados is unlikely to be a major concern for the development of sargassum based fertilizers. A key limitation of Paper 5 however, is the estimation of dry weight concentrations based on moisture content sourced from literature data (Milledge et al., 2020; Tonon et al., 2022). Prior to the development of fertilizers, or any sargassum application, it is important to conduct further arsenic analyses based on dry weight concentrations to attain a better assessment against standards set by the European Union. In addition to the valorisation barriers arsenic contamination presents, Devault et al. (2021) alludes to environmental threats associated with long term accumulation of sargassum on Caribbean shorelines. Sargassum piling up in the nearshore environment becomes stressed and starts to leach arsenic into the water column (Devault et al., 2020, 2021). With millions of metric tons of pelagic sargassum arriving yearly (United Nations Environment Programme - Caribbean Environment Programme et al., 2021; United Nations Environment Programme, 2018) arsenic pollution within the nearshore environment (Devault et al., 2020, 2021) and its incorporation into food webs (Modestin et al., 2022) is a serious concern. Frequent in-water harvesting presents an opportunity to collect large volumes of fresh (sand-free) sargassum whilst minimising costly shoreline clean-ups and mitigating arsenic accumulation within the nearshore environment.

There are great uncertainties and complexities surrounding the management and valorisation of sargassum influx events. As a result, most efforts of valorisation are still relatively small-scale (Chávez et al., 2020; Desrochers et al., 2022). In order to harness the full potential of influx events, management initiatives need to be based on interdisciplinary and transdisciplinary research (Robledo et al., 2021). This research provides a small piece of the puzzle to a very complex problem. However, findings from the biodiversity, morphotype and arsenic analyses conducted in this thesis address key valorisation constraints and contribute to the growing body of knowledge on pelagic sargassum in the Caribbean; that is also directly relevant to West Africa where similar sargassum inundations are occurring (Almar et al., 2022; Ofori & Rouleau, 2021; Sowah et al., 2022). Moreover, with a global increase in macroalgal blooms (Fidai et al., 2020; Joniver et al., 2021; Kraan, 2008; Smetacek & Zingone, 2013; Zhang et al., 2019), this body of work provides key insights on the research needed and approaches to data collection for countries beyond the WCR.

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Appendix: Papers included in this dissertation

Paper 1	Alleyne, K. S. (2022). How is pelagic sargassum-associated biodiversity assessed? Insights from the literature. Gulf and Caribbean Research 33 (1): GCFI 14-GCFI 23. DOI: https://doi.org/10.18785/gcr.3301.08.
Paper 2	Alleyne, K. S. T., Neat, F., & Oxenford, H. A. (2023). A baseline assessment of the epiphytic community associated with pelagic sargassum in the Tropical Atlantic. Aquatic Botany, 186, 103635. https://doi.org/10.1016/j.aquabot.2023.103635.
Paper 3	Alleyne, K. S. T., Small, M., Corbin, M., Vallès, H., & Oxenford, H. A. (2023). Free-swimming fauna associated with influxes of pelagic sargassum: Implications for management and harvesting. Frontiers in Marine Science, 10, ISSN=2296-7745. https://www.frontiersin.org/articles/10.3389/fmars.2023.109074
Paper 4	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, 13(1), 3753. https://doi.org/10.1038/s41598-023-30969-2
Paper 5	Alleyne, K. S. T., Neat, F., & Oxenford, H. A. (2023). An analysis of arsenic concentrations associated with sargassum influx events in Barbados. Marine Pollution Bulletin, 192, 115064. https://doi.org/10.1016/j.marpolbul.2023.115064

Paper I

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How is Pelagic *Sargassum*-Associated Biodiversity Assessed? Insights from the Literature

Kristie S.T. Alleyne
World Maritime Univeristy, w2005361@wmu.se

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HOW IS PELAGIC *SARGASSUM*—ASSOCIATED BIODIVERSITY ASSESSED? INSIGHTS FROM THE LITERATURE[§]

Kristie S. T. Alleyne
World Maritime University – Global Ocean Institute, Fiskehamnsgatan 1, 211 18 Malmö, Sweden; email: w2005361@wmu.se

ABSTRACT: Over the past decade unprecedented blooming of pelagic *Sargassum* has occurred across the Equatorial Atlantic from West Africa to the Caribbean. Although pelagic *Sargassum* mats are considered beneficial in the open ocean, providing valuable habitat for a diverse array of endemic and associated species, they also inundate coastal areas and cause a plethora of management challenges for fisheries, tourism, nearshore coastal ecosystems, public health and the socioeconomic welfare of coastal communities. In—water harvesting has been suggested as a desirable management solution to prevent shoreline inundation, but destruction of the associated biodiversity is a concern with this approach and has not been adequately examined. Furthermore, in—water harvesting methods within the Tropical Atlantic and Caribbean have been ad hoc and highly variable with no established sampling protocol. Here we review 30 published studies detailing methods to collect information on the biodiversity associated with pelagic *Sargassum*. Nets, hook and line, video recordings, bare—hands and plastic bags have all been used to collect epiphytic, clinging and free—swimming fauna associated with *Sargassum*. Net sampling was the predominant method; however, in the absence of a standardized approach a wide range of net types and sizes were used. Similarly, separation, identification and preservation methods were all unstandardized. This review highlights the need for standardization and provides the first set of guidelines for the collection and assessment of *Sargassum*—associated biodiversity. Nevertheless, these approaches are labor intensive and require extensive replication in time and space to produce a reasonable assessment of the biodiversity associated with the *Sargassum* community.

KEY WORDS: epiphytic fauna, clinging fauna, free—swimming fauna, literature review

INTRODUCTION

Floating mats of *Sargassum* (hereon referred to simply as 'pelagic *Sargassum*') typically comprise several morphotypes of 2 holopelagic species (*Sargassum natans* and *S. fluitans*) and provide essential habitat, refuge, nursery ground and foraging habitat for a wide variety of associated and endemic species (Butler et al. 1983, Witherington et al. 2012, Moser and Lee 2012, Martin 2016, Martin et al. 2021). Much of this knowledge comes from assessments in the Sargasso Sea where pelagic *Sargassum* has existed for centuries (Parr 1939, Fine 1970, Butler et al. 1983, Lapointe et al. 2014), and significant steps have been taken to protect it (Laffoley et al. 2011).

Unlike in the Sargasso Sea, the mass blooming of pelagic *Sargassum* across the North Equatorial Recirculation Region (NERR) of the Atlantic presents both a potential asset and a hazard for Caribbean and West African countries (UNEP 2021). Over the past decade unprecedented blooms of pelagic *Sargassum* in the NERR have resulted in devastating shoreline inundations, with mass accumulation and decomposition of the seaweed along the coasts of Caribbean and West African countries (Milledge and Harvey 2016). Clean—up efforts across the region has cost millions of dollars to national economies, strained local resources, and significantly affected coastal livelihoods (Milledge and Harvey 2016, Chávez et al. 2020). While pelagic *Sargassum* mats function as healthy biodiverse ecosystems at sea, the mass shoreline inundations present a plethora of management challenges for fisheries, tourism, public health and nearshore coastal ecosystems (Milledge and Harvey 2016, Ramlogan et al. 2017, van Tussenbroek et al. 2017, Resiere et al. 2018, Oxenford et al. 2019). Furthermore, mass inundations from this newly established source region are now considered the new 'normal' to which countries must adapt (Desrochers et al. 2020).

In—water removal has been suggested as a desirable management solution to prevent the multiple negative impacts associated with shoreline inundation and the problems associated with clearing the seaweed from onshore, especially from sandy beaches which can be significantly damaged by repeated removal efforts and use of heavy equipment (Hinds et al. 2016, Chereau 2019, Dutch Caribbean Nature Alliance 2019, Webber and Maddix 2021). Furthermore, considerable attention is now being given to valorization of pelagic *Sargassum* (Desrochers et al. 2020, Oxenford et al. 2021, UNEP 2021) and in—water harvesting is likely to be an attractive option for obtaining fresh 'clean' *Sargassum* for applications that require high quality fresh *Sargassum*, given the issues associated with separating fresh from partially decayed *Sargassum* (Oxenford et al. 2021).

However, destruction of the associated biodiversity is a concern with in—water removal, as elaborated by the Dutch Caribbean Nature Alliance (2019) who state that there is a need for

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[§] *This article is based on presentations given in November 2021 at the virtual 74th meeting of the Gulf and Caribbean Fisheries Institute and in November 2022 at the 75th meeting of the Gulf and Caribbean Fisheries Institute, Ft. Walton Beach, FL.*

a clear set of guidelines when harvesting pelagic *Sargassum* at sea to minimize any disturbance to or loss of marine life. Despite these concerns, the potential impacts of in–water collection of pelagic *Sargassum* on the associated biodiversity have not been adequately examined to provide appropriate guidance for this management intervention. *Sargassum* is well known to support diverse taxa (Coston–Clements et al. 1991, Casazza and Ross 2008, Laffoley et al. 2011, Moser and Lee 2012, Witherington et al. 2012), thus the impact of in–water harvesting could be significant. To date, the lack of consistency in biodiversity assessment studies in the tropical Atlantic and Caribbean limits the understanding to the patterns of diversity and thus the ability to understand the potential impact of large–scale removal. However, Monroy–Velázquez et al. (2019) noted that pelagic *Sargassum* found close to the coastline had diminished diversity, perhaps due to intensive foraging by coastal fishes and seabirds; within this context, removal of pelagic *Sargassum* may not pose a significant threat.

The faunal community associated with pelagic *Sargassum* is known to consist of sessile and motile organisms which can be found attached to, within and beneath floating mats (Weis 1968, Dooley 1972, Monroy–Velázquez et al. 2019, Martin et al. 2021). This associated community plays an important role in pelagic food webs (Laffoley et al. 2011, Martin et al. 2021). Even the most inconspicuous sessile epifauna have an important role to play, as they provide feeding opportunities for higher trophic level organisms (Martin et al. 2021) which may have commercial importance. Assessing the sessile epiphytic fauna can also prove useful for age determination of the pelagic *Sargassum* (Stoner and Greening 1984, Shadle et al. 2019) and subsequently help determine which valorization applications may or may not be appropriate. For this reason, biodiversity assessments should pay attention to both sessile and motile associated fauna, noting that there will always be inherent and significant variability in pelagic *Sargassum* according to the morphotype, age, and prevailing and past patterns of recruitment to the *Sargassum* (Stoner and Greening 1984, Martin et al. 2021).

This study reviews the variety of methods used to collect, identify and analyze the biodiversity associated with pelagic *Sargassum* that have been documented in the published literature. The purpose of this review is to provide guidance to Caribbean and West African countries on the steps they can take to assess pelagic *Sargassum*–associated biodiversity in easy, practical and reproducible ways so that data collected over time and across the region are comparable.

Materials and Methods

Literature search process

To identify the most relevant literature, 22 scientific and environmental databases (Supplementary Table S1) were searched to identify primary studies focused on biodiversity of pelagic *Sargassum* communities. Key search phrases used to identify relevant articles included: '*Sargassum* AND Biodiversity', '*Sargassum* AND Faunal Communities', 'Sargasso Sea AND Faunal Communities', '*Sargassum* AND Fauna' and 'Sargasso Sea AND Biodiversity'. Under each search phrase, only journal articles and M.S. or Ph.D. theses were selected for further consideration. In addition to the listed databases (Supplementary Table S1), the *Sargassum* Reference Repository hosted by the Centre for Resource Management and Environmental Studies (CERMES), at the University of the West Indies in Barbados, was also used to identify relevant articles. Selected documents from the database search and the repository were imported into Zotero Reference Manager and SRA–Dedupe–Ui was used to remove duplicates.

The reference lists of all relevant papers selected from the database and repository search were then loaded into an excel document to search for additional articles regardless of publication type. After relevant articles were identified using this 'snowballing' technique, all duplicate articles were removed (Supplementary Figure S1).

Selection and exclusion criteria

Article titles with key words relating to the topic under investigation were selected and all non–relevant records were excluded. After initial selection, the abstracts of articles were read to determine relevance. Non–*Sargassum* algae and detached benthic *Sargassum* species are structurally different from pelagic species; thus, the methods used to collect non–pelagic species may not be appropriate for adequately assessing pelagic *Sargassum* influx events. Articles selected for the assessment process focused only on the assessment of biodiversity associated with pelagic *Sargassum* (Supplementary Table S2).

Articles which looked exclusively at the genetic diversity of pelagic *Sargassum* species (i.e., *S. natans* or *S. fluitans*) were excluded from this study. For articles which examined the biodiversity of species associated with pelagic *Sargassum* mats compared to open water, only methods used to assess the biodiversity of pelagic *Sargassum* mats were considered. No limitations were placed on the year of publication and, as a result, articles included in this review dated from 1968 to the time of writing.

Data analysis

In this paper, 30 articles were selected and each article was reviewed carefully to answer 5 research queries covering aspects relating to the collection, identification and assessment of pelagic *Sargassum*–associated species, sample method and post–collection handling:

1. What type of *Sargassum*–associated biodiversity is identified?
2. What method(s) are used to collect pelagic *Sargassum* associated biodiversity?
3. How are the samples sorted and preserved?
4. How are the species identified?
5. How are the data analyzed?

Biodiversity associated with pelagic *Sargassum* mats is classified into 3 main groups: epiphytic fauna, clinging fauna, and free–swimming fauna which expands from the 'sessile' and 'motile' groups described by Weis (1968). Epiphytic fauna refers to any sessile animal which grows on pelagic *Sargassum*, such as hydroids, tube worms and encrusting bryozoans, etc. Clinging fauna refer to animals that exhibit very limited range of movement and spend their time clinging to or climbing around the *Sargassum*, such as crustaceans, polychaetes, molluscs, flatworms, the *Sargassum* frogfish, seahorses and turtle hatchlings. Free—swimming fauna refer to species that swim inside and beneath the *Sargassum* thalli such as juvenile turtles, adult turtles, vertical migrating fishes and pelagic fishes.

TABLE 1. *Net types and specifications used to collect pelagic* Sargassum*-associated biodiversity. Reference numbers refer to numbered studies listed in Supplementary Table S3.*

Net type	Frame opening (m^2)/ Net length (m)	Mesh size (mm)	Number of studies	Reference
Hand operated	0.07-0.25 m^2	0.3-13	21	1, 2, 3, 4, 5, 7, 9, 11, 13, 16, 17, 20, 21, 22, 23, 24, 25, 27, 28
Towed	0.28-2.64 m^2	0.3-25	10	2, 4, 10, 18, 19, 22, 23, 24, 26
Encircling	30.5 m by 5.2 m	1-12.5	4	7, 19, 29, 30

RESULTS AND DISCUSSION

The selected articles were diverse in their aims; some studies examined the relationship between the pelagic *Sargassum* mat morphology and associated biodiversity (Moser et al. 1998) or the species associated with pelagic *Sargassum* compared to open water (Casazza and Ross 2008), and others investigated pelagic *Sargassum* for free—swimming, clinging and epiphytic fauna (Fine 1970, Dooley 1972, Butler et al. 1983, Wells and Rooker 2003, Monroy—Velázquez et al. 2019). Across the 30 reviewed articles, 37% (11 articles) collected information on epiphytic fauna, 43% (13 articles) on clinging fauna and 77% (23 articles) reported on free—swimming fauna (Supplementary Table S3).

Collection methods

Five different methods have been reported in the literature to collect biodiversity associated with pelagic *Sargassum*: a variety of nets, hook and line, video recording, bare—handed collections, and collection of fauna with plastic bags (Supplemental Table S4). Overall, nets were used across the majority of studies (93%; 28 articles), with hook and line (11%; 3 articles), video recordings (7%; 2 articles), hand collections (7%; 2 articles) and plastic bags (4%; 1 article) being used to a lesser extent. Using the identified methods, biodiversity samples were collected from floating clumps of pelagic *Sargassum* (82%), along transects (11%) set at varying distances from shore, and from beach—cast pelagic *Sargassum* (7%).

Net types

Three distinct groups of nets were employed: hand operated nets such as dipnets, landing nets and hand nets, towed nets such as bongo nets, neuston nets, trawls and plankton nets, and encircling nets such as purse seines. Over the different studies, nets varied in size both across and within net types (Table 1).

Of the 3 net types, hand operated nets were the most used with 70% of the studies (Table 1) using various sizes to capture organisms across the 3 biodiversity groups. Researchers using other net types also demonstrated selective use of hand operated nets when the density of pelagic *Sargassum* was too thick for other net types (Casazza and Ross 2008) or when the seas were rough and caused mats to scatter (Dooley 1972). Towed and encircling nets were the second and third most frequently reported collection method (respectively), and were used predominantly for the capture of free—swimming fauna. Hook and line (including one multi—hook longline), and video recordings were only used to assess free—swimming fauna, and hand collections were used solely to collect pelagic *Sargassum* for the assessment of epiphytic fauna (Figure 1).

This preliminary assessment provides an overview of the potential sampling options researchers could use to investigate the biodiversity associated with pelagic *Sargassum*. However, no clear guidance emerges on which net type and/or size should be used. There was no indication why some researchers chose hand operated nets whilst others chose towed nets to sample organisms across all 3 biodiversity groups simultaneously.

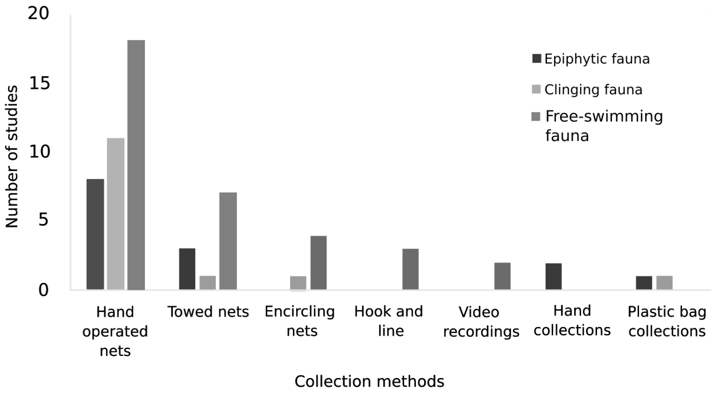

FIGURE 1. *Methods used across studies (n=30) to assess various types of epiphytic fauna, clinging fauna and free-swimming fauna associated with pelagic* Sargassum.

Other gear

Organisms associated with pelagic *Sargassum* are found throughout the mass of floating thalli, as well as several meters below it (Casazza and Ross 2008, Martin 2016). However, sampling depth was not specified in the majority (80%) of studies. In the few studies where depth was specified, net sampling took place within the upper surface waters (0 – 5 m) regardless of net type, whilst the predominantly used hand operated nets were likely to have been limited to the upper layer of floating *Sargassum*. For example, Martin (2016) stated that hand operated nets are not very effective at targeting the larger more mobile species, especially those found at greater depths below the seaweed. Similarly, Moser et al. (1998) reported a high abundance of juvenile and cryptic fish in their dipnet collections, but minimal capture of larger species.

To assess larger free—swimming fauna, Moser et al. (1998) and Casazza and Ross (2008) used a combination of dip net sampling and video recordings. Free floating cam recorders and remotely operated vehicles (ROVs) were deployed approximately 1 m below pelagic *Sargassum* mats. Both these studies indicated a higher presence of juvenile fish within pelagic *Sargassum* mats with larger fish being found in 'layers' below the mat. These studies provide insights into the distribution of species associated with *Sargassum* mats and can help researchers decide which sampling technique they require based on the target biodiversity.

Bearing in mind that studies which solely use video recordings are only able to assess free—swimming organisms below and/or adjacent to the mat, and studies which use nets are limited to the smaller more cryptic organisms, combining net sampling with video observations will play an important role in providing a better understanding of the biodiversity associated with *Sargassum* influx events. Given the inefficiencies of net sampling when targeting free—swimming fauna, biodiversity assessments of pelagic *Sargassum* should include the use of underwater video footage to give a more representative quantitative view of the overall biodiversity associated with pelagic *Sargassum*. While broad assessment methodologies will provide a better understanding of the pelagic *Sargassum* community, motile species may never be fully assessed and are likely to escape in the event of large—scale harvesting in any case.

Treatment of samples

Separation and preservation

Subsequent to collection, samples are generally sorted on board research vessels or taken back to laboratories for sorting and identification. To separate collected motile organisms some studies immediately placed the collected pelagic *Sargassum* in a bag containing seawater (Schell et al. 2016) or freshwater (Stoner and Greening 1984) where it was vigorously shaken for several minutes to remove organisms. Alternatively, collected samples were soaked in buckets of freshwater (Dooley 1972, Monroy—Velázquez et al. 2019) to induce osmotic shock and encourage the release of organisms attached to the pelagic *Sargassum*.

After rinsing, the residual water is typically filtered through a mesh sieve ranging between 0.28—1 mm in size. Dislodged organisms collected in the mesh are then fixed with 5 or 10% formalin (Weis 1968, Bortone et al. 1977, Niermann 1986, Calder 1995, Huffard et al. 2014) or immediately preserved in 40% isopropanol (Bortone et al. 1977, Casazza and Ross 2008), 70% ethanol (Bortone et al. 1977, Martin 2016, Schell et al. 2016, Monroy—Velázquez et al. 2019, Martin et al. 2021), or 95—96% ethanol (Settle 1993, Comyns et al. 2000, Taylor 2015, Shadle et al. 2019, Mendoza—Becerril et al. 2020) for later analyses. In rare cases, fish species were preserved with dry ice (Wells and Rooker 2003, Wells and Rooker 2004).

Species identification

Organisms associated with *Sargassum* were identified to genus/species level in all of the studies; however, the reference manuals/guides used were only noted by a minority (17%) of studies, with the most frequently used being Morris and Mogelberg (1973, Table 2). In addition to the above manuals/guides, several studies alluded to the use of dissecting (Calder 1995, Schell et al. 2016, Martin et al. 2021) and compound (Schell et al. 2016) microscopes to aid in the morphological identification of species.

Quantitative assessment of biodiversity

To date, studies on pelagic *Sargassum*—associated fauna have been diverse in their aims, and have included objectives to investigate species diversity and evenness, test the relationship between *Sargassum* biomass and species richness and density, test the effect of environmental parameters on observed patterns, assess video footage for relative abundance, and quantify epiphytic fauna. This section provides a brief overview of the key assessment procedures used by the reviewed studies.

Species richness/density

Several studies assessed the relationship between pelagic *Sargassum* biomass and associated species using a beam balance (Dooley 1972) or spring scales (Settle 1993, Schell et al. 2016; Taylor et al. 2017, Martin et al. 2021) to record weights, or a volume displacement method (Fine 1970, Stoner and Greening 1984). Studies examining clinging and free—swimming fauna have defined species richness as the number of species per wet weight of *Sargassum*, and species density as the number of individuals per wet weight of *Sargassum*. Calder (1995) examined species richness of epiphytic fauna (hydroid species) using displaced volume in lieu of weight.

Video recordings

Only 2 studies (Moser et al. 1998, Casazza and Ross 2008) have used video recordings as a collection method. While Casazza and Ross (2008) provided a qualitative overview of the species present and recorded their behaviors, Moser et al. (1998) estimated relative abundance using 2 species time methods: Rapid Visual Technique (RVT) and Visual Fast Count (VFC). Since RVT and VFC both rely on a weighted scoring system to estimate the relative abundance of species, 10—min video footage was broken into 2—min segments and the RVT scores (weighted by order of encounter) and VFC scores (weighted by expected frequency) were calculated. Relative abundance was calculated by dividing the score of each species by the sum of

TABLE 2. *Identification manuals/guides used by various studies to aid identification of fauna associated with pelagic* Sargassum.

Manual Author	**Manual Title**	**Studies**
LeCroy (2002)	An Illustrated Identification Guide to the Nearshore Marine and Estuarine Gammaridean Amphipoda of Florida (vol. 2)	Monroy-Veláquez et al. 2019
LeCroy (2004)	An Illustrated Identification Guide to the Nearshore Marine and Estuarine Gammaridean Amphipoda of Florida (vol. 3)	Monroy-Veláquez et al. 2019
Kensley and Schotte (1989)	Guide to the Marine Isopod Crustaceans of the Caribbean	Monroy-Veláquez et al. 2019
Chace (1972)	The Shrimps of the Smithsonian-Bredin Caribbean Expeditions with a Summary of the West Indian Shallow-water Species (Crustacea: Decapoda:Natantia)	Monroy-Veláquez et al. 2019
Williams (1984)	Shrimps, Lobsters, and Crabs of the Atlantic Coast of the Eastern United States, Maine to Florida	Monroy-Veláquez et al. 2019
Castillo-Rodríguez (2014)	Biodiversidad de Moluscos Marinos en Mexico	Monroy-Veláquez et al. 2019
de León-González et al. (2009)	Poliquetos (Annelida: Polychaeta) de México y América Tropical	Monroy-Veláquez et al. 2019
Froese and Pauly (2011)	Fishbase	Monroy-Veláquez et al. 2019
Morris and Mogelberg	Identification Manual to the Pelagic *Sargassum* Fauna	Martin 2016, Taylor et al. 2017, Martin et al. 2021
Calder (1988)	Shallow-water Hydroids of Bermuda: The Athecatae	Mendoza-Becerril et al. 2020
Schuchert (2012)	North-west European Athecate Hydroid andTheir Medusae	Mendoza-Becerril et al. 2020
Coston-Clements et al. (1991)	Utilization of the *Sargassum* Habitat by Marine Invertebrates and Vertebrates- a Review	Shadle et al. 2019

scores for all species (Moser et al. 1998).

Quantifying epiphytic fauna

Many of the earlier studies that investigated the epiphytic fauna associated with pelagic *Sargassum* gave a qualitative account of their findings. These studies recorded the presence or absence of species (Weis 1968), visually determined rare, common, or dominant organisms (Weis 1968, Calder 1995) or categorized the 'age' of *Sargassum* based on the number of organisms associated with the pelagic *Sargassum* (Butler et al. 1983, Calder 1995).

Later studies (Huffard et al. 2014, Shadle et al. 2019, Mendoza—Becerril et al. 2020) quantitatively analyzed epiphytic fauna using percentage cover. Although each of these studies expressed the associated epiphytic fauna as percentage cover, slightly different approaches were used. Huffard et al. (2014) estimated percentage cover by placing each *Sargassum* strand in a tray and taking a photograph directly above the *Sargassum*. This photograph was then cropped into growth zones (previously described by Ryland (1974)) and ImageJ was used to place 250 random dots on each image to ensure at least 25 dots fell onto the bladder, stem and leaf of the *Sargassum*. Estimates of percent cover were calculated by recording the number of randomly placed dots that fell on epiphytic taxa versus those that fell on *Sargassum* with no epiphytes. Similarly, Shadle et al. (2019) took digital images (front and back) of the *Sargassum*; however, this was achieved with a Zeiss dissecting microscope that was fitted with a Canon digital camera. iSolution Lite software was then used to find the total area of the *Sargassum* sample as well as the basal area covered by each type of encrusting epiphyte present; once both measures were obtained, the total epiphytic percentage cover was calculated. Mendoza—Becerril et al. (2020) on the other hand, investigated the hydroid cover on *Sargassum* by placing the thallus between 2 clear rectangular acrylic plates which were subdivided into 1 x 1 cm squares. Percentage cover of hydroids was estimated by counting the number of squares occupied by *Sargassum* and those occupied by hydroids on both sides of the plate.

To determine the total biomass of epiphytic fauna, pelagic *Sargassum* samples were oven dried and weighed with epiphytic fauna still intact. Once the initial weight was obtained, epiphytic fauna was scraped off with the use of forceps and the sample was reweighed. The difference in the 2 weights was used as the total dry weight for epiphytic fauna (Shadle et al. 2019).

Recommendations

There is a real need to conduct site—specific biodiversity studies that are comparable across sites and over time. The type of question to be answered will dictate the best method and level of replication required and each method will have their own set of challenges. When conducting biodiversity assessments to better understand and mitigate the impacts of in—water harvesting, it is important to:

1. Acknowledge the inherent and significant variation associated with pelagic *Sargassum* communities. Components within the *Sargassum* community vary in time

and space within the Atlantic and the Gulf of Mexico (Butler et al. 1983, Stoner and Greening 1984, Martin et al. 2021). To determine seasonality of the fauna associated with pelagic *Sargassum* in the Tropical Atlantic, intensive sampling efforts will be required.

2. Understand the limitations of biodiversity assessments. Given the variation in *Sargassum* communities, it is ill—advised to generalize the findings of one biodiversity assessment to identify a specific time or place where *Sargassum* should be harvested. With that said, Monroy—Velázquez et al. (2019) reported that once pelagic *Sargassum* is close to shore the quantity and diversity of associated fauna is diminished. The rationale is that pelagic *Sargassum* in shallower water is intensively foraged by fishes, thus its removal prior to imminent stranding can be accepted as having the least impact. However, spatial configuration, nearshore slope, the presence of reefs and hydrography of the different coastlines will likely influence the distance from shore where biodiversity decreases.
3. Recognize that not all fauna within the *Sargassum* community will be affected in the same way from in—water harvesting. Large vagile fish are likely to be the least impacted taxa, given their capacity to escape, if large—scale removal is developed. Similarly, sea birds that use *Sargassum* mats for foraging (Haney 1986, Moser and Lee 2012) will also disperse when approached by harvesting vessels. Clinging fauna are more likely to be captured during harvesting events, and special efforts will be required to reduce the impacts on endangered sea turtle species. Epiphytic communities such as hydroids and tubeworms may be of lesser concern than clinging species with inherent rarity (i.e., Sargassum Frogfish, pipefish and juvenile sea turtles). However, the presence of attached flyingfish egg masses (Oxenford et al. 2019) does elevate concern for impact on the epiphytic communities, and preliminary scans to assess the presence of egg masses may be required prior to in—water harvesting.

Based on the reviewed literature, preliminary guidelines for developing a simple, easy to follow protocol for the collection and assessment of pelagic *Sargassum*—associated biodiversity that is suitable for wide use by a variety of researchers and other stakeholders is presented here.

Targeted biodiversity group

Prior to data collection, the targeted biodiversity should be classified as epiphytic, clinging or free—swimming fauna. These broad groupings will help to determine which collection methods are likely to be most suitable.

Given the nature of epiphytic and clinging fauna, both biodiversity groups can be collected using similar net types, as the results are likely to be much less sensitive to differences in net types and/or sizes than when assessing free—swimming fauna. Free—swimming fauna, on the other hand, may require nets with larger frame openings, larger mesh sizes and the additional use of video footage. Tools and techniques used to investigate the free—swimming fauna associated with pelagic *Sargassum* mats will depend on whether assessments are striving to 1) simply record the presence or absence of a species or 2) record the sizes of individuals associated with pelagic *Sargassum*. In the first instance net sampling may not be required as this can be assessed with the use of video. However, in the second case, researchers may want to employ a mixed approached (net and video sampling) bearing in mind that net type and size have the potential to bias results.

Net requirements

Whilst hand operated, towed and encircling nets can all be used to collect organisms across the 3 biodiversity groups, biodiversity assessments should strive to use the net type most suitable for each group. For example, if researchers only want to assess epiphytic and/or clinging fauna, hand operated nets may be the most suitable since these organisms are found attached and clinging to the pelagic *Sargassum*. On the other hand, a study assessing free—swimming fauna should consider using either towed or encircling nets, since large vagile species are likely to escape hand operated nets.

In addition to net type and size, it is also necessary to consider mesh size when conducting biodiversity assessments. According to Tanaka and Leite (1998), a mesh size of 0.5 mm is sufficient for capturing amphipods and gastropods, however the presence/abundance of larger fish may be underestimated (Moser et al. 1998). This is because water resistance is greater for smaller mesh sizes, resulting in slower pulling/towing speeds and thus allowing fast free—swimming fauna to escape. For this reason, it is important that collection protocols for pelagic *Sargassum*—associated biodiversity carefully consider the targeted biodiversity group(s) and their net requirements. Using the net specifications identified in this review, Table 3 provides a list of recommended net types, net sizes and mesh sizes which can be used to collect organisms across the 3 biodiversity groups.

Sampling depth

The sampling depths (0—5 m) used in this review is a reasonable range for future studies, and these depths can extend to deeper waters if the target group for the assessment is free—swimming fauna. These depths are not required when targeting epiphytic and clinging fauna; however, biodiversity assessments of clinging and epiphytic fauna should account for the entire depth/thickness of the mat being sampled.

Separating organisms from pelagic Sargassum

Once collected, the entire *Sargassum* sample should be placed in a container of seawater and transported to the laboratory. To separate the collected fauna from the *Sargassum*, the entire contents of the container should be placed in buckets of freshwater to induce osmotic shock. Alternatively, smaller samples can be placed in bags of freshwater and shaken vigorously to remove clinging and small free—swimming fauna. The rinse water in either case should be filtered through a mesh sieve to collect all detached organisms. Within the reviewed

TABLE 3. *List of recommended net specifications to be used to collect epiphytic, clinging and free-swimming fauna from pelagic* Sargassum. *Recommendations are based on the findings of 30 reviewed articles and serve as a starting point for future biodiversity assessments.*

Biodiversity group	Recommended net types(s)	Recommended frame opening (m^2)/ net length (m)	Recommended mesh size
Epiphytic fauna	Hand operated nets	0.07–0.25 m^2 No optimal size identified	0.5 mm
Clinging fauna	Hand operated nets	0.28–2.64 m^2 No optimal size identified	0.5 mm
Free-swimming fauna	Towed nets	0.28–2.64 m^2 No optimal size identified	3–25 mm No optimal size identified
Free-swimming fauna	Encircling nets Based on a single study	30.5 m by 5.2 m No optimal size identified	12.5 mm No optimal size identified

literature, sieves used to collect organisms after rinsing ranged between 0.28—1 mm mesh size. Keeping the mesh size <1 mm will reduce the likelihood of losing any of the small and often cryptic clinging fauna (i.e., amphipods, shrimps, molluscs) associated with the collected pelagic *Sargassum*. Ideally, the sieve used to collect organisms from the rinse water should be equal to or finer than the mesh size used to collect organisms in—water. Unlike clinging and free—swimming fauna, epiphytic fauna will remain attached to the pelagic *Sargassum*, and can be assessed without removal.

Identifying species

The manuals listed in Table 2 can serve as a starting point for the identification of fauna associated with pelagic *Sargassum*. Morphological identifications can be further validated with the use of genetic approaches using DNA barcoding libraries such as the Barcode of Life DataSystems (BOLD) and GenBank (Ratnasingham and Hebert 2007, Benson et al. 2017). In cases where it is equally important to identify the morphotypes of pelagic *Sargassum* in addition to their associated biodiversity, Parr (1939), Schell et al. (2015) and Martin et al. (2021) provide useful accounts of the various morphotypes.

Preserving specimens

If the species cannot be identified immediately, samples should be preserved for later analysis. Although several of the reviewed articles indicated the use of formalin and alcohol solutions to preserve organisms, there was no indication as to why a particular substance or concentration was chosen. According to Collins (2014), formalin is preferred for taxonomic purposes because it preserves tissue morphology over long periods. However, organisms can be preserved directly in 70% ethanol as it is an effective biocide. Ethanol concentrations >70% may result in the dehydration of samples, and those <70% will not be an effective biocide. This review suggests the use of 70% ethanol as opposed to formaldehyde solutions for preserving epiphytic and clinging fauna until they can be identified, as ethanol is more cost effective, less toxic and readily accessible across Caribbean and West African countries. Additionally, specimens preserved in ethanol can be used for molecular taxonomic identification, whereas those preserved in formalin cannot. On the other hand, large free—swimming pelagic fish captured during biodiversity assessments should be photographed and released back into the ocean. Sea turtles should only be captured with the proper permits and under specific regulations.

Other considerations

Acknowledging the benefits of combined net and video sampling, assessments of pelagic *Sargassum*—associated biodiversity will likely include underwater footage when assessing free—swimming fauna. Within the reviewed studies, cameras and ROVs were both used to visualize the free—swimming fauna associated with pelagic *Sargassum*; however, within the Caribbean and West Africa context it may be more feasible to conduct underwater assessments using cameras since access to ROVs is likely to be limited across countries and more costly.

CONCLUSION

With increasing numbers of *Sargassum* researchers and actors across the Caribbean and West Africa, there is a pressing need for the development of a clear set of guidelines for the collection and assessment of pelagic *Sargassum*—associated biodiversity. This would allow data to be collected across different countries in easy, practical and reproducible ways. The adoption of such guidelines would help to develop a clearer sense of the homogeneity or heterogeneity of pelagic *Sargassum* communities and achieve comparable results for future studies. It should be noted, however, that while the recommendations provided in this study are straightforward and require very little cost, extensive replication in time and space is required to achieve a reasonable assessment of the biodiversity associated with the pelagic *Sargassum* community.

Biodiversity associated with pelagic *Sargassum* varies over time and space, and therefore impacts associated with in—water harvesting and the trade—offs against coastal impacts will also vary. Studies comparing the biodiversity associated with pelagic *Sargassum* in nearshore and offshore environments are needed to better understand when, where and if in—water harvesting should occur. While establishing a clear set of guidelines for biodiversity assessments cannot directly inform managers of the impact(s) of bulk removal of massive quantities of pelagic *Sargassum* at sea, guidelines can improve conservation efforts by clarifying the value of *Sargassum* to the broader pelagic ecosystems of the Tropical Atlantic and the Caribbean Sea.

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Paper II

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

Kristie S.T. Alleyne [a,*], Francis Neat [a], Hazel A. Oxenford [b]

[a] *WMU-Sasakawa Global Ocean Institute, World Maritime University (WMU), Malmö, Sweden*
[b] *Centre for Resource Management and Environmental Studies, Cave Hill Campus, University of the West Indies, Bridgetown BB11000, Barbados*

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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

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* 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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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 (~ 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 × 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 (× 10 magnification) and compound microscopes (× 40 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.

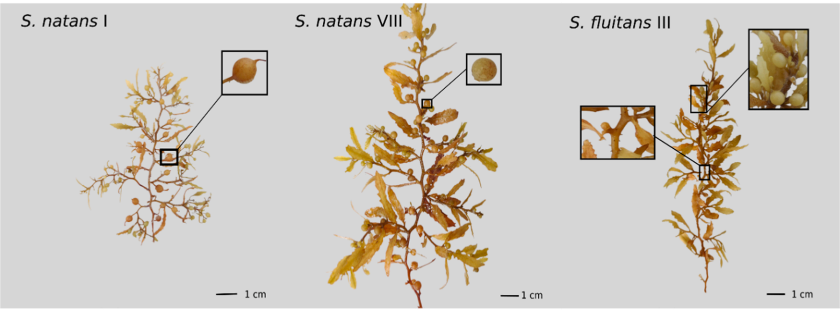

Fig. 1. General appearance of the three pelagic sargassum morphotypes collected at Conset Bay, Barbados.

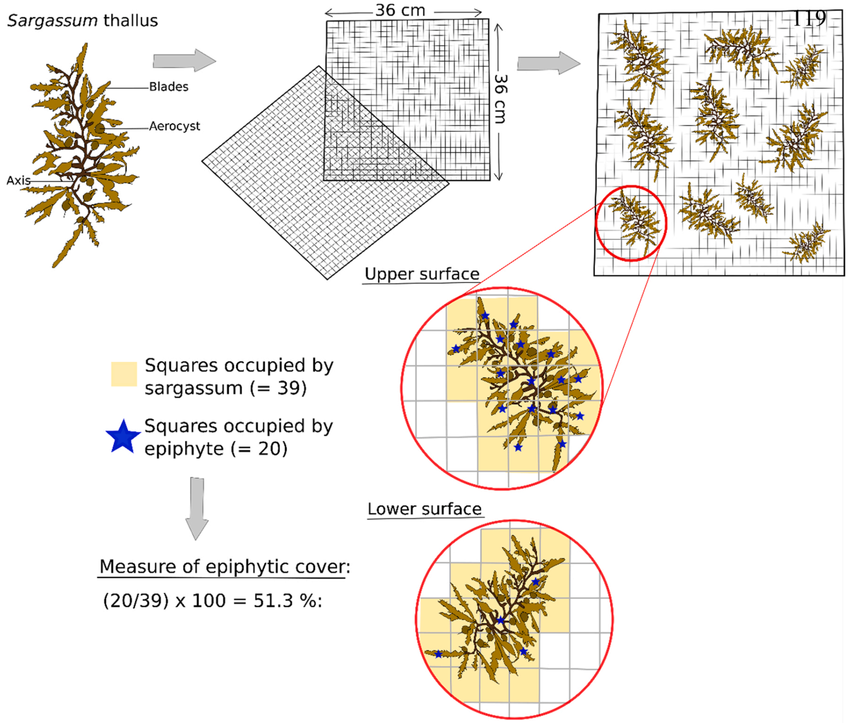

Fig. 2. Schematic of the method of measuring epiphytic cover found on pelagic sargassum samples.
Adopted from the methodology described in Mendoza-Becerril et al. (2020).

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:

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

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 ± 2 SD), *S. natans* I (n = 170; specimen mean wet weight = 11.2 g ± 3 SD) and *S. natans* VIII (n = 170; specimen mean wet weight = 19.5 g ± 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°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°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, 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.

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	33.4 ± 16.9
	Aglaophenia latecarinata	Aglaopheniidae	Hydroid	13.0 ± 19.3
	Clytia noliformis	Campanulariidae	Hydroid	6.8 ± 17.3
	Spirorbis spirorbis	Serpulidae	Polychaete	5.0 ± 4.9
	Obelia dichotoma	Campanulariidae	Hydroid	3.7 ± 5.7
	Plumularia strictocarpa	Plumulariidae	Hydroid	0.1 ± 0.5
Flora	Unid. filamentous alga	Chlorosarcinaceae	Algae	0.7 ± 1.5

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 substrate 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*

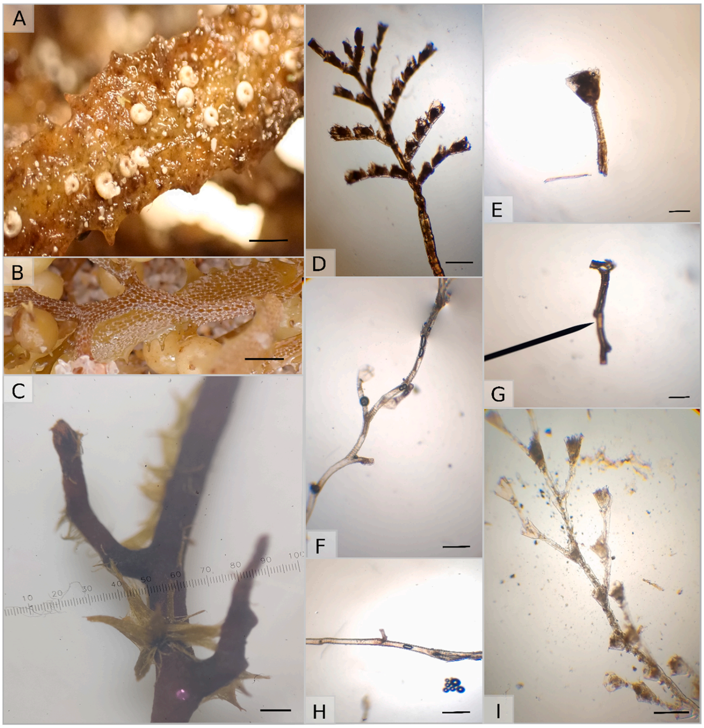

Fig. 3. Epiphytes associated with *Sargassum fluitans* III, *S. natans* I and *S. natans* VIII arriving in Barbados. (A) *Spirorbis spirorbis*; (B) *Membranipora tuberculata*; (C) filamentous alga; (D) *Aglaophenia latecarinata*; (E) *Clytia noliformis*; (F–H) *Obelia dichotoma*; (I) *Plumularia strictocarpa*.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

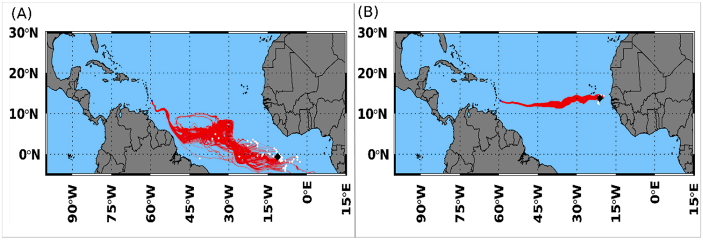

Fig. 4. Backtracks of pelagic sargassum collected from Conset Bay beach in Barbados. Panel (a) shows sample backtracks that originate close to the equator and travel along northeast Brazil before arriving in Barbados; origin/transport pathway A. Panel (b) shows backtracks that originate further north 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

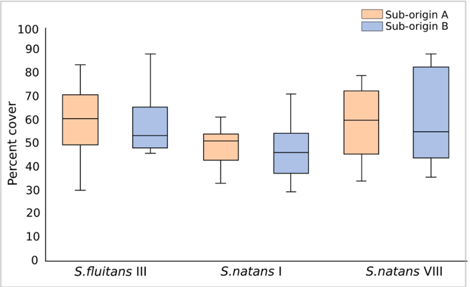

Fig. 5. Percent cover of epiphytes on the three prevalent sargassum morphotypes (*Sargassum fluitans* III, *S. natans* I, *S. natans* VIII) arriving in Barbados from sub-origins within the NERR.

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 associated with pelagic sargassum. The ability 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, 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

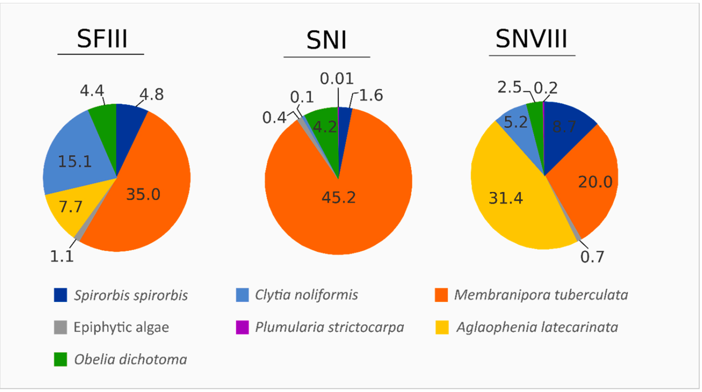

Fig. 6. Epiphytic percentage cover of *Sargassum fluitans* III (SFIII), *S. natans* I (SNI) and *S. natans* VIII (SNVIII) arriving in Barbados.

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.

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Free-swimming fauna associated with influxes of pelagic sargassum: Implications for management and harvesting

Kristie S. T. Alleyne[1]*, Micaela Small[2], Makeda Corbin[2], Henri Vallès[3] and Hazel A. Oxenford[2]

[1]WMU-Sasakawa Global Ocean Institute, World Maritime University (WMU), Malmö, Sweden, [2]Centre for Resource Management and Environmental Studies, The University of the West Indies, Bridgetown, Barbados, [3]Department of Biological and Chemical Sciences, The University of the West Indies, Bridgetown, Barbados

EDITED BY
Aleke Stöfen-O'Brien,
World Maritime University, Sweden

REVIEWED BY
Lydia Ladah,
Center for Scientific Research and Higher Education in Ensenada (CICESE), Mexico
Lindsay Martin,
National Science Foundation (NSF),
United States

*CORRESPONDENCE
Kristie S. T. Alleyne
✉ w2005361@wmu.se

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Mass accumulations of pelagic sargassum (*Sargassum natans* and *S. fluitans*) in the Tropical Atlantic, across the Caribbean and off the coast of West Africa, are causing extensive ecological and socioeconomic harm. The extraordinary volumes of sargassum influxes could also provide a business opportunity if innovative ways are developed to utilise the raw material. In-water harvesting provides the best opportunity to collect substantial amounts of 'fresh' sargassum that can be used in a variety of applications. However, sargassum rafts are living and diverse ecosystems with a range of associated fauna including fish that are targeted by fishers. The consequences of in-water harvesting of sargassum on the biodiversity, including associated fishes, remain poorly understood. Characterisation of this biodiversity within nearshore and offshore environments is needed to help guide best harvest practices and assess possible impacts on fishing opportunities. We assessed the free-swimming fauna associated with sargassum rafts at various distances from shore with the use of underwater video recordings. Over a three-month period, a total of 35 underwater surveys were conducted off the eastern and southern coastline of Barbados. Thirteen species (12 fishes and one comb jelly) from 8 families were identified, with the family Carangidae representing the greatest number of species (n=6). Application of the MaxN metric (maximum number of individuals of a species seen during deployment) revealed significant correlations with raft characteristics notably raft volume, raft distance from shore and water depth. The three environmental variables accounted for 9% of the variation (adjusted R^2) in the free-swimming community composition with raft volume being the major driver of species richness. This aligns with ecological theory and supports our hypothesis that larger rafts would host greater species richness. The results demonstrate a strong affiliation between pelagic sargassum rafts and species biodiversity and abundance that will need to be considered by managers when seeking a best compromise between protecting beaches from inundation by sargassum and protecting biodiversity and fishing opportunities.

KEYWORDS

pelagic sargassum, associated biodiversity, motile fauna, Barbados, fishing opportunities

Introduction

Vast quantities of pelagic *Sargassum* spp. (*Sargassum natans* and *S. fluitans*) subsequently referred to simply as 'sargassum' continue to inundate the coasts of Caribbean, South American and West African countries (Wang et al., 2019; Chávez et al., 2020; Cox et al., 2021). This proliferation of sargassum in the Tropical Atlantic has been linked to a new source region known as the North Equatorial Recirculation Region (NERR) (Franks et al., 2016; Wang et al., 2019). Influx events are episodic in nature with volumes varying from year to year (Cox et al., 2021). In 2018, the Caribbean recorded the highest volumes of sargassum influxes leading to states of national emergency being declared in some countries. This has continued in 2022 with strandings just as extreme as 2018, if not worse in places (The Sargassum Watch System (SaWS), 2022; Centre for Resource Management and Environmental Studies, 2022).

Sargassum influx events are now considered the new 'normal' for the region (Desrochers et al., 2020) and show a trend of increasing severity (The Sargassum Watch System (SaWS), 2022). As the region continues to adapt to this new reality, there has been a surge in research and publications on impacts (Milledge and Harvey, 2016; Ramlogan et al., 2017; van Tussenbroek et al., 2017; United Nations Environment Programme, 2018; Resiere et al., 2019), forecasting (Wang and Hu, 2017; Johnson et al., 2020; Marsh et al., 2021; Marsh et al., 2022), potential uses (Desrochers et al., 2020; Thompson et al., 2020; Amador-Castro et al., 2021; Oxenford et al., 2021; United Nations Environment Programme - Caribbean Environment Programme et al., 2021) and chemical composition (Devault et al., 2019; Davis et al., 2020; Nielsen et al., 2021; Devault et al., 2022; Tonon et al., 2022). Research into the sargassum phenomenon reveals considerable spatial and temporal complexities associated with management due to its transboundary nature and unpredictability (Cox et al., 2021). Management efforts to date have been largely focused on protecting fisheries and tourism sectors as these are severely impacted during influx events and contribute approximately US $370 million (Patil et al., 2016) and US$29.2 billion (Milledge and Harvey, 2016), respectively, to the region's economy. Considerable attention is also now being given to the valorization of pelagic sargassum to ameliorate the economic damage generated in the region (Desrochers et al., 2020; Oxenford et al., 2021; United Nations Environment Programme - Caribbean Environment Programme, 2021; Robledo et al., 2021).

In-water harvesting provides an opportunity to reduce mass shoreline inundations and provide large volumes of sargassum for valorization (Robledo et al., 2021). Government agencies and the private sector have been working together to carry out clean-ups at considerable cost (running into tens of millions of US dollars per year), to help reduce the impacts of influx events (Milledge and Harvey, 2016; Chávez et al., 2020). These harvesting efforts were initially carried out in response to stranding events and placed significant strain on the economy of Caribbean Small Island Developing States (SIDS) (Cox et al., 2021; Liranzo-Gómez et al., 2021). Furthermore, shoreline harvesting contributed to coastal erosion (Liranzo-Gómez et al., 2021) and negatively impacted sea turtle nests and hatchlings (Maurer et al., 2015; Schiariti and Salmon, 2022). In-water harvesting is currently being developed to reduce the impacts associated with mechanical shoreline harvesting and provide the large quantities of fresh clean (high quality) sargassum required for many applications (Liranzo-Gómez et al., 2021; Webber and Maddix, 2021).

While urgent solutions to sargassum strandings are needed and turning a challenge into an opportunity is commendable, it should also be recognized that pelagic sargassum hosts a diverse assemblage of endemic and associated fauna that rely on the sargassum for food and shelter (Dooley, 1972; Bortone et al., 1977; Butler et al., 1983; Settle, 1993; Moser et al., 1998; Wells and Rooker, 2003; Hoffmayer et al., 2005; Huffard et al., 2014). Whilst studies from the Sargasso Sea highlight the importance of pelagic sargassum to a diverse assemblage of fauna, there have been very few studies (Schell et al., 2016; Monroy-Velázquez et al., 2019; Mendoza-Becerril et al., 2020; Martin et al., 2021) focused on understanding the biodiversity associated with pelagic sargassum from the new source region. Recent evidence (Martin et al., 2021) suggests important differences in biodiversity associated with the three prevalent sargassum morphotypes (*S. natans* I, *S. natans* VIII and *S. fluitans* III). Given the seasonal and interannual shifts in morphotype composition (Schell et al., 2016; García-Sánchez et al., 2020; Machado et al., 2022) and the influence of sub-origins on morphotype composition (Alleyne et al.; unpublished data) addressing the current knowledge gaps on biodiversity can play a pivotal role in guiding best harvest practices.

Fishes have long been known to associate with the rafts of sargassum, attracting fishers, but the sheer scale of the recent influxes has also caused problems for fishers. Fishers across the region have reported damage to fishing gear, predominantly propeller and net entanglements, and damage to boat engines from overheating when navigating through extensive sargassum accumulations (Speede et al., 2018). Sargassum also hinders fishers' ability to launch their boats leading to loss of fishing days (Franks et al., 2012; Caribbean Regional Fisheries Mechanism and Japanese International Cooperation Agency, 2019). In Barbados, there has also been a reduction in catches of key fisheries species like flyingfish and adult dolphinfish; however, there have been increases in catch of other species such as almaco jacks (Caribbean Regional Fisheries Mechanism and Japanese International Cooperation Agency, 2019). These impacts are especially concerning since most Caribbean countries are categorised as SIDS, meaning that they already experience unique social, economic and environmental challenges (United Nations, no date), and their economic growth is intrinsically linked to the marine environment. It is therefore a priority to understand the association of fishes with sargassum influxes and thus be able to advise managers on the impacts of interventions such as in-water harvesting on fishing opportunities.

The purpose of this study was to characterise the free-swimming fauna associated with pelagic sargassum arriving in Barbados and identify what factors (if any) drive changes in community assemblage. Following Alleyne (2022), free-swimming fauna in this study refer to motile species that swim inside and beneath floating sargassum such as juvenile turtles, adult turtles, vertical migrating fishes and pelagic fishes. Drawing from ecological theory, we hypothesized that larger rafts would host greater species richness (Simberloff, 1976; Lomolino, 2000).

Materials and methods

Sampling method

During three periods of high sargassum abundance (August 2021, March, and May 2022), a total of 35 underwater videos of sargassum rafts were conducted offshore between (613 and 2,368 m off) the eastern and southern coastline of Barbados. Videos were conducted from a small open boat (length 5 m) with an outboard engine, using a free-floating underwater recording device. Each recording device consisted of a U-shape aluminum frame on which a GoPro camera HERO 8 (1920 x 1080 pixels with 30 frames per second) or HERO 9 (1920 x 1080 pixels with 60 frames per second) was mounted. Cameras were set to 'wide- angle' view and suspended below the water surface by two one-meter lengths of rope attached to the aluminum frame that was kept afloat with a surface buoy (Figure 1).

Cameras were deployed under two types of pelagic sargassum aggregation states: mats and windrows (Figure 2). Mats were classified as densely packed aggregations of sargassum with an irregular to round shape and measured 5 to 100s of meters in diameter (distance across) (Marmorino et al., 2011; Goodwin et al., 2022). Windrows were defined as aggregations of sargassum generally arranged in a line and ranged from 0.5 meter to several meters in diameter (Marmorino et al., 2011; Goodwin et al., 2022). The term 'raft' is hereinafter used to refer to aggregations of mats and/or windrows.

Each targeted sargassum raft was defined as a sampling station. Small stations (5-25 m length) were sampled with one camera and larger stations (> 40 m length) were sampled with 2 to 3 cameras spanning the extent of the sampling station. Stations ranging between 26-40 m in length were not encountered. Camera deployments on larger stations were done at a minimal distance of 30 m apart and each deployment was treated as an individual sample during video analysis. For each deployment the camera was set to record video footage and submerged approximately 1 m below the water's surface (angled slightly upwards) to record the free-swimming fauna in the water column directly beneath the sargassum raft. After deployment, cameras were left adrift for a period of 15 minutes and the boat maintained a minimal distance of 10 m from the raft to limit interference.

At each sampling station several dimensions were recorded: the length of the sargassum raft; the diameter of the sargassum raft; the thickness of the sargassum raft; the depth of the water; and the distance from shore. The length and diameter of the station was estimated using the boat length as a reference. The thickness of the sargassum raft was determined (to the nearest 5 cm) with the use of a graduated pole. Water depth was recorded (to the nearest 0.1 m) with a handheld depth sounder (Speedtech SM-5A) and GPS coordinates were recorded *via* a handheld GPS device (Garmin GPS 72). Subsequent to field sampling, GPS coordinates were uploaded into Google Earth to determine the distance from shore of each sampling station.

Video analysis

To minimise any interference caused by the sampling boat during camera deployment and retrieval, 2.5 minutes of footage were removed from the beginning and end of each video, resulting in 10-minute surveys. Following Priede et al. (1994), the maximum number of individuals sighted in any one field of view (i.e., frame) (hereafter referred to as MaxN) was recorded for each species within each survey. Within each survey free-swimming fauna were identified to species level where possible, using FishBase (Froese and Pauly, 2011) or the FAO species identification guides (Carpenter, 2002) where necessary.

MaxN was chosen as a conservative measure of abundance as it avoids repeated counts of individuals (Priede et al., 1994; Willis and Babcock, 2000; Harvey et al., 2007). For each species, relative abundance was determined by dividing the MaxN of an individual species by the sum of MaxN values across all species.

$$Relative\ Abundance\ (by\ species) = \frac{MaxN\ of\ species\ A}{Sum\ of\ MaxN\ for\ all\ species\ (A\ to\ Z)}$$

The total number of species observed (species richness) and the species frequency (as number of surveys in which a species occurred) across surveys were also recorded. The relative frequency of each species was calculated by dividing its frequency by the sum of frequencies across all species.

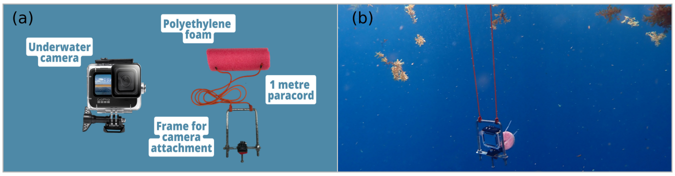

FIGURE 1
Materials used to construct underwater recording device **(A)** and a still image of the device deployed underwater **(B)**.

FIGURE 2
Pelagic sargassum aggregation states sampled off the coast of Barbados. **(A)** Large mat (>100 m in diameter), **(B)** small mat (10 m in diameter) and **(C)** windrows (7 m in diameter).

$$Relative\ \ Frequency\ \ (by\ \ species) = \frac{Species\ \ A\ \ frequency\ \ across\ \ all\ \ surveys}{Sum\ \ of\ \ Taxa\ \ A\ \ to\ \ Z\ \ frequencies}$$

To assess the dominance and the spatiotemporal consistency of dominant species within the community, we used Sanders Biological Value Index (BVI). BVI assesses dominance within a community by assigning ranks (based on the number of species) and corresponding points to individual species (Loya-Salinas and Escofet, 1990). The number of species to be considered in the overall calculation was identified by assessing patterns of dominance across the 35 surveys. Within each survey the number of species making up 95% of the cumulative relative abundance was identified and the maximum number of species across all surveys that accounted for 95% of the cumulative relative abundance (in our case 6 species) was used to assign ranks and points to species across all surveys (Supplementary Table S1).

Within each survey, ranks from 1 to 6 were assigned to species in order of abundance in a survey with a rank of 1 being the highest and equivalent to a value of 6 points (Supplementary Table S1). If there were more than 6 species in any survey, species after the 6th species received a value of 0 for that sample. With this method if a species ranks first across all surveys (35) it would receive a value of 210, that is, the maximum possible value.

Statistical analysis

The 35 surveys yielded species abundance estimates that differed by more than three orders of magnitude (Supplementary Figure 2). Since, *ceteris paribus*, species richness estimates will tend to increase non-linearly with individual abundance, we standardized species richness estimates across the surveys using rarefaction curves to facilitate cross-survey comparisons. We used a sample size of eight individuals to generate the rarefied species richness for each survey, since the maximum number of species observed in any given survey was eight. Two surveys had zero individuals observed, and so their species richness estimates were manually set to zero. Six other surveys had fewer than eight individuals (but more than zero); these surveys were manually and conservatively set to one species, since this is the minimum value that can be produced *via* rarefaction. Rarefied species richness was produced using the rarefy function in "vegan" (Oksanen et al., 2018) in R (R Core Team, 2022). Associations between the rarefied species richness estimates and distance from shore, water depth, and raft volume were assessed using Spearman rank correlations. Raft volume was calculated by multiplying raft length, raft width and raft depth, which provided a single estimate of raft size.

We also performed a redundancy analysis (RDA) to assess the effects of depth, distance from shore, and raft volume on community assemblage composition. Prior to running the RDA, the species data were first turned into species presence/absence matrix and subsequently Hellinger-transformed. These analyses were conducted using the "vegan" package in R (Oksanen et al., 2018). To assess the independent and shared effects of raft volume, distance from shore, and depth on assemblage composition, we conducted a variance partitioning (Borcard et al., 1992) using the varpart command in the "vegan" package.

Finally, we also assessed the extent to which changes in assemblage composition across surveys, i.e., beta diversity, reflected species replacement versus losses in species richness and whether any such potential process was associated with any of the three environmental variables. This implied first decomposing beta diversity into species replacement and species losses variance components using the beta.div.comp function in the "adespatial" package in R (Dray et al., 2022). These two variance components were subsequently and separately used to create a response matrix in a distance-based redundancy analysis where each environmental variable was used as predictor (after removing the effect of the two other variables *via* linear regression).

Results

A total of 35 underwater surveys were conducted off the eastern and southern coastline of Barbados during August 2021, March 2022 and May 2022. Species assemblages and abundances (0-250 individuals) varied across surveys (Figure 3); some rafts were teeming with life while 6% of rafts were unoccupied. Species richness was low (0-8 species) across surveys, with the majority (74%) of sargassum rafts occupied by 5 or fewer species.

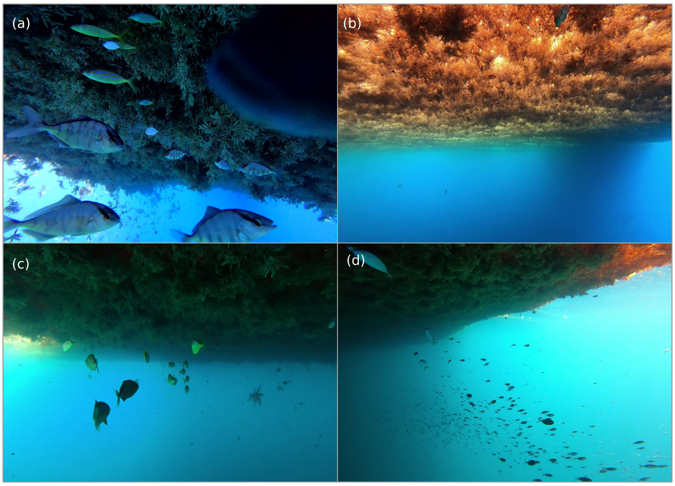

FIGURE 3
Still images collected from underwater videos of pelagic sargassum rafts. Smaller rafts **(A)** (5 m in diameter) and **(B)** (7 m in diameter). Larger rafts **(C)** (20 m in diameter) and **(D)** (100 m in diameter).

Relative abundance, relative frequency, and Sanders biological value index for observed species

We identified 1958 individuals representing 13 species (12 fishes and one comb jelly) across 8 families (Table 1 and Supplementary Figure 1). Carangidae represented the majority (96.1%) of species observed with pelagic sargassum and had high frequencies across all surveys.

Across the 35 surveys, *Caranx latus* (horse-eye jack) had the highest overall abundance but obtained a lower BVI score than *Seriola rivoliana* (almaco jack), which had a higher frequency across surveys resulting in spatiotemporal dominance (Table 2). Irrespective of total abundance or BVI ranking, Carangidae species dominated pelagic sargassum arriving in Barbados.

Effect of distance from shore, depth, and raft volume on species assemblage composition

The RDA revealed that 16.9% of the variance across surveys in species assemblage composition could be significantly explained by the environmental data (Pseudo-F= 1.96, p=0.008). The main axis of the RDA accounted for 51% of the explained variance and reflected primarily raft volume effects and secondarily depth effects (Figure 4). The second axis accounted for an additional 29% of the explained variance and reflected primarily the effect of distance from shore and secondarily depth effects (Figure 4). Testing the effect of distance from shore, depth, and raft volume separately indicated that species assemblage composition was significantly related to raft volume and depth (Pseudo-F≥ 2.94, p ≤ 0.006), whereas the relationship with distance from shore was marginally non-significant (Pseudo-F=2.05, p=0.053).

A variance partitioning to assess the independent and shared contributions of the three environmental variables indicated that they jointly accounted for 8.5% of the adjusted variance (adjusted R^2) in species assemblage composition (Figure 5). Of this, 2.1% of the explained variance was shared among the three variables, whereas approximately 1.0% was shared between distance from shore and depth and between depth and raft volume, respectively (Figure 5). Raft volume independently accounted for the biggest fraction of the explained variance (2.5%; Figure 5), which was statistically significant (Pseudo-F=2.56, p=0.007). Depth and distance from shore independently accounted for 1.7% and 1.0% of the explained variance (Figure 5), respectively, but these independent fractions were not statistically significant (Pseudo-F ≤ 1.29, p≥0.228).

Depth was highly positively correlated with distance from shore (r_s=0.76, p<0.001) and raft volume (r_s =0.43, p=0.009), but raft volume and distance from shore were not significantly correlated (r_s =0.25, p=0.146) (Supplementary Figure 3). Raft volume was positively correlated with species richness (p<0.010) (Supplementary Figure 3), rarefied species richness (p= 0.001), and individual abundance (p<0.001) (Figure 6). In contrast, there was no significant correlation between distance or depth with species richness or rarefied species richness (p>0.050) (Figure 6 and Supplementary Figure 3). Distance and depth were positively correlated with abundance (p<0.05) (Figure 6).

The analysis of beta-diversity revealed that species replacement and species richness losses were equally important as each

TABLE 1 Total and relative abundance and frequency of free-swimming fauna observed under pelagic sargassum by family and species.

Family	Species	Environment	MaxN Abundance values		Relative frequency (%)
			Total	Relative (%)	
Carangidae	*Caranx latus*	Coastal pelagic	1316	67.2	15.9
	Seriola rivoliana	Oceanic pelagic	178	9.1	18.2
	Caranx ruber	Coastal pelagic	94	4.8	6.8
	Caranx spp.	–	90	4.6	1.5
	Caranx bartholomaei	Coastal pelagic	89	4.5	10.6
	Caranx crysos	Coastal pelagic	75	3.8	9.1
	Elagatis bipinnulata	Oceanic pelagic	41	2.1	8.3
Monacanthidae	*Aluterus scriptus*	Coastal pelagic	35	1.8	9.8
Ocyropsidae	*Ocyropsis maculata*	–	17	0.9	8.3
Balistidae	*Balistes capriscus*	Coastal pelagic	11	0.6	5.3
Lobotidae	*Lobotes surinamensis*	Oceanic pelagic	9	0.5	3.8
Antennariidae	*Histrio histrio*	Oceanic pelagic	1	0.1	0.8
Sphyraenidae	*Sphyraena barracuda*	Coastal pelagic	1	0.1	0.8
Kyphosidae	*Kyphosus* sp.	Coastal pelagic	1	0.1	0.8

Abundance values were derived using MaxN method.

accounted for half (50%) of the variation in beta-diversity. The species replacement component was not significantly linked to any of the three environmental variables (Pseudo-F ≤ 1.09, p≥0.125). In contrast, the species richness loss component was significantly linked to raft volume (Pseudo-F=1.97, p=0.011), but not to depth nor distance from shore (Pseudo-F ≤ 0.79, p≥0.809), supporting that species were being lost from the original species assemblage as the rafts got smaller.

TABLE 2 Sanders biological value index (BVI) for species observed under pelagic sargassum, based on the total points obtained per species from 35 underwater surveys.

Species	BVI	Importance rank		MaxN Abundance values		
		BVI	Total abundance	Total	Relative (%)	Cumulative (%)
Caranx latus	105	2	1	1316	67.2	67.2
Seriola rivoliana	111	1	2	178	9.1	76.3
Caranx ruber	48	5	3	94	4.8	81.1
Caranx spp.	11	11	4	90	4.6	85.7
Caranx bartholomaei	57	3	5	89	4.5	90.2
Caranx crysos	55	4	6	75	3.8	94.1
Elagatis bipinnulata	40	7	7	41	2.1	96.2
Aluterus scriptus	41	6	8	35	1.8	98.0
Ocyropsis maculata	31	8	9	17	0.9	98.8
Balistes capriscus	21	9	10	11	0.6	99.4
Lobotes surinamensis	19	10	11	9	0.5	99.8
Histrio histrio	2	13	12	1	0.1	99.9
Sphyraena barracuda	4	12	13	1	0.1	99.9
Kyphosus sp.	2	13	14	1	0.1	100.0

Also shown are the importance ranks based on the BVI value, and based on the total MaxN abundance value. The three MaxN abundance indices used in calculating the BVI are displayed in the righthand columns.

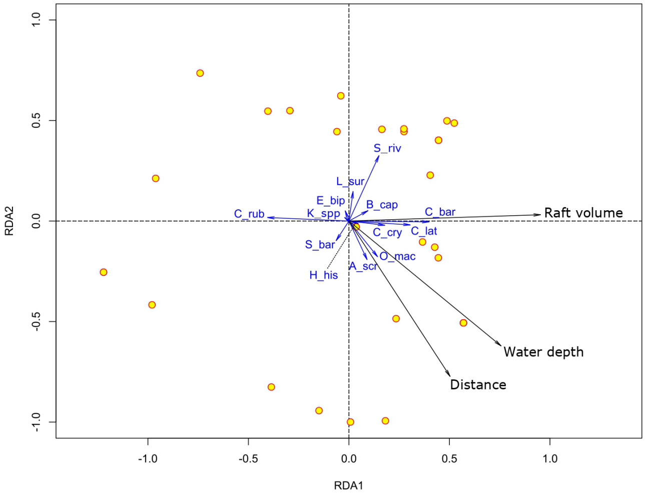

FIGURE 4
Redundancy analysis (RDA) ordination plot showing the effect of distance, water depth and raft volume on species composition of the free-swimming fauna associated with pelagic sargassum. *S. rivoliana* (S_riv), *B. capriscus* (B_cap), *C. bartholomaei* (C_bar), *L. surinamensis* (L_sur), *C. latus* (C_lat), *C. crysos* (C_cry), *C. ruber* (C_rub), *E. bipinnulata* (E_bip), *Kyphosus* spp. (K_spp), *S. barracuda* (S_bar), *H. histrio* (H_his), *A. scriptus* (A_scr), *O. maculata* (O_mac).

Discussion

Pelagic sargassum arriving in Barbados during 2021 and 2022 influx events was associated with 12 fish species (predominantly (67%) coastal pelagic) and one comb jelly (*Ocyropsis maculata*). This first account of free-swimming fauna associated with pelagic sargassum for the Eastern Caribbean is considerably lower than that reported by earlier studies (36-110 species) conducted across the Gulf of Mexico, the Gulf Stream, and various parts of the North Atlantic (Dooley, 1972; Bortone et al., 1977; Settle, 1993; Wells and Rooker, 2003; Hoffmayer et al., 2005). This was also the case when compared with Moser et al. (1998) (29 species, Gulf Stream) despite

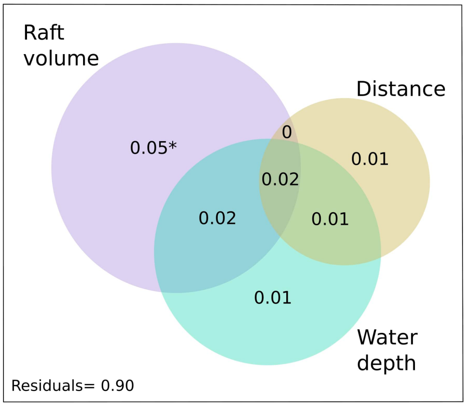

FIGURE 5
Venn diagram representing the shared and independent effects of each environmental variable on the assemblage of free-swimming fauna associated with pelagic sargassum. The variance jointly explained by distance, water depth and raft volume is represented in the region where all three circles overlap. Note that the sizes of the various shared and non-shared effects are only approximations.

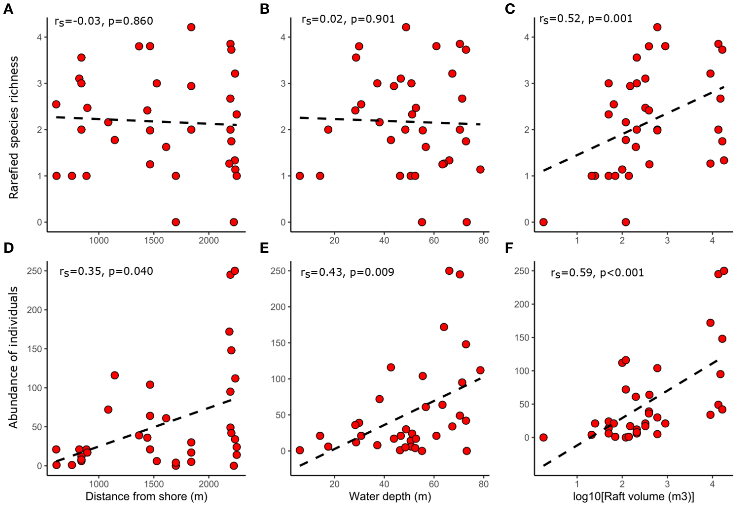

FIGURE 6
Scatter plots showing relationships between distance vs rarefied species richness **(A)**, water depth vs rarefied species richness **(B)**, raft volume vs rarefied species richness **(C)**, distance vs abundance of individuals **(D)**, water depth vs abundance of individuals **(E)** and raft volume vs abundance of individuals **(F)**. Spearman rank correlation coefficients and associated p-values are also shown. A best fit line was inserted to help interpret trends.

the use of video surveys in both studies. Differences in sampling methodologies between the present study and earlier studies (Dooley, 1972; Bortone et al., 1977; Settle, 1993; Wells and Rooker, 2003; Hoffmayer et al., 2005) may have contributed to the differences in species diversity (Alleyne, 2022). However, given the fact that species diversity increases with the amount of time a drifting structure, such as pelagic sargassum, is available (Kingsford, 1992), we postulate that earlier studies with ties to the well-established Sargasso Sea would have greater diversity when compared to the newly established bloom region in the Tropical Atlantic. This observation is supported by anecdotal information from local fishers in the Eastern Caribbean, who report finding increasing numbers and greater diversity of fish species associated with sargassum over time since the first influxes in 2011.

Across surveys, Carangidae was the dominant family observed making up 50% of the total fish species. Similarly, earlier studies (Moser et al., 1998; Hoffmayer et al., 2005) have also reported high abundances of Carangidae associated with pelagic sargassum. Within the Carangidae family, *C. latus* (horse-eye jack) was the most abundant species with large schools observed under some rafts. In Barbados, Carangidae are important to the coastal pelagic fishery (Maraj et al., 2011; Food and Agriculture Organization (FAO), 2022) making up 98.4% of the total catch in the seine fishery (Maraj et al., 2011). These species help to support the livelihood of fishers during the oceanic pelagic fishery 'off-season' and contribute to the island's food security (Maraj et al., 2011).

The fisheries sector of Barbados, like much of the Eastern Caribbean, is an integral component of the culture, economy and food security (Oxenford and Monnereau, 2018). The mass proliferations and subsequent influx events of pelagic sargassum brought new navigation and harvesting challenges to the fishery sector (Ramlogan et al., 2017; Speede et al., 2018). Prior to the onset of large-scale sargassum strandings in 2011, *Hirundichthys affinis* (flyingfish) made up approximately 60% of the annual fish landings in Barbados and accounted for the highest value-added benefits of all landed species (Oxenford et al., 2019). By 2019, prolonged sargassum influx events resulted in extremely low catches in the flyingfish industry with a 51.5% decrease in the mean monthly landings (Oxenford et al., 2019). This decrease was followed by a rapid increase in catches of almaco jack (*S. rivoliana*) not previously known to Eastern Caribbean fishers or consumers (Caribbean Regional Fisheries Mechanism and Japanese International Cooperation Agency, 2019). Within this study, almaco jacks showed the highest spatiotemporal dominance of the 13 identified species. The association of almaco jacks with pelagic sargassum is now widely recognised in Barbados with iceboat and longline fishers actively targeting almaco jacks in periods of low flyingfish abundance. Over the last two years, Barbadian fishers have been using satellite images, provided by the University of South Florida, to target large sargassum rafts in pursuit of almaco jacks (Dr. Shelly-Ann Cox, pers. comm., Barbados).

Within this study, distance from shore, water-depth and/or raft volume jointly accounted for approximately 9% of the variation (adjusted R^2) in the free-swimming community associated with pelagic sargassum. The effect of raft volume, distance from shore and water depth on community composition is complicated by the fact that water depth is correlated with both distance from shore and raft volume. That said, the variance partitioning and pairwise correlation tests do support that raft volume, a proxy for raft size, is the major structuring factor (among those measured here) of the free-swimming community associated with pelagic sargassum arriving in Barbados. As raft size decreased, individual abundance and species richness also decreased, as expected by ecological theory (Simberloff, 1976; Lomolino, 2000). The observed positive relationships between sargassum raft size and species richness and abundance is consistent with the earlier studies (Settle, 1993; Moser et al., 1998; Casazza and Ross, 2008; Martin et al., 2021; Goodwin et al., 2022) and explains why Barbadian fishers target larger rafts. Our results also support the findings of Wells and Rooker (2003) and Monroy-Velázquez et al. (2019), who reported reduced abundances within nearshore environments. Moreover, our beta-diversity analyses supported that the losses in species richness with decreasing raft size were due to a gradual loss of resident species (nestedness) rather than to progressively having smaller assemblages of new species (species replacement) (Legendre, 2014).

Interestingly, Monroy-Velázquez et al. (2019) noted that the occurrence of sargassum-brown-tide events in nearshore waters may account for the lower abundance of motile sargassum-associated fauna close to shore. They suggested that the reduction in available oxygen in these brown-tides may force fish to abandon the rafts as they approach the shore. In our study, however, none of the surveys were close enough to shore to experience the sargassum-brown-tide phenomenon. Regardless of cause, reduced abundances of associated biodiversity nearshore have been put forth as an argument for encouraging in-water harvesting of sargassum close to shore, rather than in the open sea. Furthermore, nearshore rafts are more likely to strand, resulting in the loss of any remaining biodiversity (Hinds et al., 2016; López-Contreras et al., 2022).

In order to reduce the environmental and economic impacts associated with shoreline accumulation of sargassum, affected countries need integrated management plans with adaptive strategies geared towards the creation of sustainable sargassum opportunities (Liranzo-Gómez et al., 2021; Robledo et al., 2021). Harvesting at sea will likely be required in the future to obtain the large quantities of sargassum needed for industrial-scale applications, or the high quality clean sargassum needed for many other applications, given the issues associated with separating partially decayed sargassum from fresh sargassum, other macroalgae, seagrasses and sand after stranding (Oxenford et al., 2021). However, a key question remains for providing best practice guidance: at what point (distance from shore) should sargassum be harvested to minimize biodiversity loss? The answer will likely vary on a case-by-case basis as coastal morphology, hydrography and presence of nearshore habitats will likely influence the distance from shore at which biodiversity decreases (Alleyne, 2022).

To date, the destruction of biodiversity associated with pelagic sargassum has been the primary concern raised with in-water harvesting (Dutch Caribbean Nature Alliance, 2019; Robledo et al., 2021). However, given the utilization of pelagic sargassum by Eastern Caribbean fishers, large-scale harvesting of pelagic sargassum will result in the loss of fishing opportunities. Fishers in this region are no longer merely 'coping' with sargassum as they did in the initial years (Speede et al., 2018) but rather they are adapting and now depend on the incoming rafts to target alternative species that are now well accepted by the market (e.g., almaco jacks, *C. bartholomaei* (yellow jacks). In fact, all species (with the exception of *Histrio histrio* (sargassum frogfish), and *Ocyropsis maculata* (comb jelly) found to be closely associated with pelagic sargassum in this study are considered commercial species and provide fishing opportunities, and contribute to the local economy and food security. In addition to reducing fishing opportunities, large-scale removal of sargassum could potentially affect commercially important flyingfish populations since they are known to use sargassum as a spawning substrate (Oxenford et al., 2019). A recent study in West Africa by Ofori and Rouleau (2021) using agent-based modelling to demonstrate the effects of sargassum harvesting on fisheries, showed that when all of the incoming sargassum is harvested, the fishery sector is denied the opportunities that sargassum offers to enhance fish growth and abundance. On the other hand, if no sargassum is removed, fishers will likely experience challenging fishing conditions with high volumes of sargassum in nearshore environments, and tourism sectors will also be negatively affected (Ofori and Rouleau, 2021). These findings, supported by our own results suggest that a best comprise should be sought with regard to in-water sargassum harvesting and preserving fishing opportunities. Therefore, as the region explores the use of in-water harvesting to minimize beaching events and increase valorization, efforts should also be made to maintain fishing opportunities. Additionally, if large-scale harvesting is developed, endangered species that use sargassum rafts, such as turtle hatchlings (known to be present as part of the clinging-fauna community in the rafts off Barbados but not captured in our video surveys of the free-swimming community) will need to be considered (Oxenford et al., 2021). Such concerns have already led to pelagic sargassum being given special management attention in the USA through its designation as 'essential fish habitat' resulting in regulations restricting the harvesting of sargassum in waters under the jurisdiction of the South Atlantic Fishery Management Council (South Atlantic Fishery Management Council (SAFMC), 2002; National Marine Fisheries Service (NMFS), 2003). Furthermore in 2014 sargassum was designated as 'critical habitat' for loggerhead turtles in the US Gulf of Mexico and NW Atlantic (National Oceanic and Atmospheric Administration (NOAA), 2014) resulting in its legal protection.

A significant conundrum highlighted here in the management of sargassum is the conflicting needs of two important commercial sectors. Large scale in-water removal of sargassum has the potential to reduce fishing opportunities but it is also likely to greatly improve tourist experience. It is well established that clean beaches, clear waters and healthy coral reefs provide the principal settings for tourism activity in Barbados (Schuhmann et al., 2017) and play a critical role in tourists' return visitation decisions (Schuhmann et al., 2019).

In conclusion, this preliminary study provides the first insights for the Eastern Caribbean on the free-swimming fauna associated with incoming pelagic sargassum rafts originating from the NERR, and reveals the management dilemma between the fisheries and tourism sectors. We have also demonstrated the usefulness of the relatively simple and low-cost video technique for recording free-swimming fauna associated with sargassum. Even with the use of a conservative assessment of the associated biodiversity (MaxN) and the crude estimates for raft size, we have revealed a significant positive correlation between raft size and community assemblage that aligns well with ecological theory that biodiversity should increase with patch/habitat size (e.g., Simberloff, 1976; Kohn and Walsh, 1994; Lomolino, 2000; Munguía-Rosas and Montiel, 2014).

However, there are limitations to our study and generalisations across years or countries should not be made on the basis of samples taken over a limited period. Additionally, our camera design would have inherently missed some of the cryptically colored species swimming directly beneath the raft. Within this study, about 90% of the variation in the free-swimming community associated with pelagic sargassum was not explained by distance from shore, water-depth and/or raft volume. This suggests that there are likely to be other important unmeasured variable(s) influencing the community associated with pelagic sargassum. These could include variability in sargassum morphotype composition of the rafts (Martin et al., 2021), age of the sargassum (Stoner and Greening, 1984) source area of sargassum within the NERR which varies with season (Beron-Vera et al., 2022), oxygen levels and changes in hydrography.

To better understand where, when or if in-water harvesting of sargassum should be permitted, future studies should compare the fish community in offshore and nearshore environments over a greater range of distance and over a longer time period than the current study. Ideally sampling should be carried out closer than 500 m from shore for applicability of assessing the impact of harvesting sargassum along the outside of barriers deployed to prevent sargassum reaching the shore. Sampling should also occur in oceanic waters for applicability of assessing the impacts of industrial-scale harvesting or sinking of sargassum. Likewise, sampling should be expanded to cover summer and winter influx events that bring sargassum from different source areas in the NERR (Beron-Vera et al., 2022). Moreover, studies that quantify the utilization of pelagic sargassum by fishers in Barbados and the Eastern Caribbean are needed to better assess the impacts of loss of fishing opportunities.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

Author contributions

KA, MC and HO conceptualized the work. KA, MC and MS participated in the data collection process and the data was analyzed by KA and HV. All authors contributed to the writing of the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1090742/full#supplementary-material

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Paper IV

scientific reports

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Seasonal variation in morphotype composition of pelagic *Sargassum* influx events is linked to oceanic origin

Kristie S. T. Alleyne[1]✉, **Donald Johnson**[2], **Francis Neat**[1], **Hazel A. Oxenford**[3] & **Henri Vallès**[4]

The recent proliferation of pelagic *Sargassum* spp. in the Tropical Atlantic causes major ecological and socioeconomic impacts to the wider Caribbean when it washes ashore, with regional fisheries and tourism industries particularly affected. The Caribbean influxes have been tracked to a new bloom region known as the North Equatorial Recirculation Region (NERR) encompassing the area between the South Equatorial Current and the North Equatorial Counter Current and extending from Africa to South America. The vast biomass of *Sargassum* presents serious problems when it washes ashore but also represents significant commercial opportunities, especially with biofuel and fertilizer. The floating *Sargassum* mats are themselves diverse ecosystems that vary both in their biodiversity and biochemical attributes. Two major species (*Sargassum fluitans* and *S. natans*) have been identified as well as several distinguishable morphotypes of each. Oceanic mixing tends to blend the morphotypes together making it difficult to determine if there are regions of the NERR that favour bloom and growth of the distinct types. In this study, we quantify the species and morphotype composition of *Sargassum* strandings in Barbados and test if this is related to separate oceanic origins and routes travelled using a backtracking algorithm based on ocean drifter data. We found significant seasonal variation in the relative abundance of three morphotypes and this could be traced to two distinct easterly sub-origins and/or transport pathways; one area around 15° N that travels directly E–W across the Atlantic, and another area generally south of 10° N that takes a more meandering route coming close the coast of South America. These findings contribute towards our understanding of why the Tropical Atlantic bloom is presently occurring as well as towards addressing valorisation constraints surrounding variation in the supply of the three commonly occurring morphotypes.

Pelagic *Sargassum* spp. (*Sargassum natans* and *S. fluitans*) subsequently referred to simply as '*Sargassum*' forms a floating oceanic ecosystem that provides habitat, shelter and foraging opportunities for a wide diversity of endemic and associated species[1–3]. Historically, this structural habitat was largely confined to the Sargasso Sea and the Gulf of Mexico[4,5] with very low abundance in the northern Caribbean and Tropical Atlantic[6,7]. This dramatically changed in 2011, when massive quantities of *Sargassum* began to strand and decompose along the coasts throughout the Caribbean, NE South America and West Africa[8–10] seriously impacting regionally important industries. This proliferation of *Sargassum* in the Tropical Atlantic has continued and increased, and has been linked to a bloom region bounded latitudinally by the South Equatorial Current (SEC) and the North Equatorial Counter Current (NECC) lying between Africa and South America and defined, for simplicity, as the North Equatorial Recirculation Region (NERR)[9,10]. Ocean eutrophication and climate change are likely driving factors[11–13] although little is known about the effects of ocean circulation patterns on the taxonomic composition of *Sargassum* blooms. In this study, the distribution of *Sargassum* morphotypes within the Tropical Atlantic is determined as a first step in unravelling this complex problem.

The negative impacts of decomposing *Sargassum* have been well documented in nearshore ecosystems[8,14], fisheries[15–17], tourism and other coastal businesses[8,18,19] and human health[20–22]. Clean-up efforts have cost

[1]WMU-Sasakawa Global Ocean Institute, World Maritime University (WMU), Malmö, Sweden. [2]Center for Fisheries Research & Development, The University of Southern Mississippi-Gulf Coast Research Laboratory, Ocean Springs, MS, USA. [3]Centre for Resource Management and Environmental Studies, The University of the West Indies, Cave Hill Campus, Bridgetown, Barbados. [4]Department of Biological and Chemical Sciences, The University of the West Indies, Cave Hill Campus, Bridgetown, Barbados. ✉email: w2005361@wmu.se

hundreds of millions of dollars to national economies[8,23]. Influx events are now considered a new norm to which countries must adapt[12,24]. There is a rapidly growing interest in utilizing *Sargassum* and turning it into business opportunities[25–28]. However, what constitutes sustainable harvesting and the human and/or environmental health risks of utilizing *Sargassum* are currently not well understood[29].

Sargassum mats originating in the Tropical Atlantic are widely recognised as composing of two species (three dominant morphotypes); *Sargassum natans* I, *S. natans* VIII and *S. fluitans* III (Fig. 1). Whilst there remains some controversy over the taxonomy and nomenclature[30–34], these three morphotypes are genetically distinct[30] and have distinctive ecological, biological, and chemical traits[3,35] and even accumulate toxic heavy metals at different rates[36,37].

There is evidence of substantial interannual and/or intra-annual variation in the morphotype composition of *Sargassum* mats originating from the NERR[29,39–41]. Initial influxes were reported to be dominated by *S. fluitans* III and *S. natans* VIII, whilst more recent observations report a dominance of *S. fluitans* III and *S. natans* I[29,40]. To date, however, the variability in relative abundance of *Sargassum* morphotypes remains poorly understood[29]. Furthermore, given that morphotype composition can influence both the biodiversity associated with *Sargassum*[3] and chemical composition[35,37], variations in the relative abundances of the three commonly occurring morphotypes will have implications for sustainable harvesting strategies and for the utilization of *Sargassum* by entrepreneurs.

Recent findings[42] revealed two potential pathways for *Sargassum* transport into the Caribbean. We hypothesised that the morphotype composition of *Sargassum* influx events varies seasonally and that this is related to its oceanic origin and transport pathway across the Atlantic. We assessed variation in relative abundance of the three morphotypes in *Sargassum* strandings in Barbados during 2021–2022 and analysed their origins with the use of a backtracking algorithm based on ocean drifter data with addition of 0.5% wind[43]. Barbados is uniquely positioned as a study site, being near the 15° N latitude 'separation' line between North Atlantic gyre water and tropical water entering the Caribbean[44] and the most easterly of the Caribbean islands, thus among the first to receive *Sargassum* influxes from the NERR. Therefore, it serves as an ideal site to test our hypothesis regarding seasonal variation and oceanic origins of *Sargassum* influxes.

Results

Changes in morphotype compositions.

Monthly analyses of the relative abundance of *S. natans* I, *S. natans* VIII and *S. fluitans* III revealed temporal differences in the predominant morphotype (Fig. 2, Fig. S1).

While *S. fluitans* III was the predominant morphotype in 80% of the samples, there were notable exceptions (Fig. 2). For example, in November, January, and February samples were dominated by *S. natans* VIII, which was generally the least abundant of the three morphotypes.

Linking morphotype compositions to sub-origins.

The extent to which the observed variation in the relative abundance of *Sargassum* morphotypes reflects distinct origins was investigated via sample backtracking for 365 days from the date of stranding using 100 particles to represent each sample. This revealed two distinct sub-origins/transport pathways (Fig. 3). *Sargassum* stranding in Barbados between March and early August apparently originated close to the equator and travelled along northeast Brazil before arriving in Barbados (Fig. 3a). In contrast, *Sargassum* arriving between late August and February originated further north and travelled a relatively direct route to Barbados (Fig. 3b).

The two identified transport pathways differed in the average distance travelled by the particles and average latitude at the origin of each particle backtrack (Fig. 4a). Simulations were attributed to sub-origin/transport pathway A or B based on the route travelled, distance travelled and the approximate location of the origins.

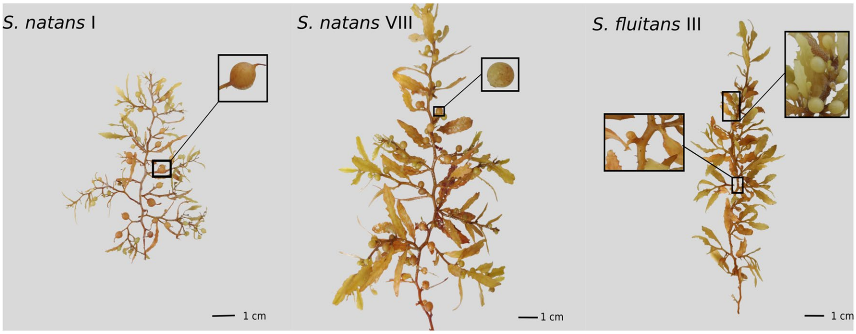

Figure 1. General appearance of the three pelagic *Sargassum* morphotypes collected on Morgan Lewis beach, Barbados. Inset on *S. natans* I shows the presence of spines on the circular air bladders. Inset on *S. natans* VIII shows the absence of spines on the circular air bladders. The top right inset on *S. fluitans* III shows the absence of spines on the elongated air bladders and the bottom left inset shows the presence of spines along the stem. Photograph taken from Ref.[38].

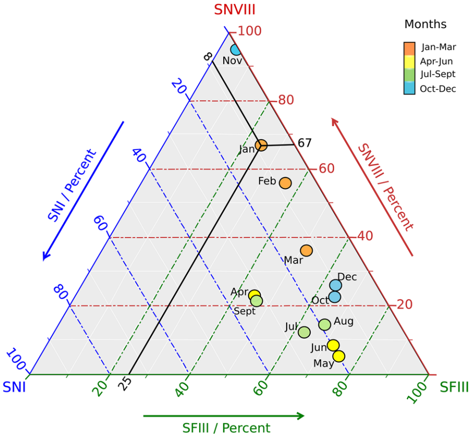

Figure 2. Ternary plot illustrating monthly variation in morphotype composition of *Sargassum* stranding in Barbados over a 12-month period. *Sargassum natans* I (SNI), *S. natans* VIII (SNVIII) and *S. fluitans* III (SFIII). Black lines indicate the average percent contribution of each morphotype in the January samples (67% SNVIII, 25% SFIII, 8% SNI). Quarterly periods are represented by orange (Jan–Mar), yellow (April–Jun), green (Jul–Sept) and blue (Oct–Dec) dots.

Backtracks that originated around the equator (0–7° N; Fig. 4b) and followed a convoluted trajectory along the NE coast of Brazil to the Caribbean (Fig. 3a) are referred to as sub-origin/transport pathway A. These backtracks showed both high average distances travelled (5740 to 8550 km over the 365 days) as well as high variability in the distance travelled among replicate backtracks for any given date (indicated by the relatively large 95% confidence intervals in Fig. 4a). In contrast, backtracks referred to as sub-origin/transport pathway B originated relatively far north (9–18° N; Fig. 4b) and travelled a more direct westerly route covering a much shorter distance over the 365 days (4080–4870 km) than *Sargassum* from sub-origin/transport pathway A (Fig. 3a,b) and showed greater consistency in the distance travelled among the replicate backtrack particles for any given date (Fig. 4a). This partitioning of the 25 simulations into two "homogenous" groups of sub-origins was supported with the use of K-means partitioning (Fig. S2).

A Permutational Multivariate Analysis of Variance (PERMANOVA) indicated that the relative abundance of *S. natans* I, *S. natans* VIII and *S. fluitans* III morphotypes differed significantly between the two sub-origins/transport pathways ($p = 0.0131$) (Table S1). Sub-origin/transport pathway A (March-early August) showed a predominance of *S. fluitans* III (Fig. 5a). In contrast, sub-origin/transport pathway B (late August–February) showed higher levels of *S. natans* VIII, with reduced quantities of *S. fluitans* III (Fig. 5b).

Oceanographic parameters and sub-origins. We investigated whether environmental conditions, i.e., Sea Surface Temperature (SST) and nutrient load (inferred from Chlorophyll a concentration) derived from satellite imagery, differed between the two sub-origins at the initial locations ('origins' (Fig. 4b)) and mid-way (6 months) along the average backtrack trajectory of *Sargassum* (for a given date). A PERMANOVA indicated that environmental conditions differed significantly between the two sub-origin/transport pathways ($p = 0.0039$) but not between time periods (origin vs mid-way) ($p = 0.3179$) (Table S1). Pooling the data across both time periods for each sub-origin supported that environmental differences between the two sub-origins/transport pathways were driven by higher SST at the sub-origin/pathway A (Fig. 6).

Discussion

Since the onset of *Sargassum* influx events in 2011, there has been notable annual variability in the relative abundance of *S. natans* I, *S. natans* VIII, and *S. fluitans* III, with broadscale spatial and temporal differences observed across the Caribbean[29,39–41]; however, to date there has been little understanding of what drives this. This study supports for the first time that the morphotype composition of *Sargassum* influxes over the course of a full year varies significantly and appears to be linked to their origin/transport pathway. By using a backtracking algorithm based on ocean drifter data with 0.5% wind, *Sargassum* from Barbados was traced to two distinct sub-origins/transport pathways within the Tropical Atlantic. Identified pathways align with the findings of Ref.[42]. In our assessment, *Sargassum* mats arriving in Barbados between March to early August are likely to take the more southerly transport pathway, linked to the Gulf of Guinea, (arriving from sub-origin A) that passes along the coast of South America. Satellite imagery in Refs.[7,45] suggest that *Sargassum* enters this pathway from south of the equator, which is south of the NERR. Alternatively, *Sargassum* arriving between late-August and

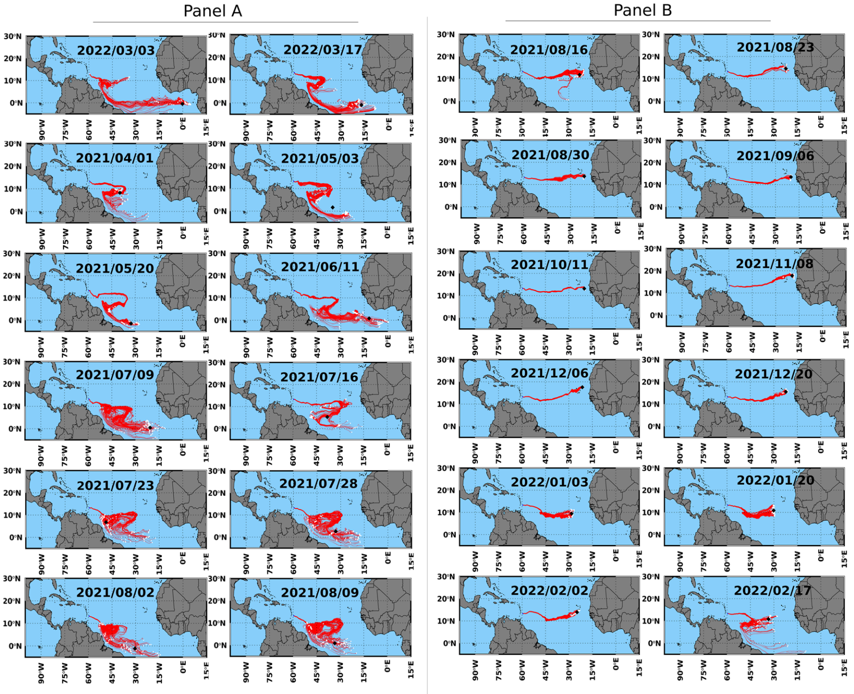

Figure 3. Backtracks of *Sargassum* (mixed-morphotype samples) collected from Morgan Lewis beach in Barbados over the period of 1 year (2021–2022). Panel (**a**) shows sample backtracks from early March to early August and panel (**b**) shows backtracks from late August through February. All backtracks 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). Dates are presented in year/month/day format. Maps were generated using IDL 8.8.1 (https://www.l3harrisgeospatial.com/Software-Technology/IDL).

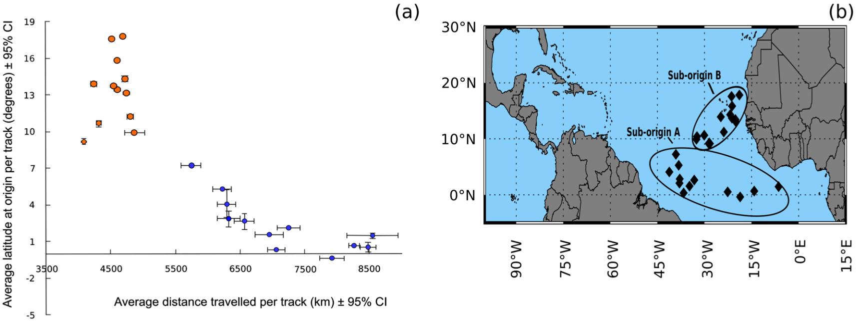

Figure 4. *Sargassum* sub-origins and transport pathway metrics within the Tropical Atlantic as determined from backtracking monthly *Sargassum* samples stranded in Barbados. Part (**a**) shows the average (±95% CI) distance travelled per track and the average (±95% CI) latitude of each origin for a given date. Blue dots indicate samples from sub-origin A and orange dots indicate samples from sub-origin B. Part (**b**) shows the two distinct sub-origins identified. Black square represents the average latitude at the origin of each track for a given date. Map was generated using IDL 8.8.1 (https://www.l3harrisgeospatial.com/Software-Technology/IDL). All backtracks started from the Morgan Lewis beach, located on the east coast of Barbados and were run over a 365-day period using 100 particles. All averages represent mean value of the 100 particles.

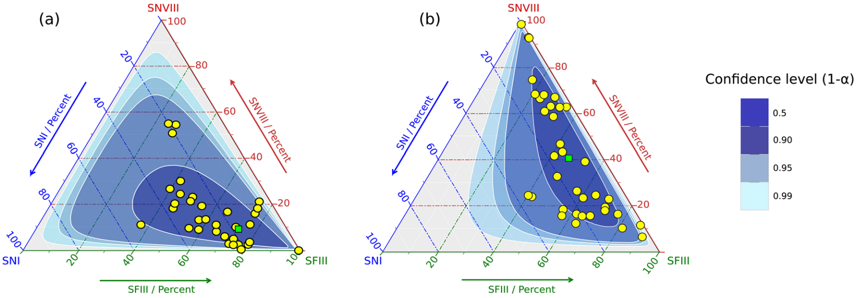

Figure 5. Ternary plots showing morphotype composition of *Sargassum* samples stranding in Barbados over a 12-month period. Part (**a**) shows *Sargassum* samples from sub-origin/transport pathway A (March–early August). Part (**b**) shows *Sargassum* samples from sub-origin/transport pathway B (late August–February). *Sargassum natans* I (SNI), *S. natans* VIII (SNVIII) and *S. fluitans* III (SFIII). Samples are represented by yellow dots and the mean value is represented by a green square.

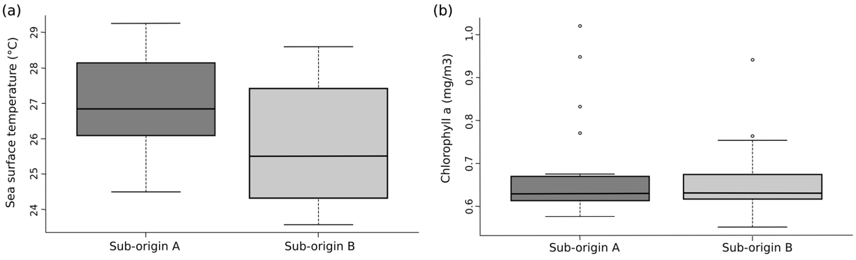

Figure 6. Boxplots of sea surface temperature (**a**) and chlorophyll a concentration (**b**) for sub-origin/transport pathway A and B (n = 48 in all groups).

February are likely to take the more northerly transport pathway (arriving from sub-origin B). This matches the seasonal distribution of *Sargassum* in the NERR as detected by satellites[13]. *Sargassum* arriving from sub-origin/transport pathway A were *S. fluitans* III-dominated while those arriving from sub-origin/transport pathway B had significantly higher amounts of *S. natans* VIII.

Interestingly, our monthly observations of relative abundance of the three *Sargassum* morphotypes aligns with morphotype compositions reported in the literature[39–41]. Starting with the November 2014 to May 2015 period[41], *S. natans* VIII was the predominant form observed across the Caribbean. This was especially interesting since no earlier studies had ever reported *S. natans* VIII-dominated mats throughout the region. Subsequent studies[39] in the Mexican Caribbean, also reported large volumes of *S. natans* VIII during the peak arrival of *Sargassum* in August 2015. In contrast, recent investigations into the morphotype composition arriving in Jamaica during July and August[40] showed a clear dominance of *S. fluitans* III. Based on the findings of our study, a possible explanation for the large-scale variations observed by Refs.[39–41] can be linked to the identified sub-origins/transport pathways. It is plausible that 2015 reports of *Sargassum*[39,41] recorded high amounts of *S. natans* VIII because the majority of their data collection took place during the late August-February (sub-origin/transport pathway B) period, which was associated with significantly higher abundances of *S. natans* VIII in our analyses. On the other hand, the 2020 summer report[40] of *Sargassum* influx events reported dominance of *S. fluitans* III; according to the findings of the current study *Sargassum* mats arriving during this time would have likely arrived from sub-origin/transport pathway A, which shows a significantly higher abundance of *S. fluitans* III.

While the presence of a southern sub-origin/transport pathway A and a northern sub-origin/transport pathway B provides a plausible explanation for the observed spatial and temporal variations in the relative abundances of *S. natans* I, *S. natans* VIII and *S. fluitans* III, the question remains: why are these sub-origins/transport pathways favouring different morphotypes? In Florida, the two *Sargassum* species are reported to have different maximum growth rates under optimal conditions, with *S. fluitans* apparently capable of growing considerably faster than *S. natans*[46]. The same study also indicated a difference in thermal tolerances between the two species, stating that *S. natans* has a broader optimal temperature range (18–30 °C) than *S. fluitans*. Furthermore, recent studies have also indicated similar differences in growth rates between species, as well as differences among morphotypes from the Tropical Atlantic[47]. Studies by Lapointe and colleagues comparing growth rates have also indicated that both pelagic species grow significantly faster with nutrient enrichment[5,48,49]. Therefore, given the two distinct sub-origins/transport pathways, oceanographic conditions between the two areas may have been the proximal cause for the observed morphotype compositions. Our analysis suggests that differing SST within sub-origins/transport pathways influenced the morphotype composition of *Sargassum* arriving in Barbados. *S. fluitans* III-dominated mats arriving from the southerly transport pathway A, close to the equator, experienced higher SST when compared to the northerly transport pathway B. Recent studies[12] indicate that *Sargassum* blooms are enhanced by nitrogen-rich neritic waters and that nutrient variability is a key driver of *Sargassum* variability[13]. In this study we used chlorophyll a concentration as a direct proxy for nutrient concentration. However, we found high variability in this proxy within each of the two sub-origins/transport pathways, which precluded a clear understanding of its possible role on morphotype composition. Moreover, it is possible that chlorophyll concentration per se might not be a good indicator of nutrient availability for *Sargassum*. The Equatorial Atlantic has a heterogenous surface environment with contributing nutrient-rich water masses from the Amazon River, the Congo River and equatorial and coastal upwelling[50,51]. Thus, mats originating close to the equator (sub-origin/transport pathway A) are likely to experience nutrient-rich environments in addition to higher SST than *Sargassum* from the more northerly sub-origin/transport pathway B, allowing *Sargassum* to flourish and perhaps amplifying physiological differences among morphotypes that result in differential growth and mortality and thus in different morphotype composition. However, discussions surrounding optimal growth conditions for the three morphotypes remain largely speculative and the extent to which the rate of nutrient uptake varies among morphotypes is not well understood. Interestingly, *S. natans* VIII and *S. fluitans* III collected from around 10° N showed different levels (albeit not significant) of %N enrichment; with *S. natans* VIII having higher %N on average than the other two morphotypes[12]. If *S. natans* VIII is indeed capable of absorbing nutrients faster than its counterparts above 10° N, valorisation of this morphotype may be affected. Low phosphate environments increase the uptake of arsenic[37], therefore, mats traversing low phosphate environments at and above 10° N may result in *S. natans* VIII absorbing higher levels of arsenic compared to *S. natans* I and *S. fluitans* III, ultimately reducing the applications for which *S. natans* VIII can be used. Intriguingly, biomass composition of *Sargassum* arriving in Jamaica during February 2019 had lower quantities of metals in *S. natans* VIII than *S. natans* I and *S. fluitans* III; but when looking at arsenic specifically, *S. natans* I and *S. natans* VIII on average contained higher levels of arsenic when compared to *S. fluitans* III[35]. Studies on growth and mortality of the three morphotypes in various conditions are required to understand their optimal conditions, the effects of source and dispersal routes on morphotype composition, biomass composition and the potential consequences for valorisation.

The observed seasonality *in S. fluitans* III and *S. natans* VIII may also influence the biodiversity associated with *Sargassum* mats at different times of the year. The greater structural complexity of *S. fluitans* III supports more organisms when compared to the less foliated *S. natans* VIII[3]. This means that *S. fluitans* III-dominated mats arriving from sub-origin/transport pathway A during March to early August may have greater biodiversity than mats arriving from sub-origin/transport pathway B (late August to February). With more innovative strides being made towards *Sargassum* valorisation[26], in-water harvesting may be the solution to providing large quantities of fresh *Sargassum* for a variety of uses. However, in-water harvesting may pose a threat to associated biodiversity especially during months where *S. fluitans* III is the dominant morphotype. To better understand the implication(s) of changing morphotype composition on *Sargassum* associated biodiversity and valorisation efforts, further research into the seasonality of *Sargassum* morphotypes is required. Studies should ideally be conducted across the Caribbean to provide a comprehensive understanding of the situation and aid in the region's continued adaptation to *Sargassum* influx events.

There are limitations to our study. As such generalizations within or across years or countries should not be made with only one year of data. We cannot say if the results of 2021–2022 reflect a typical year or if the findings were unique to Barbados given that it is one of the first islands to receive *Sargassum* from the NERR. As *Sargassum* travels from eastern to western countries across the Caribbean and experiences different environments, differential growth and mortality will undoubtedly play a role in *Sargassum* quantities and morphotype composition. A further potential limitation of this study arises from the simple classification of simulations into sub-origin/transport pathway A and B. This simple classification into two pathways points to resolvability of the complex problem of blooms; why now, why here, what are the dominant parameters that influence growth and mortality? Nevertheless, the findings of this study are relevant to the developing *Sargassum* industry by providing insights into the potential causes of variation in morphotype composition arriving in the Caribbean; and by extension provide a baseline for further studies on the predictability of seasonal patterns. The identification of the two sub-origins/transport pathways has implications for advancing the region's understanding of the factors responsible for the continued proliferation and extensive interannual variability of *Sargassum* in the Tropical Atlantic since the initial bloom in 2011.

Methods

Sample collection and sorting.

For each date of sampling effort, three clumps of newly beached, wet, "fresh gold" *Sargassum* were collected from Morgan Lewis beach, Barbados (13° 16′ 4.86″ N–59° 33′ 48.41″ W) (Fig. S3). Clumps (~ 0.27 kg each) were collected using both hands at approximately 10 m intervals along the shoreline. Using gross morphological features (following[52]), each of the three clumps was carefully separated into its component morphotypes, *Sargassum natans* I, *S. natans* VIII and *S. fluitans* III (Fig. 1). The displacement volume of each morphotype from each clump was then obtained using a measuring cylinder filled with a known volume of seawater. Sampling occurred opportunistically from February 2021 to March 2022, with at least one sample being collected each month. Sampling efforts resulted in 24 collection days over a 1-year period.

Backtracking of pelagic *Sargassum*.

Satellite tracked mix-layer drifters (drogue element at 15 m) from the Global Drifter Program (GDP)[53] have been deployed around the globe since ~ 1979. These drifters provide reliable tracking of water particles at drogue depth and are equipped with batteries that can last in excess of

450 days; however, loss of drogue is common. Using a Surface Velocity Program (SVP), data are provided on position, temperature and drogue on/off[54]. Current vector components are calculated at 6-h intervals from sequential positions and can be retrieved from https://www.aoml.noaa.gov/phod/gdp/. This study used a compiled file of the GDP data set consisting of: year, day, hour, longitude, latitude, east-current, west-current and drogue-on/drogue-off flag from 1979 to 2020. For tracking, the data were interpolated to a 1/12th degree resolution grid at 365 year-day intervals. The exact steps taken to achieve this dataset can be found in Ref.[43].

To determine potential origins of the sampled *Sargassum*, each of the 24 collection days were backtracked using IDL 8.8.1 programming software (https://www.l3harris.com/all-capabilities/idl). Using a simple backtracking algorithm based on the drifter data set and 0.5% windage, *Sargassum* was tracked back 365 days from collection points on Morgan Lewis beach to determine the origin of each sample within the Tropical Atlantic. The selected 365-day time for backtracking was based on an experiment that assessed the dispersion of *Sargassum* from the NERR (Fig. S4). Our results showed that approximately 90% of the *Sargassum* population within the NERR is dispersed within 365 days. Recent studies[44] also found that *Sargassum* present in the NERR has a high probability of entering the Caribbean within a year's time.

Backtracks were simulated using 100 particles launched simultaneously from the collection location at Morgan Lewis beach, applying sub grid-scale turbulent motions (Lagrangian Stochastic Model[55]) to each particle's current component:

$$\mathrm{u}' = \mathrm{u} + 0.1 \times \text{ current speed } \times \mathrm{P}(1) \tag{1}$$

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. This simple turbulence addition to each of the east–west (u) and north–south (v) current components acknowledges that the gridded current database is smoother than reality. End points of each particle's back-trajectory were obtained by center-of-mass calculations of the 100 ending locations.

The tracking methodology used in this study was developed by Ref.[43] and is currently used to obtain 3-month *Sargassum* forecasts for the Lesser Antilles, published in the Sargassum Sub-Regional Outlook Bulletin (https://www.cavehill.uwi.edu/cermes/projects/sargassum/outlook-bulletin.aspx). Forecasts from the Outlook bulletin are well suited for monitoring *Sargassum* within the Lesser Antilles and are in close agreement with observed influxes[56].

Data analysis. Monthly changes in relative abundance of *Sargassum* morphotypes (volume of morphotype/total volume of *Sargassum* sample) were calculated by averaging compositional sample data first by date (if multiple *Sargassum* samples were collected the same date) and then by month (if multiple dates were sampled within the same month). Differences in relative abundance of *Sargassum* morphotypes between the two sub-origins were tested using a PERMANOVA with the sample compositional data (transformed into a bivariate matrix following[57] to address non-independence of the three percent estimates) as response matrix and sub-origin as independent factor, while implementing a constrained nested permutation scheme with sample data nested within dates and dates serving as independent statistical replicates for each sub-origin. This test was conducted using the adonis function of the "vegan" package in R[58,59]. Data were also checked for homogeneity of dispersion using the betadisper function of the same package (Table S1). Given that *Sargassum* compositional samples involved three morphotypes, we used ternary plots to display these data; these plots were produced using the "ggplot2", "ggtern", "ggpubr", and "lattice" packages in R[59–63].

Environmental data were retrieved using Giovanni (https://giovanni.gsfc.nasa.gov/giovanni/) time-series area-average oceanic data. The data sources were Sea Surface Temperature at 4 microns (Night) 8-daily 4 km (MODIS-Aqua) and Chlorophyll a concentration 8-daily 4 km (MODIS-Aqua MODISA_L3m_CHL_8d_4km). These data were retrieved for each collection date for (1) the location and time of origin (i.e., 365 backtracked days; 1 year) and the location and time of the mid-point (183 backtracked days; 6 months). For example, when assessing the initial SST conditions at time of origin for a sample collected on the 10th of January 2022 in Barbados, we used the 8-day SST average data from the closest available time intervals the year before (i.e., January 2021) at the estimated point of origin. To do this, a box of approximately 93,500 sq km was drawn centred around the point of origin. Then, the SST 8-day average for the entire box area was downloaded. To test for differences in SST and chlorophyll a between sub-origins a PERMANOVA test using SST and chlorophyll as response bivariate matrix data and time period (initial vs mid-way point) and sub-origin location (A vs B) (and their interaction) as independent factors. This test was also conducted using the adonis function of the "vegan" package in R[58,59]. Chlorophyll a data were square-root transformed to minimize the effect of extreme values. The significance level of 0.05 was used for all analyses.

Data availability

All data generated or analysed during this study are included in this published article [and its Supplementary Information files].

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Author contributions

K.A., H.O. and F.N. conceived the project. K.A. collected the *Sargassum* compositional data and wrote the first draft. K.A. and D.J. generated the *Sargassum* backtrack data. K.A. and. H.V. analysed and interpreted the data. All authors contributed to the writing of the article and approved the submitted version.

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Competing interests

The authors declare no competing interests.

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Correspondence and requests for materials should be addressed to K.S.T.A.

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An analysis of arsenic concentrations associated with sargassum influx events in Barbados

Kristie S.T. Alleyne[a,*], Francis Neat[a], Hazel A. Oxenford[b]

[a] World Maritime University, Sasakawa Global Ocean Institute, P.O. Box 500, SE 201 24 Malmö, Sweden
[b] Centre for Resource Management and Environmental Studies, Cave Hill Campus, University of the West Indies, Bridgetown BB11000, Barbados

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ABSTRACT

Tropical Atlantic blooms of pelagic *Sargassum* spp. present major socioeconomic and ecological challenges for Caribbean and West African nations. Valorisation of sargassum provides an opportunity to ameliorate some of the damage to national economies; however, the active uptake of arsenic by pelagic sargassum creates significant barriers to its use. When defining valorisation pathways, it is important to understand arsenic speciation in pelagic sargassum, given the different levels of toxicity associated with different arsenic species. In this study, we assess the temporal variability of total arsenic and inorganic arsenic in pelagic sargassum arriving in Barbados; and test whether arsenic concentrations are linked to oceanic sub-origins. Results indicate that inorganic arsenic, the most toxic form, represents a consistent and substantial percentage of the total arsenic present in pelagic sargassum, and that variability in arsenic concentration does not appear to be driven by sample months, years or oceanic sub-origins/transport pathways.

1. Introduction

Tropical Atlantic blooms of pelagic *Sargassum* spp. (*Sargassum natans* and *S. fluitans*), hereafter referred to as 'sargassum', result in sargassum influx events with extraordinary levels of sargassum biomass appearing along the coasts of Caribbean and West African countries (Chávez et al., 2020; León-Pérez et al., 2021; United Nations Environment Programme, 2018; Wang et al., 2019). These unparalleled proliferations present major threats to fisheries (Oxenford et al., 2019; Ramlogan et al., 2017; Speede et al., 2018), tourism (Bartlett and Elmer, 2021; Chávez et al., 2020; Engel, 2018), coastal ecosystems (Engel, 2018; Maurer et al., 2015, 2022; Rodríguez-Martínez et al., 2019; van Tussenbroek et al., 2017) and public health (Resiere et al., 2018, 2021). Franks et al. (2016) identified the North Equatorial Recirculation Region (NERR) as the source of these sargassum influx events; with ocean eutrophication and climate change being driving factors (Johns et al., 2020; Lapointe et al., 2021; Skliris et al., 2022). Influx events are episodic in nature, with quantities varying from year to year (United Nations Environment Programme – Caribbean Environment Programme, 2021); however, yearly mass proliferations form what is now known as the Great Atlantic Sargassum Belt (GASB) with extensive quantities of sargassum biomass extending from West Africa to the Gulf of Mexico (Wang et al., 2019). Recurrent blooms in the Tropical Atlantic are expected to continue into the foreseeable future (Desrochers et al., 2022; Wang et al., 2019); thus, countries affected by sargassum influx events must adapt.

In an effort to turn a 'threat' into opportunities, research on biochemical and elemental characteristics of sargassum originating from the NERR has been undertaken (e.g., Botelho Machado et al., 2022; Cipolloni et al., 2022; Davis et al., 2020; Devault et al., 2021, 2022; Gobert et al., 2022; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020) to help identify potential valorisation pathways. Differences in biochemical and elemental composition among the three prevalent morphotypes (*Sargassum natans* I, *S. natans* VIII, and *S. fluitans* III; Cipolloni et al., 2022; Davis et al., 2020; Gobert et al., 2022) suggest that morphotypes may be more or less suited for specific applications. In an effort to defray the costs associated with shoreline strandings and clean-ups (Chávez et al., 2020; Oxenford et al., 2021) researchers and entrepreneurs are working arduously to find innovative business ideas (Desrochers et al., 2022). Potential uses within the Caribbean have been identified for 15 different sectors (Desrochers et al., 2022); however, reports of the high arsenic content associated with pelagic sargassum (Davis et al., 2020; Devault et al., 2021, 2022) raise concern for applications involving direct consumption of lightly or unprocessed biomass (Oxenford et al., 2021; Tonon et al., 2022; Gobert

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[*] Corresponding author.
E-mail address: w2005361@wmu.se (K.S.T. Alleyne).

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et al., 2022).

Pelagic sargassum, like many other brown seaweeds, bioaccumulate micropollutants (e.g., trace metals) from their surroundings (Barquilha et al., 2019; Devault et al., 2022; Saldarriaga-Hernandez et al., 2020). Among the different trace metals and metalloids, arsenic is of particular concern due to its notorious toxicity (Devault et al., 2021, 2022). Arsenic is ubiquitous in the environment, naturally occurring in various inorganic (toxic) and organic (low or non-toxic) states (Devault et al., 2021). Inorganic forms of arsenic, namely trivalent arsenite (AsIII) and pentavalent arsenate (AsV) are highly toxic and found naturally in anoxic and aerobic environments respectively (Agency for Toxic Substances and Disease Registry [ATSDR], 2007; Devault et al., 2021). The active uptake of inorganic arsenic by pelagic sargassum results in high concentrations within the cell walls and cell membranes (Gobert et al., 2022) and presents significant barriers for valorisation given that inorganic arsenic exposure can have serious dermal, cardiovascular, respiratory, gastrointestinal, and neurological effects on humans (Agency for Toxic Substances and Disease Registry [ATSDR], 2007).

The exploitation of pelagic sargassum and creation of sargassum businesses requires thorough knowledge of biomass composition (Davis et al., 2020) especially concerning arsenic. To date, there is significant variation among studies reporting arsenic concentrations, with total arsenic levels varying from 5 to 231 mg kg^{-1} (dry weight) of sargassum biomass (Bam et al., 2022; Cipolloni et al., 2022; Davis et al., 2020; Devault et al., 2021, 2022; Gobert et al., 2022; López-Contreras et al., 2021; Milledge et al., 2020; Nielsen et al., 2021; Vázquez-Delfín et al., 2021) across the Caribbean. Many reports on arsenic concentrations in sargassum from the Tropical Atlantic exceed the maximum levels authorized for agricultural soil (20 mg kg^{-1} dry weight) and fertilizers (40 mg kg^{-1} dry weight) (Desrochers et al., 2022; European Union, 2019b; Rahaman et al., 2013). Moreover, reports on arsenic have largely focused on total arsenic content (Bam et al., 2022; Cipolloni et al., 2022; Davis et al., 2020; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020) with very few studies (Devault et al., 2022; Gobert et al., 2022; López-Contreras et al., 2021) providing information on levels of the highly toxic inorganic arsenic. With feed businesses limited to a recommended maximum value of 2 mg kg^{-1} of feed for inorganic arsenic (European Union, 2019a) and required to provide the ratio of inorganic arsenic to total arsenic (European Union, 2022); it is important to understand the arsenic 'speciation' (different forms) in pelagic sargassum when determining valorisation pathways, especially those linked to consumptive and contact uses.

In this study, we assess the temporal variability of total arsenic (As_t) and inorganic arsenic (As_i) in pelagic sargassum arriving in Barbados. Observed variations are compared with transport pathways to determine the effect (if any) of the route travelled on arsenic concentrations. We hypothesize that arsenic variation will be linked to sub-origins/transport pathways within the Tropical Atlantic. Barbados is one of the first islands to receive sargassum from the Tropical Atlantic and being positioned east of the island chain it receives sargassum directly from the open ocean making it an ideal place to examine variation in arsenic concentration of sargassum entering the Caribbean Sea. The assessment of As_t and As_i in this study will add important knowledge towards understanding one of the key constraints to valorisation of sargassum, and will provide essential baseline data for sargassum management and the potential for turning the threat into economic opportunities in Barbados.

2. Methods

2.1. Sample collection

Wet 'fresh gold' pelagic sargassum was collected from Consett Bay (13°10′47″N 59°27′57″W) and Morgan Lewis beach (13°16′4.86″N 59°33′48.41″W) Barbados during 2021 and 2022. Mixed samples (*Sargassum natans* I, *S. natans* VIII and *S. fluitans* III) of sargassum were collected in-water, within 40 m of the shoreline. Immediately after collection, sargassum was placed on ice and transported to the laboratory where it was rinsed with tap water, packaged into polypropylene vials (of similar weight (~30 g)) and frozen at −80 °C. A total of 23 frozen samples were subsequently shipped (on ice) to Brooks Applied Labs (BAL) in Washington for the analyses of total recoverable arsenic (As_t) and inorganic arsenic (As_i) (the sum of AsIII and AsV).

Fresh samples sent for analyses were assessed 'as received' resulting in arsenic concentration per wet weight (ww). Estimates of arsenic concentration per dry weight (dw) were obtained following (Warburton and Seagarst, 1993; Agriculture & food Systems Institute [AFSI], 2023). An average moisture percentage value of 82 %, reported in previous analyses (Milledge et al., 2020; Tonon et al., 2022) for mixed pelagic sargassum species samples, was applied to the below equation.

$$\textit{Dry weight conc.} = \frac{\textit{wet weight conc.}}{1 - \left(\frac{\textit{moisture\%}}{100}\right)}$$

2.2. Arsenic analyses

2.2.1. Total arsenic quantitation by ICP-QQQ-MS

Once thawed, the samples were homogenized using pre-cleaned commercial grade homogenization equipment. A known mass of each sample homogenate was weighed into a microwave digestion vessel, and then aliquots of concentrated hydrogen peroxide and nitric acid were added to all samples and prepared for quality control. All vessels were sealed and then digested at elevated temperature and pressure in a laboratory microwave system. All resulting digests were diluted to a known final volume and then analysed for As_t content via inductively coupled plasma triple quadrupole mass spectrometry (ICP-QQQ-MS). The ICP-QQQ-MS uses advanced interference removal techniques, including multiple collision/reaction gases, to ensure accuracy of the sample results.

2.2.2. Arsenic speciation quantitation by IC-ICP-CRC-MS

Each sample for As_i quantitation was prepared via a modified ISO EN 16802:2016. In summary, a known mass of each sample homogenate was extracted using dilute nitric acid and hydrogen peroxide on a hot block apparatus. All resulting extracts were then analysed for arsenic species using Ion Chromatography Inductively Coupled Plasma Collision Reaction Cell Mass Spectrometry (IC-ICP-CRC-MS). For total As_t and As_i content, values for the Method Detection Limit (MDL) of wet samples were approximately 4.5 μg/kg and 1.0 μg/kg respectively. Values for each sample were adjusted to account for the exact mass of sample prepared and all dilutions applied during the analysis.

2.3. Backtracks

To determine the potential origins of the sampled sargassum, each of the 23 collection days were backtracked 365 days from collection points in Barbados. Following Alleyne et al. (2023), a compiled file from the 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 was used to produce the backtracks. Within IDL 8.8.1 programming software a windage component of 0.5 % was applied to the drifter data set. Each track was simulated using 100 particles launched simultaneously from the collection location applying subgrid-scale turbulent motions (Lagrangian Stochastic Model) to each particle's current component:

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

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. The exact steps taken to achieve backtracks are described by Alleyne et al. (2023).

2.4. Statistical analyses

To investigate drivers of differences in arsenic concentration, a Permutational Multivariate Analysis of Variance (PERMANOVA) test using As_t and As_i as response bivariate matrix data and sub-origin location (A vs B), year (2021 vs 2022), and month as independent factors was conducted using the adonis function of the "vegan" package in R (Oksanen et al., 2018; R Core Team, 2022).

Phosphate data were retrieved from Copernicus Marine Service (CMS) (doi:10.48670/moi-00015). Phosphate maps representing monthly mean concentrations (mmol/m^3) of phosphate in sea surface water were generated from the 'global-analysis-forecast-bio-001-028-monthly' dataset and the area of interest (N: 32.97, S: −7.94, E: 12.56, W: −103.92) was selected using a bounding box. Generated maps were imported into ArcMap 10.8.2 and overlayed with backtracks.

3. Results

A total of 23 sargassum samples were collected between 2021 (May, July, August) and 2022 (February–June) (Table 1). Across samples, As_i was highly positively correlated with As_t ($r_s = 0.97$, $p < 0.001$) (Fig. 1a) and accounted for up to 62 % of the As_t content (Table 1). On average, pelagic sargassum arriving in Barbados contained As_t and As_i concentrations of 9.0 μg g^{-1} (wet weight) and 5.0 μg g^{-1} (wet weight) respectively (Fig. 1b). Considerable variation was observed in As_t (2.3–17.8 μg g^{-1} wet weight) and As_i (0.3–11.3 μg g^{-1} wet weight) concentrations with July being particularly low compared to other months.

Despite the observed variation, a PERMANOVA indicated that there was no significant difference in As_t or As_i concentrations of pelagic sargassum collected across years (Pseudo-F = 1.248, $p = 0.265$) (Fig. 1c) or months (Pseudo-F = 1.332, $p = 0.316$) (Fig. 1d).

The extent to which the observed variation in arsenic concentration reflected distinct origins, was investigated with the use of backtracking. Backtracks separated into two putative sub-origins/transport pathways within the NERR. Samples collected between March and early August ($n = 16$) originated close to the equator (0–7°N) and travelled a somewhat circuitous route along northeast Brazil before arriving in Barbados (hereafter referred to as sub-origin/transport pathway A) (Fig. 2a). Samples collected between late August and February ($n = 7$) originated further north (10–15°N) and travelled a relatively direct westerly route to Barbados (hereafter referred to as sub-origin/transport pathway B) (Fig. 2b). Sub-origins/transport pathways align with and are named after those identified in Alleyne et al. (2023).

We investigated whether phosphate conditions, derived from satellite imagery, differed between the two sub-origins/transport pathways for specific dates. In the absence of any significant effect of collection year on arsenic concentration, the data were pooled across the two years. Maps of average phosphate concentrations for March-early August (2021/03/01–2021/08/09) and late August–February (2021/08/10–2022/02/28) were used to visualise phosphate levels likely to have been experienced by sargassum from sub-origin/transport pathway A and sub-origin/transport pathway B respectively. Overlays of backtracks on phosphate maps show that sargassum originating in sub-origin/transport pathway A is likely to have been exposed to slightly higher concentrations of phosphate across its transport pathway compared to sargassum originating from sub-origin/transport pathway B (Fig. 2). However, a PERMANOVA indicated that arsenic concentrations of pelagic sargassum arriving from sub-origin/transport pathway A did not differ from those originating from sub-origin/transport pathway B (Pseudo-F = 0.121, $p = 0.754$).

4. Discussion

Efforts to valorise the massive quantities of pelagic sargassum originating in the Tropical Atlantic continue to be hindered by reports of arsenic contamination (Milledge et al., 2020; Oxenford et al., 2021; Tonon et al., 2022). Here we present baseline data on As_t and As_i concentrations in pelagic sargassum arriving in Barbados. Acknowledging that industrial processes utilising large volumes of sargassum are unlikely to sort/distinguish among species/morphotypes unless returns on investment are large enough to cover the effort required (Tonon et al., 2022); this study assessed As_t and As_i concentrations in samples from mixed sargassum rafts. On average, As_t concentrations (49.8 ± 21.1 μg g^{-1}dw: mean ± standard deviation) reported in this study were at the low end of the general range (5–231 mg kg^{-1} dw) reported in the literature (Bam et al., 2022; Cipolloni et al., 2022; Davis et al., 2020; Devault et al., 2022; Gobert et al., 2022; López-Contreras et al., 2021; Milledge et al., 2020; Nielsen et al., 2021; Vázquez-Delfín et al., 2021). For example in Mexico the reported range is 24–172 μg g^{-1}dw (Alzate-Gaviria et al., 2021; López-Contreras et al., 2021; Rodríguez-Martínez et al., 2020; Tonon et al., 2022), in Jamaica it is 56.03–91.95 μg g^{-1}dw (Davis et al., 2020; Tonon et al., 2022), in Turks and Caicos it is 20.94–123.69 μg g^{-1}dw (Milledge et al., 2020; Nielsen et al., 2021; Tonon et al., 2022), in Bonaire it is 74–89 μg g^{-1} dw (López-Contreras et al., 2021) and in Antigua and Barbuda it is 170 μg g^{-1} dw (Bam et al., 2022). Contrastingly, As_i concentrations (27.8 ± 15.1 μg g^{-1}dw: mean ± standard deviation) reported here were similar to or higher than those observed in the Dutch (18–99 μg g^{-1}dw) and French Caribbean (41.8 ± 25.2 μg g^{-1}dw for AsV and 3.8 ± 5.2 μg g^{-1}dw for AsIII) (Devault et al., 2022; López-Contreras et al., 2021). It should be noted, however, that dry weight concentrations provided in this study are estimates based on wet weight conversions using 82 % moisture content and therefore lack exact comparability with previous studies.

Arsenic toxicity varies with its oxidation state. Inorganic 'species' (arsenite (AsIII) and arsenate (AsV)) are highly toxic whilst organic 'species' (organoarsenic, methylarsonic acid (MMS), dimethylarsinic acid (DMA)) are not particularly harmful (Agency for Toxic Substances and Disease Registry (ATSDR), 2007; Devault et al., 2022). Reports on As_t concentrations (Bam et al., 2022; Cipolloni et al., 2022; Davis et al., 2020; Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020) associated with Tropical Atlantic sargassum blooms have so

Table 1

Arsenic concentrations (mean ± SD) in mixed samples of pelagic sargassum. Concentrations are expressed as μg g^{-1} for wet weights (ww) and dry weights (dw). The symbol (*) indicates that only a single collection occurred.

Month	Number of samples	Year	Total arsenic (ww)	Inorganic arsenic (ww)	Total arsenic (estimated dw)	Inorganic arsenic (estimated dw)	% of inorganic arsenic
Feb	3	2022	8.66 ± 4.56	5.40 ± 3.19	48.11 ± 25.34	30.0 ± 17.75	62.4
March	4	2022	10.47 ± 4.36	5.78 ± 3.19	58.14 ± 24.24	32.1 ± 17.1	55.2
April	4	2022	8.27 ± 2.17	4.63 ± 1.58	45.96 ± 12.07	25.7 ± 8.76	56.0
May	2	2022	8.04 ± 0.45	4.90 ± 0.66	44.67 ± 2.51	27.2 ± 3.65	60.9
May	1	2021	12.30*	7.22*	68.33*	40.1*	58.7*
June	3	2022	11.61 ± 5.46	6.77 ± 4.05	64.50 ± 30.33	37.6 ± 22.48	58.3
July	2	2021	3.30 ± 1.46	1.41 ± 0.73	18.31 ± 8.13	7.8 ± 4.05	42.6
August	4	2021	8.85 ± 3.28	4.42 ± 2.88	49.17 ± 18.21	24.6 ± 16.00	50.0

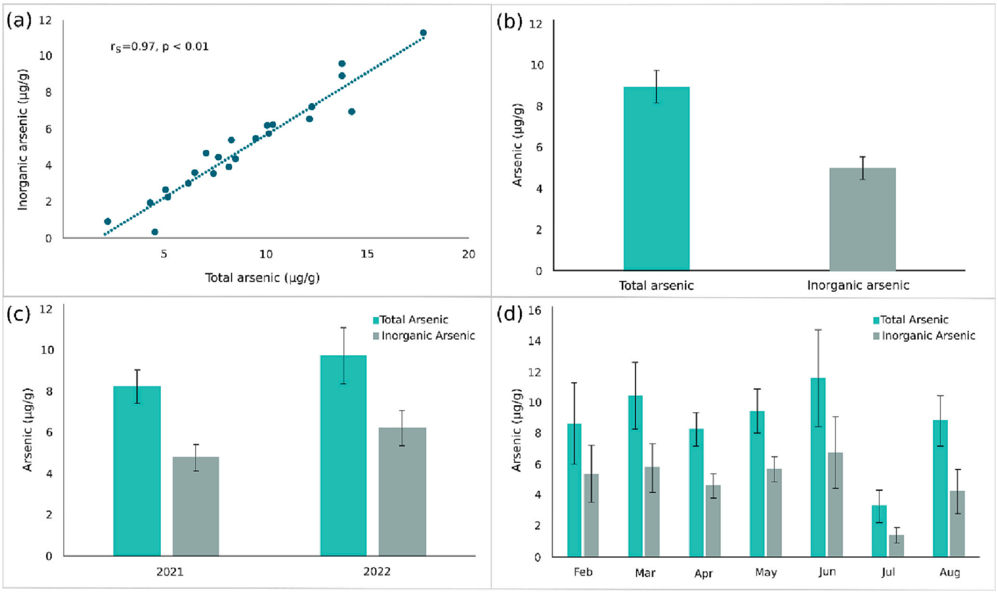

Fig. 1. Variation in total arsenic (As_t) and inorganic arsenic (As_i) concentrations (µg g^{-1} wet weight) of pelagic sargassum arriving in Barbados. Scatter plot showing the relationship between As_t and As_i (Panel a). Spearman rank correlation coefficient and associated *p*-values are also shown in Panel (a) and a best fit line was inserted to help interpret the trend. Bar charts showing average As_t and As_i concentrations (b), average As_t and As_i concentration by year (c) and average As_t and As_i concentration by month (d). All error bars represent standard error (SE).

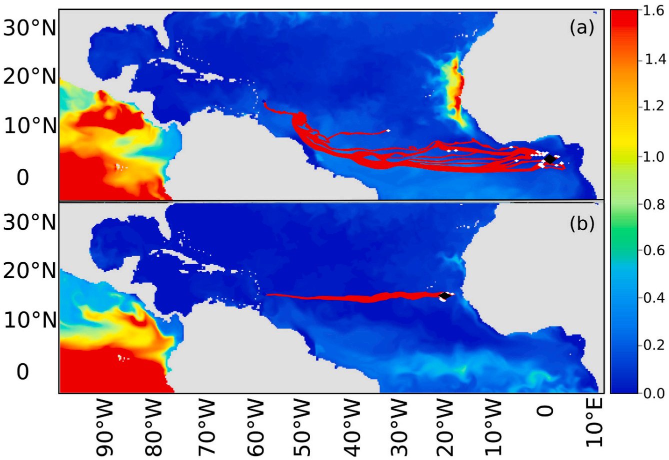

Fig. 2. Backtracks of pelagic sargassum collected in Barbados overlayed on phosphate (mmol/m^3) maps retrieved from Copernicus Marine Service (CMS) (doi:10.48670/moi-00015). Panel (a) represents sample backtracks that originate close to the equator and travel along northeast Brazil before arriving in Barbados; origin/transport pathway A. The map displayed in Panel (a) shows average phosphate concentrations for March-early August (2021/03/01–2021/08/09). Panel (b) represents backtracks that originate further north and travelled a relatively direct westerly route to Barbados; sub-origin/transport pathway B. The map displayed in Panel (b) shows average phosphate concentrations for late August–February (2021/08/10–2022/02/28). 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 in Barbados) and the black square represents the origin of highest probability (mean of all backtrack particles).

far provided invaluable information on the potential dangers associated with arsenic that has helped to shape a precautionary approach to sargassum management and valorisation to date. However, the ratio of organic vs. inorganic arsenic must be understood to better determine the actual potential toxicity and thus help advance beyond current precautionary use for products linked to consumption and contact.

The principal chemical form of As in surface waters of the temperate and tropical North Atlantic is inorganic pentavalent arsenate (AsO_4^{3-}), which is known to be taken up by microbial communities (phytoplankton) in phosphorous-limited oligotrophic ocean water masses

(Wurl et al., 2015). Similarly, Gobert et al. (2022) report that arsenic uptake by pelagic sargassum appears to be linked to (negatively correlated with) availability of phosphate, with pelagic sargassum taking up high levels of the inorganic pentavalent arsenate ion (AsO_4^{3-}) in phosphorous-limited waters due to its similarity in size and geometry to the phosphate ion (PO_4^{3-}). Previous reports indicate that As_i can account for as much as 76.2 % (Devault et al., 2022) and 50 % (Gobert et al., 2022) of As_t concentrations. Similarly, our results show that As_i represents a substantial percentage (up to 62.4 %) of the As_t in pelagic sargassum. Furthermore, the concentration of As_i in our study is highly correlated with the As_t concentration, with an overall mean of 49.8 (±21.1) μg g^{-1}dw of As_t corresponding to a mean As_i concentration of 27.8 ± 15.1 μg g^{-1}dw. This has implications for future analyses of arsenic, suggesting that there is no need to routinely test sargassum samples for inorganic arsenic, thus reducing the cost. Moreover, only 17 % of samples ($n = 23$) exceeded regulations set by the EU (40 μg g^{-1}dw) for the allowable level of As_i in organic fertilizers (European Union, 2019b), suggesting potential for developing fertilizers at least partially based on sargassum. However, with 22 out of the 23 samples exceeding the maximum (20 mg kg^{-1} dw) level of arsenic authorized for agricultural soil (Desrochers et al., 2022; Rahaman et al., 2013); the use of sargassum based fertilizers requires a precautionary approach. As_i concentrations in all of our samples exceeded the maximum limits (2 mg kg^{-1} (12 % moisture)) for seaweed-based animal feed material (European Union, 2002, 2019a) as well as limits set for cereals and rice based products for human consumption (European Union, 2015, 2023).

Previous reports of variation in arsenic concentrations in pelagic sargassum indicate elevated levels during the rainy season (Ortega-Flores et al., 2022) and differences among locations at several spatial scales (e.g., López-Contreras et al., 2021; Tonon et al., 2022; Bam et al., 2022; Gobert et al., 2022). These findings suggest that arsenic uptake by pelagic sargassum in the Caribbean is likely a function of local and/or regional hydrographic parameters which may vary over time (Bam et al., 2022) including, but perhaps not limited to, the availability of phosphates. To better understand the factor(s) influencing arsenic uptake, we first compared samples collected at different times of the year (Feb–Aug) and within different years (2021 and 2022). Our results suggest that there is no significant difference in As_t or As_i among sampling months or between years for sargassum arriving in Barbados. Given the influence of phosphate availability on arsenic concentration, we then assessed the effect of oceanic sub-origin on arsenic contamination. Pelagic sargassum affecting the Caribbean originates from two putative pathways within the NERR (Alleyne et al., 2023; Beron-Vera et al., 2022; Skliris et al., 2022) that are exposed to differing levels of nutrients (Oviatt et al., 2019). Sub-origins identified in this study align with those identified in Alleyne et al. (2023). Given that samples originating close to the equator (Sub-origin A) are likely to traverse what are generally accepted as relatively high phosphate water masses stemming from Amazon River outflows as well as equatorial and coastal upwelling areas (Djakouré et al., 2017; Oviatt et al., 2019; Skliris et al., 2022); we postulated that lower levels of arsenic would be associated with sargassum from sub-origin A compared to sub-origin B that has a transport pathway located further away from direct nutrient inputs. However, we found no significant difference in As_t or As_i between the two sub-origins/transport pathways. Whilst this was not initially expected, it is clear from the visualised phosphate maps that there is a marked temporal difference in the generally accepted areas of higher nutrient concentrations in the Tropical Atlantic. As such, the appearance of high nutrient concentrations, especially in the upwelling areas of West Africa (Fig. 2a) and the equator (Fig. 2b) did not coincide with either of the two sub-origins/transport pathways. Furthermore, the expected higher phosphate levels in the Amazon plume were not apparent. As such, sargassum from both sub-origins/transport pathways, observed during the 2021–2022 period, appear to have been exposed to similar phosphate concentrations at the low end of the spectrum albeit slightly higher phosphate concentrations for sub-origin/transport pathway B. It is therefore not surprising that our results showed no apparent effect of phosphate concentrations on arsenic levels between origins, although limited sample sizes from sub-origin A ($n = 16$) and sub-origin B ($n = 7$) may have precluded a clear understanding of the effect of oceanic origins on arsenic concentration. Furthermore, it is important to acknowledge limitations of the backtracking methodology. This study used satellite-tracked drifter data from 1979 to 2020 to understand the probable transport pathways of the 23 samples, based on ocean circulation dynamics of the Equatorial Atlantic. Using a climatology of ocean and wind conditions, the drifter dataset provides the likely transport pathways of sargassum for a given day of the year. However, the occurrence of tropical storms, or shifts in currents that differ among years, has the potential to influence the trajectory and distribution of pelagic sargassum (Putman and Hu, 2022; Sosa-Gutierrez et al., 2022). Without accounting for such occurrences, it is plausible that tracks allocated to sub-origin A/B may not reflect the actual pathway taken; thus, limiting our understanding on the effect of sub-origins/transport pathways on arsenic concentration.

Valorisation of pelagic sargassum will be integral to the Caribbean region's ability to adapt to the continuing mass influxes, and arsenic contamination remains a primary concern for valorisation (Milledge et al., 2020; Oxenford et al., 2021; Tonon et al., 2022). The findings of this study contribute to the growing body of knowledge regarding trace metal contamination of pelagic sargassum and confirm the uncertainties surrounding the variation in arsenic concentrations over time. Whether the region can effectively and safely utilise the high amounts of minerals and bioactive compounds found in pelagic sargassum (e.g. Milledge et al., 2020; Nielsen et al., 2021; Rodríguez-Martínez et al., 2020) over the long term remains an important unanswered question. Whilst significant contaminant dilution could be achieved through mixing sargassum with other biomass to produce high-quality fertilizers (Sembera et al., 2017), and animal feeds, arsenic could still accumulate and reach unsafe levels with sustained applications. In Bonaire, efforts to utilise pelagic sargassum as a fertilizer resulted in elevated arsenic concentrations in both the produce and soil (Dutch Caribbean Nature Alliance [DCNA], 2022). Pre-treatment of sargassum to detoxify inorganic arsenic may offer a solution for consumptive uses. A sequential pre-treatment procedure involving hot water, citric acid and fermentation has recently been reported to effectively reduce arsenic concentrations in *Sargassum fusiforme* for human consumption (Wang et al., 2022), but is unlikely to be cost effective in this region. Forging ahead, resolution of the complexities surrounding arsenic contamination and valorisation will likely require long term assessments, effective arsenic mitigation strategies and the development of regional safety standards for sargassum-based products.

CRediT authorship contribution statement

KA and HO conceptualized the work. KA conducted the fieldwork and analysed 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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