

Assessing growth of pelagic sargassum in the Tropical Atlantic

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ABSTRACT

Pelagic sargassum species, historically endemic to the North Atlantic, have now been identified in the Tropical Atlantic. For over a decade, massive blooms of pelagic sargassum have dispersed seasonally from this 'new' Tropical Atlantic source region, negatively impacting the coasts of Caribbean and West African countries. Significant strides have been made towards adaptation to this new 'hazard', yet many knowledge gaps remain that constrain improvements to these efforts. The key objective of this study was to add to the knowledge of pelagic sargassum growth rates in the Tropical Atlantic to better inform forecasting and innovative applications. Growth rates of the three commonly occurring morphotypes from the Tropical Atlantic source region, *S. fluitans* III, *S. natans* I and *S. natans* VIII, were studied *in-situ* using novel 'growth mesocosms' in neritic waters of Barbados under cool and warm ambient conditions. Overall, results reveal a significant difference in growth rates among all pelagic sargassum morphotypes, with *S. fluitans* III on average doubling its biomass in 13 days, *S. natans* I in 22 days and *S. natans* VIII in 31 days. Furthermore, growth rates of *S. fluitans* III decreased significantly with an increase in ambient temperature from the cool (mean 27.6 °C) to warm (mean 29.6 °C) water period. During both periods *S. fluitans* III grew significantly faster than the other two morphotypes. However, *S. natans* I only grew significantly faster than its conspecific morphotype, *S. natans* VIII, during the cool period. These findings highlight the different growth responses among sargassum morphotypes under varying conditions and add to the considerable variability in growth rates reported by recent similar studies conducted elsewhere in the Tropical Atlantic. As such, it is clear that further research will be needed to unravel the complex mechanisms affecting pelagic sargassum growth rates before they can confidently inform improvements in management applications.

1. Introduction

1.1. Pelagic sargassum source regions

Sargassum is a genus of brown algae of the family Sargassaceae which contains approximately 361 taxonomically accepted species (Godínez-Ortega et al., 2021). The majority of species are benthic, however two species *Sargassum natans* and *Sargassum fluitans*, hereafter collectively referred to as 'pelagic sargassum' or simply 'sargassum', are uniquely holopelagic spending their entire life history floating on the ocean's surface (Schell et al., 2015). While historically considered endemic to the Sargasso Sea (North Atlantic Ocean) (Godínez-Ortega et al., 2021), in 2011 satellite imagery revealed pelagic sargassum blooming and accumulating across the equatorial Atlantic, representing a new source region within the Tropical Atlantic termed the 'North Equatorial Recirculation Region' (NERR) (Franks et al., 2016). For over a decade Caribbean and West African countries have continued to

grapple with the socio-economic and ecological consequences brought about by repeated coastal inundations of massive quantities of pelagic sargassum transported from the Tropical Atlantic NERR.

1.2. Pelagic sargassum taxonomy and growth

Early taxonomic work by Parr (1939) described a total of six pelagic sargassum morphotypes based on differences in morphological characteristics, however only three: *S. fluitans* III, *S. natans* I and *S. natans* VIII regularly occur in the North Atlantic and Tropical Atlantic (Godínez-Ortega et al., 2021). Recent studies using mitochondrial gene markers (cox2, cox3, nad6 and mt16S rRNA) have revealed interspecific genetic distinctions between *S. natans* and *S. fluitans*, and an intraspecific distinction between *S. natans* I and *S. natans* VIII morphotypes (Amaral-Zettler et al., 2017; Dibner et al., 2022), corroborating Parr's (1939) morphological classifications of these three morphotypes and supporting current recognition of these distinct forms.

Abbreviations: NERR, North Equatorial Recirculation Region; SGR, specific growth rate; SST, sea surface temperature.

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Variability in the relative abundance of pelagic sargassum morphotypes, and total abundance of the sargassum biomass have been reported over space (between source regions) and time (seasons and years) (Schell et al., 2015; Wang et al., 2019; García-Sánchez et al., 2020). In the North Atlantic *S. natans* I is the predominate morphotype, while *S. fluitans* III and *S. natans* VIII occur in relatively smaller abundances with the latter being rare. In contrast, in the Tropical Atlantic pelagic sargassum populations were initially dominated by *S. natans* VIII. In subsequent years however, *S. fluitans* III has become the dominant morphotype with progressive reductions in *S. natans* VIII and variable increases in *S. natans* I (García-Sánchez et al., 2020). These variable spatial and temporal trends have proven difficult to explain, as multiple abiotic factors could be influencing these differences.

Despite pelagic sargassum's long presence in the North Atlantic and acknowledged ecological importance (Laffoley et al., 2011), aspects of its biology such as its growth dynamics remain poorly understood. To date there have only been a small number of sargassum growth studies and considerable variability exists among their findings. Furthermore, most of these studies have examined growth of sargassum from the North Atlantic (Sargasso Sea, Gulf of Mexico, and Northern Caribbean), although two very recent studies have now examined growth within the Tropical Atlantic (Mexico).

Early studies considering the sustainability of the Sargasso Sea population, speculated that the sargassum population (an estimated standing stock biomass of about 7.2 million tons) grew relatively slowly and “does not produce in excess of 10 times their own weight per year” (Parr, 1939). Low productivity of sargassum was also suggested by various other authors (e.g., Howard and Menzies, 1969; Carpenter and Cox, 1974; Mann et al., 1980). This opinion changed with the first direct growth measurements of pelagic sargassum by Lapointe (1986) and Hanisak and Samuel (1987) who reported that sargassum could, under optimal conditions, double its biomass in a matter of days or weeks.

Whilst these early studies agreed that the growth rates of pelagic sargassum species were fast, contrary results have been reported when comparing growth rates between the two species. Hanisak and Samuel (1987) reported that *S. fluitans* grew at a faster rate than *S. natans* under similar conditions. In contrast, a more recent study by Lapointe et al. (2014) found no difference between species growth rates in neritic waters across a wide range of locations. Interestingly two very recent studies from the Tropical Atlantic (Magaña-Gallegos et al., 2023a, 2023b) report sargassum growth rates in the same broad range as those reported by earlier studies from the North Atlantic, and they also report interspecific as well as intraspecific growth rate differences among *S. fluitans* and *S. natans* species and morphotypes.

Previous studies from the North Atlantic have also shown considerable spatial variability in sargassum growth, with faster rates in nutrient rich neritic regions (GOM, Gulf Stream, Florida Straits, and Caribbean Sea) compared with oligotrophic oceanic regions (Sargasso Sea) (Lapointe, 1986, 1995; Lapointe et al., 2014). Laboratory growth experiments by Hanisak and Samuel (1987) also revealed tolerance ranges and optimal values for salinity and temperature for sargassum from the North Atlantic population. The most recent studies by Magaña-Gallegos et al. (2023a, 2023b) from the Tropical Atlantic also demonstrate highly variable growth rates under differing temperatures and levels of nutrient enrichment.

1.3. Sargassum influx forecasting

Sargassum forecast models which predict and inform on the occurrence and severity of sargassum bloom events in the Tropical Atlantic, have been an important management tool in the Caribbean in recent years given the recurrent mass influxes of sargassum into this region (Cox and Oxenford, 2019). These forecasts currently rely on the detection and quantification of pelagic sargassum in processed satellite imagery using an Alternative Floating Algae Index (AFAI) (e.g., Wang and Hu, 2016, 2017) which identifies the red-edge reflectance of floating

vegetation. The AFAI images are then used to seed advection models which predict the passage of the inert ‘sargassum’ pixels (Franks et al., 2016; Maréchal et al., 2017; Johnson et al., 2020). However, the accuracy of these forecasts is limited as advection alone does not account for the seasonal and interannual variability in sargassum's biomass and distribution (Brooks et al., 2018; Marsh et al., 2022).

The incorporation of physiological data pertaining to pelagic sargassum growth and mortality has been tried in an attempt to improve the accuracy of forecast models (Brooks et al., 2018; Jouanno et al., 2020; Marsh et al., 2021). However, the sargassum growth and mortality data so far incorporated into ‘improved’ forecast models are subject to considerable uncertainty (Marsh et al., 2022). This uncertainty emanates from the paucity of growth and mortality studies on pelagic sargassum and the lack of agreement among them (as described in Section 1.2). This uncertainty is exacerbated by the potential for different growth and mortality attributes among the different species and morphotypes and the influence of environmental parameters, about which very little is known, especially with regard to the newly established Tropical Atlantic sargassum population. So far, the majority of the limited studies only provide growth data for putative species morphotypes *S. fluitans* III and *S. natans* I which dominate the North Atlantic sargassum population. Currently only one study provides information on the growth responses of all three sargassum morphotypes (*S. fluitans* III, *S. natans* I and *S. natans* VIII) *ex-situ*. The considerable variability in reported results of the few existing growth studies, highlights the importance of additional studies for assessing each pelagic sargassum morphotype under variable environmental conditions relevant to the Tropical Atlantic Basin (Jouanno et al., 2020; Marsh et al., 2021).

1.4. Objectives

The key objective of this study was to add to the knowledge of pelagic sargassum growth rates in the Tropical Atlantic to better inform forecasting and innovative applications. As such, the present study sought to (1) determine and compare the growth rates of each of the three common sargassum morphotypes (*S. fluitans* III, *S. natans* I and *S. natans* VIII) from the Tropical Atlantic population *in-situ* for the first time, and (2) determine and compare the growth rates of each morphotype during the cool and warm sea surface temperature periods experienced in Barbados. We hypothesize that sargassum morphotypes grow at different rates, and that growth rate differences among morphotypes are influenced by changes in temperature.

2. Methodology

2.1. Study site

Pelagic sargassum was collected in neritic waters of Conset Bay, on the windward eastern coast of Barbados in the Lesser Antilles and grown *in-situ* in neritic waters of Carlisle Bay on the island's southwest coast (Fig. 1). Barbados is among the first islands to receive sargassum as it is transported along various distribution pathways from the Tropical Atlantic source region, westwards into the Caribbean (Alleyn et al., 2023). As such, the island is in a key position to study the growth of the Tropical Atlantic sargassum population as it transitions from open ocean into the semi-enclosed Caribbean Sea. Furthermore, Barbados now receives sargassum throughout most of the year (CERMES and MABE, 2021; Degia et al., 2022), allowing comparison of sargassum growth between the two extremes of sea surface temperature experienced in this region.

2.2. Experimental design

In-situ growth studies were conducted over two study periods from May 4th – 24th (cool water period) and August 23rd – September 12th 2022 (warm water period). For each study period, three one-week

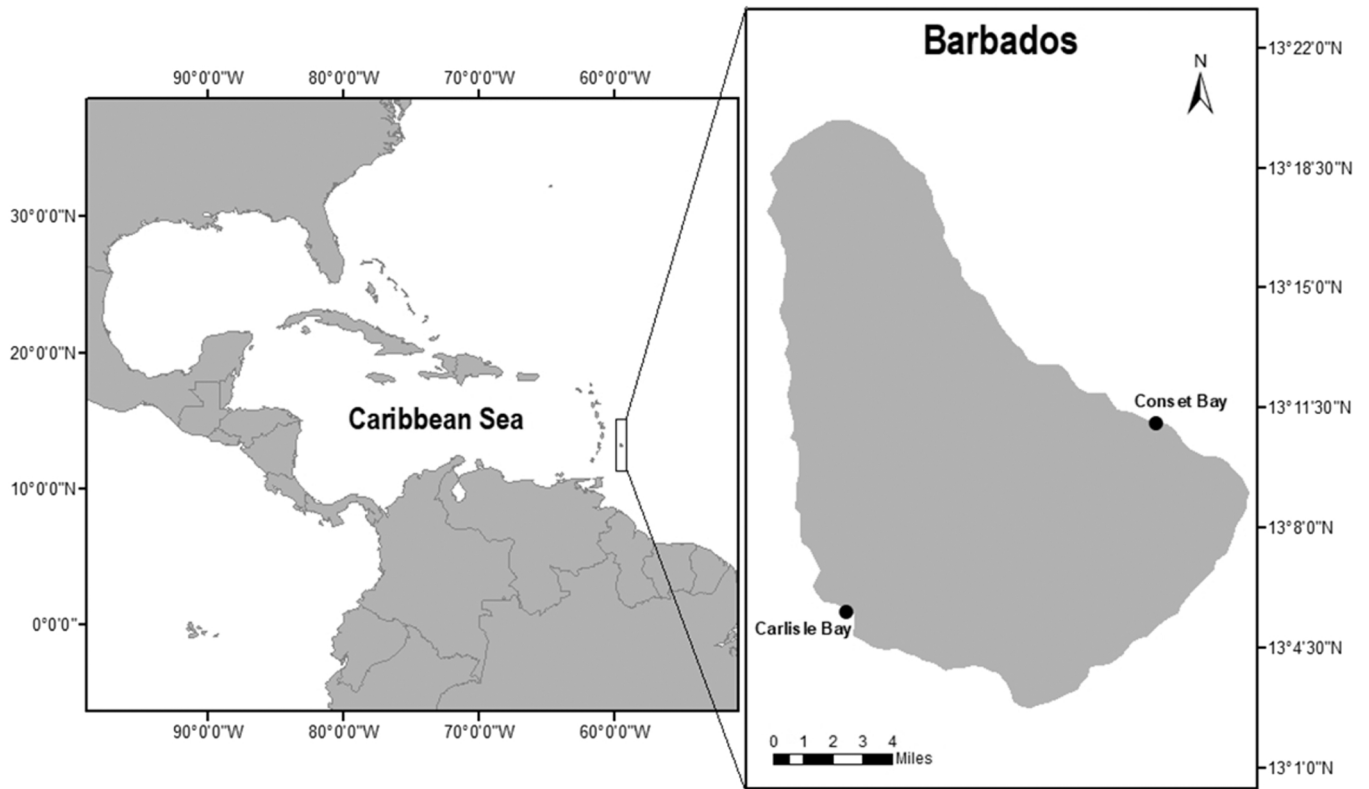


Fig. 1. Location of Carlisle Bay study site and Conset Bay collection site in Barbados, Lesser Antilles.

growth trials were conducted. The experimental design involved the use of novel ‘growth mesocosms’ secured to two moorings (Fig. 2). Three growth mesocosms were joined to form a triplicate set, and three triplicate sets (one for each morphotype) were attached to each mooring for a total of 18 replicates (6 per morphotype) per one-week trial. A maximum of six replicates per morphotype were used whenever possible, however the number of replicates per morphotype varied slightly among trails due to variability in relative morphotype abundance of sargassum arriving in Barbados at the time of the study.

perforated by rows of 6 mm diameter holes (~1 cm apart) to allow water flow. A flap was cut into the surface of each mesocosm to allow for the insertion and removal of sargassum thallus fragments and was sealed shut with cable ties. The mesocosms were strung together in triplicates and kept buoyant by polyethylene floats strung in-between (Fig. 2). The placement of floats between each mesocosm triplicate set, ensured only half of each mesocosm remained submerged. This ensured sargassum replicates maintained their natural position in the water column, interacting with both the water and atmosphere.

2.2.1. Growth mesocosms

The ‘growth mesocosms’ were constructed of 5 l clear plastic bottles

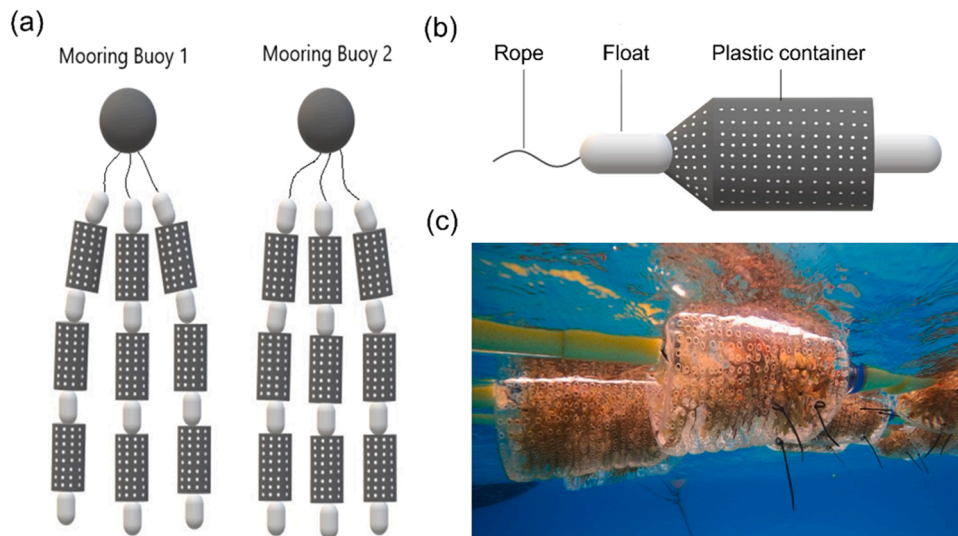


Fig. 2. Triplicate sets of growth mesocosms attached to mooring buoys (a) single growth mesocosm (b) mesocosms containing pelagic sargassum *in-situ* (c).

2.3. Sample collection and sorting

Sargassum was collected in Conset Bay, on the eastern coast of the island (Fig. 1). For each study period, a moderately large volume of mixed species sargassum (~16 kg) was collected weekly with a dipnet from a small boat 0.1–1 km from shore. The sargassum was immediately placed into a large cooler with seawater and transported to Carlisle Bay, where conditions are calm enough for the experimental set up and monitoring of sargassum growth. Sargassum was then sorted into the three respective morphotypes: *S. fluitans* III, *S. natans* I and *S. natans* VIII. Any associated fauna clinging to the sargassum were removed. For each morphotype, six replicate samples (~40 g wet weight, comprising 3–10 thallus fragments with all constituent parts: stipe, blades and aerocysts) were separated, shaken vigorously to remove excess water, and weighed on a digital scale (to the nearest gram). The degree of epiphytization on sargassum thallus fragments of each replicate sample was also noted. Epiphytes were not removed to avoid risk of damaging the thallus fragment, but only fragments exhibiting no to mild epiphytization (< 5 % surface cover) were used. Each replicate was then placed in an individual plastic ziplock bag with seawater and put into buckets to be transported to the experimental set up approximately 140 m from shore, where the morphotype replicates were placed into the growth mesocosms and deployed.

2.4. Measuring growth

The pre-weighed sargassum replicates were collected after 6 days *in-situ* and carefully re-weighed after removal of excess water. Although the density of epiphytes on sargassum thallus fragments typically increased after 6 days, tedious removal of fouling epiphytes from a subset of replicates and subsequent re-weighing, confirmed that the increase in fouling epiphytes was not detectable and therefore did not influence wet weight of sargassum thallus fragments.

Specific Growth Rate (SGR) was calculated as doublings per day (dd^{-1}), and doubling time as number of days taken to double in biomass (t_d) using Eqs. (1) and (2) respectively, following Hanisak and Samuel (1987).

$$dd^{-1} = \log_2 (W_2/W_1) / t \quad (1)$$

$$t_d = 1 / dd^{-1} \quad (2)$$

Where: W_1 = initial weight, W_2 = end weight and t = time in days.

2.5. Measuring environmental parameters

Surface water temperature and salinity were measured continuously at 3-h intervals using a HOBO Saltwater Conductivity/ Salinity Logger (U 24–002 C) throughout each study period. The HOBO Logger was placed in a protective housing to limit fouling and secured to the mooring line approximately 1 m below the water surface.

3. Results

3.1. Growth trials

Cool water growth trials were conducted during May 2022 while warm water growth trials were conducted from late August to mid-September 2022. During growth trials the number of sargassum morphotype replicates varied slightly due to variability in the relative morphotype abundance of sampled sargassum rafts (Table 1).

3.2. Environmental conditions

Mean daily water temperature remained relatively constant during each period ranging from 27.3 – 28.1 °C (mean 27.6 °C) during the 3-week cool water period and 29.4 – 29.9 °C (mean 29.6 °C) during the

Table 1

Number of sargassum morphotype replicates used during each trial for cool and warm water periods in 2022.

Temperature Period	Trial	Dates (dd/mm)	Replicates (N)		
			<i>S. fluitans</i> III	<i>S. natans</i> I	<i>S. natans</i> VIII
Cool	1	04/05–10/05	3	6	6
	2	11/05–17/05	6	6	6
	3	18/05–24/05	6	3	6
	Sub total		15	15	18
Warm	1	23/08–29/08	6	6	5
	2	30/08–5/09	6	6	6
	3	6/09–12/09	6	5	6
	Sub total		18	17	17
Overall	Total		33	32	35

warm water period (Fig. 3a) and were significantly different between periods (Mann-Whitney U, $Z = -5.477$, $p < 0.001$). Mean daily salinity was quite variable during the cool water period, ranging from 29.9‰ to 34.4‰ (mean 32.1‰) and relatively stable over the warm period, ranging from 31.3‰ to 32.5‰ (mean 32.0‰) (Fig. 3b), but did not differ significantly between the two periods (T-Test test, $T = 0.0613$, $df = 39$, $p = 0.546$).

3.3. Comparison of sargassum morphotype growth rates

This *in-situ* study has revealed a significant difference in growth rates among all three pelagic sargassum morphotypes (Fig. 4, One-way ANOVA, $F = 44.087$, $df = 2$, $p < 0.001$). The mean specific growth rate (SGR) of *S. fluitans* III was 0.077 dd^{-1} (i.e., doubling its biomass in 13 days on average) and ranged among replicates from 0.028 to 0.124 dd^{-1} (Table 2). This was considerably higher than *S. natans* I (0.046 dd^{-1} or 22 days to double biomass) and almost three times the mean SGR of *S. natans* VIII (0.032 dd^{-1} or 31 days to double biomass) (Table 2). Interestingly, the interspecific growth rate differences (*S. fluitans* III versus *S. natans* morphotypes) were much larger than the intraspecific growth rate differences (*S. natans* I versus *S. natans* VIII) (Fig. 4). Regardless, the mean SGRs of all morphotypes differed significantly from one another (Tukey HSD test: $p < 0.05$ in all cases; Table S1).

3.4. Comparison of growth rates between warm and cool water periods

Specific growth rates were higher during the cool water period (mean 27.6 °C) than the warm water period (mean 29.6 °C) for all three sargassum morphotypes (Fig. 5, Table 2). The fastest growing morphotype *S. fluitans* III dropped from a mean SGR of 0.098 dd^{-1} in the cool water period to 0.060 dd^{-1} in the warm water period, indicating an increase from an average of just 10 days to an average of 17 days to double its biomass. The other morphotypes followed this trend with the next fastest growing morphotype *S. natans* I, showing an increase in mean doubling time from 20 to 24 days, and the slowest growing morphotype, *S. natans* VIII, taking an average of 34 days to double its biomass in the warm water period, up from 29 days in cooler water (Table 2).

Despite the general decrease in growth across all morphotypes during the warm water period compared with the cool period, only the

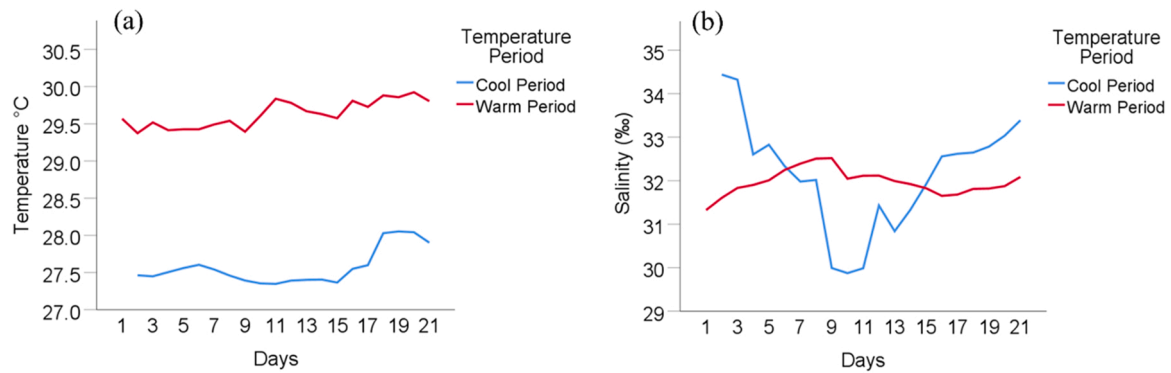


Fig. 3. Mean daily water temperature (a) and salinity (b) during cool water (May) and warm water (August-September) periods at Carlisle Bay, Barbados.

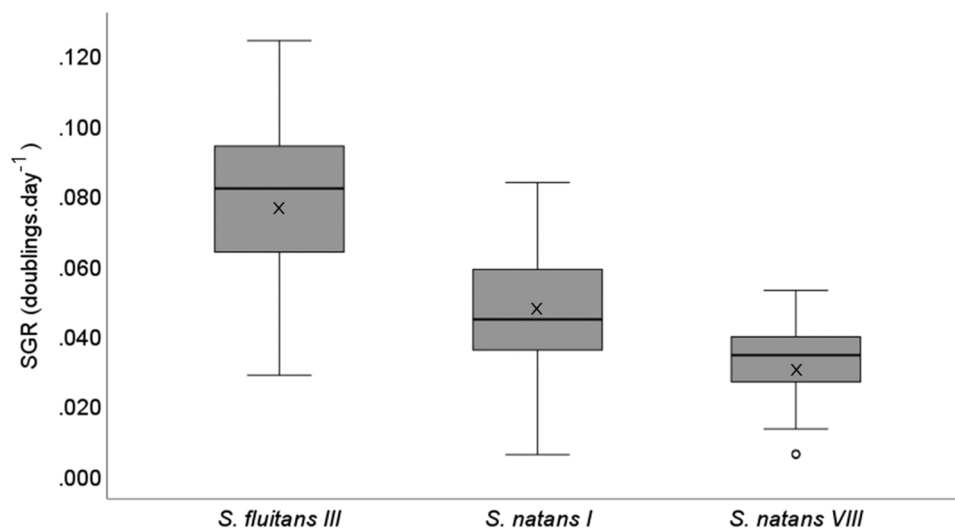


Fig. 4. Comparison of specific growth rates (SGR) of sargassum morphotypes shown across both periods combined. Boxes show the interquartile range, horizontal lines represent the median value and whiskers indicate the minimum and maximum data range excluding outliers. Mean SGR is indicated by an 'x'.

Table 2

Specific growth rates (SGR) of pelagic sargassum morphotypes (averaged across all replicates) shown overall and separately by cool and warm water periods. SGR is shown as range, mean doublings per day (dd^{-1}) and doubling time in days (t_d). *S. fluitans* III, *S. natans* I and *S. natans* VIII are denoted as SF3, SN1, SN8, respectively.

Temperature Period	Morphotype	N	Growth Rate			
			Range	Average		
			(dd^{-1})	(t_d)	($dd^{-1} \pm SD$)	(t_d)
Overall	SF3	33	0.028–0.124	8–36	0.077 ± 0.026	13
	SN1	32	0.006–0.083	12–167	0.046 ± 0.021	22
	SN8	35	0.006–0.053	19–167	0.032 ± 0.012	31
Cool	SF3	15	0.069–0.124	8–14	0.098 ± 0.014	10
	SN1	15	0.020–0.073	14–50	0.051 ± 0.015	20
	SN8	18	0.016–0.051	20–63	0.035 ± 0.010	29
Warm	SF3	18	0.028–0.088	11–36	0.060 ± 0.019	17
	SN1	17	0.006–0.083	12–167	0.042 ± 0.024	24
	SN8	17	0.006–0.053	19–167	0.029 ± 0.014	34

growth of *S. fluitans* III showed a statistically significant reduction (T-test, $T = 6.395$, $df = 31$, $p = 0.023$). The other two morphotypes had fairly high variation in SGR among replicates and did not show a statistically significant difference between cool and warm periods ($p > 0.05$ in both cases).

Regardless, *S. fluitans* III remained the fastest growing morphotype during both cool and warm water periods, growing significantly faster than both *S. natans* morphotypes (Fig. 5, Table S1). Additionally, while the mean SGR of *S. natans* I significantly exceeded SGR of *S. natans* VIII during the cool water period, during the warm water period, when

growth rates of both slowed, they were not significantly different ($p = 0.138$) (Fig. 5, Table S1).

4. Discussion

The results of the present study support our hypothesis that pelagic sargassum morphotypes grow at different rates and have different growth responses to abiotic (temperature) conditions, suggesting that they are physiologically distinct. This is consistent with reported differences among the sargassum morphotypes in their biochemistry and

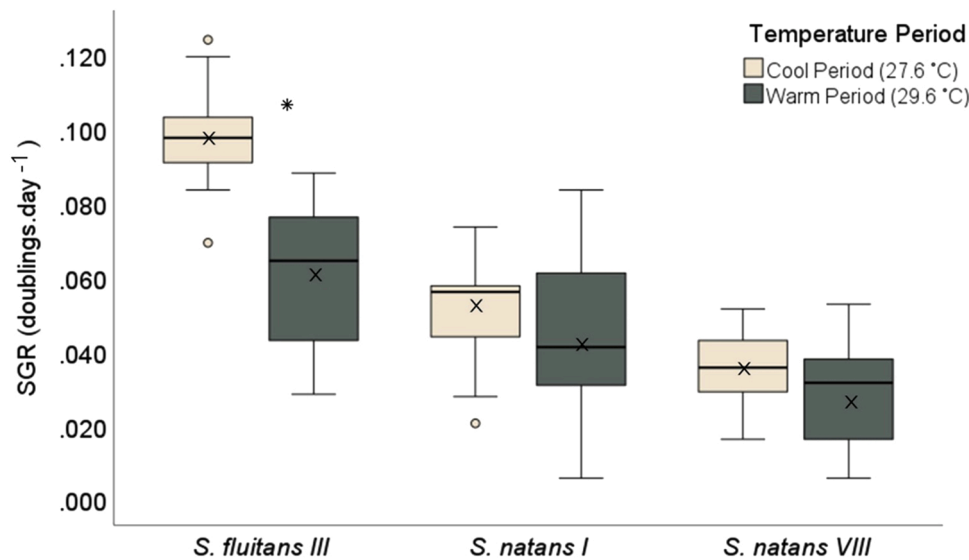


Fig. 5. Comparison of specific growth rates (SGR) of sargassum morphotypes during the cool and warm water periods. Asterisk (*) indicates significant difference in growth rates between cool and warm periods.

elemental composition (Davis et al., 2021), and their genetic identities (Amaral-Zettler et al., 2017; Dibner et al., 2022).

The present study represents the first investigation of *in-situ* growth of pelagic sargassum thalli fragments that have recently advected from a tropical oceanic to a neritic environment, given that Barbados is the most easterly Caribbean island and thus on the frontline of sargassum as

it transitions from the Tropical Atlantic Ocean into the Caribbean Sea. Furthermore, this study has served to highlight, for the first time, the variability in the *in-situ* growth among all three common sargassum morphotypes that are responsible for the Tropical Atlantic sargassum blooms, and between two different ambient temperatures.

Mean growth rates for pelagic sargassum obtained in the present

Table 3

Comparison of growth rates of North Atlantic and NERR (Tropical Atlantic) sourced sargassum species and morphotypes reported in the literature. SF represents *S. fluitans*, SN represents *S. natans* and numbers (1,3,8) denote morphotypes. All growth rate data are calculated using the specific growth rate equation of Hanisak and Samuel (1987).

Study Type	Thalli Used	Collection Region	Morph.	Mean Growth Rate		Abiotic Factors	Source
				SGR [range] (dd ⁻¹)	Doubling Time [range] (days)		
<i>Ex-situ</i>	Apical tips	N. Atlantic (Sargasso Sea)	Not given	0.037 ^a [0.006–0.078] ^a	27 ^a [13–167] ^a	-	Howard and Menzies (1969)
<i>In-situ</i>	Thallus	N. Atlantic	SF	0.036 ^b	28 ^b	28–30°C, 36‰	Lapointe (1986)
<i>Ex-situ</i>	fragments	(Straits of Florida; Sargasso Sea)		0.031 ^b	32 ^b	28–30°C, 36‰	
			SN	0.045 ^b	22 ^b	28–30°C, 36‰	
				0.035 ^b	29 ^b	Neritic	
						28–30°C, 36‰	
<i>In-situ</i>	Apical tips	N. Atlantic (Gulf Stream)	SF	0.109 ^c	9 ^c	12–30°C	Hanisak and Samuel (1987)
			SN	0.073 ^c	14 ^c	6–42‰	
<i>In-situ</i>	Thallus	N. Atlantic	SF	0.06	17	18–30°C	Lapointe et al. (2014)
<i>Ex-situ</i>	fragments	(Florida, Gulf Stream, Sargasso Sea, Belize)		[0.031–0.093]	[11–32]	Neritic	
			SN	0.06	17		
				[0.041–0.091]	[11–24]		
			SN	[0.005–0.020]	[50–200]	18–30°C Oceanic	
<i>In-situ</i>	Thallus	Tropical Atlantic	SF3	[0.035–0.039] ^d	[26,27] ^d	27–29°C, 35‰	Magaña-Gallegos et al. (2023a)
<i>Ex-situ</i>	fragments	(Mexico)	SN8	[0.049–0.056] ^d	[18–20] ^d	Neritic, <i>In-situ</i>	
			SF3	[0.04–0.067] ^d	[15–25] ^d	28, 29°C, 35‰	
			SN8	0.046 ^d	22 ^d	Neritic, <i>Ex-situ</i>	
<i>Ex-situ</i>	Thallus	Tropical Atlantic	SF3	[0.058–0.095] ^d	[11–17] ^d	22–31°C	Magaña-Gallegos et al. (2023b)
	fragments	(Mexico)	SN1	[0.054–0.067] ^d	[15–19] ^d	Neritic	
			SN8	[0.045–0.059] ^d	[17–22] ^d		
<i>In-situ</i>	Thallus	Tropical Atlantic	SF3	0.077	13	27–30°C	This study
	fragments	(Barbados)		[0.028–0.124]	[8–36]	30–34‰	
			SN1	0.046	22	Neritic	
				[0.006–0.083]	[12–167]		
			SN8	0.032	31		
				[0.006–0.053]	[19–167]		

^a Growth rate values calculated from given data. ^b Values reported for controls only. ^c Mean maximum values. ^d Values are mean minimum and maximum values across abiotic range

study are within the range of mean growth rates reported in prior *in-situ* and *ex-situ* studies of both North Atlantic and Tropical Atlantic pelagic sargassum, further supporting that on average it is capable of doubling its biomass in somewhere between 9 and 32 days (Table 3).

Our findings that *S. fluitans* III was the fastest growing morphotype, whilst *S. natans* VIII was the slowest across our ambient temperature range (27.3 – 29.9 °C) also align with the only other study to have examined all three morphotypes in the Tropical Atlantic (Mexico), but in an *ex-situ* set up (Magaña-Gallegos et al., 2023b) (Table 3). We further note a significant intraspecific difference between *S. natans* morphotypes under cooler ambient temperatures (mean 27.6 °C), with *S. natans* I growing about 1.5 times faster than its conspecific *S. natans* VIII. Magaña-Gallegos et al. (2023b) examined morphotype growth over a wider temperature range (22 – 31 °C) and also report differential growth between morphotypes *ex-situ*. However, the only significant difference in growth occurred between allospecific morphotypes *S. fluitans* III and *S. natans* VIII at 28 °C, with *S. fluitans* III growing faster. While similar to findings of the present study, it is contrary to their earlier *in-situ* study (Magaña-Gallegos et al., 2023a) in which *S. natans* VIII was the faster growing morphotype under similar ambient temperatures (27–29 °C).

In the Tropical Atlantic, both the present study and Magaña-Gallegos et al. (2023b) report a decline in growth rate of morphotypes, especially *S. fluitans* III, at the highest temperatures assessed (albeit with variation), aligning with early assessments of pelagic sargassum growth by Hanisak and Samuel (1987) in the North Atlantic. This likely indicates physiological heat stress occurring above an optimum temperature. However, contrasting results were reported by Magaña-Gallegos et al. (2023a) in Mexico, where the growth of *S. fluitans* III increased significantly with an increase in temperature from 28 °C to 31 °C in their first *ex-situ* trials.

Whilst there is agreement among studies that temperature has an effect on morphotype growth, the variation in growth responses of different morphotypes between studies or even between growth trials is not consistent and may also depend on the season when sargassum is collected, perhaps reflecting its condition (Magaña-Gallegos et al., 2023b).

In addition to the effects of temperature, Hanisak and Samuel (1987) further examined the impacts of salinity on growth of both species and reported an optimal salinity range of 36 – 40‰ and a reduction in growth rate by almost half at a salinity of 30‰ and no growth at 18‰. The fact that maximal growth rates for *S. fluitans* III and *S. natans* I in the current study (at salinities of 30 – 34‰) were very similar to those obtained under high salinity conditions (see Lapointe, 1986; Hanisak and Samuel, 1987; Lapointe et al., 2014) suggests that pelagic sargassum, at least from the NERR, has a wider salinity tolerance than previously reported elsewhere.

Our findings contribute to understanding the drivers of variation in pelagic sargassum blooms in the Tropical Atlantic. For example, the fact that the mean growth rate of *S. fluitans* III significantly exceeds the growth of *S. natans* I and *S. natans* VIII in the present *in-situ* growth trails and in the *ex-situ* study of Magaña-Gallegos et al. (2023b) over the temperatures found in this region, could explain why sargassum blooms arriving in the Caribbean from the NERR are generally dominated by *S. fluitans* III (García-Sánchez et al., 2020; CERMES data unpubl.; Alleyne et al., 2023). Furthermore, the higher variability and smaller differences in growth observed between conspecific *S. natans* morphotypes align with observations of lower relative abundance of, and fluctuations between, *S. natans* morphotypes in the rafts arriving in the Caribbean.

Furthermore, *S. natans* is reported to have optimal growth at a lower temperature than *S. fluitans* (Magaña-Gallegos et al., 2023b: 22–25 °C; Hanisak and Samuel, 1987: 24 °C) and *S. fluitans* is reported to have a sharp decrease in growth below 24 °C (Hanisak and Samuel, 1987). This may confer a strong seasonal advantage to *S. natans* over *S. fluitans* in the North Atlantic where temperatures drop to the low 20 s in the winter, and could explain the historical dominance of *S. natans* in sargassum

populations reported there, which Schell et al. (2015) note is in stark contrast to morphotype composition observed in the Tropical Atlantic. Note that in our *in-situ* study examining growth at these lower temperatures was not possible, since ambient temperatures do not drop below 26 °C in the Eastern Caribbean.

The negative correlation between sea surface temperature (SST) and sargassum growth rate for Tropical Atlantic sargassum (indicated by Wang et al., 2019), is corroborated by the massive sargassum blooms observed in the NERR in 2015 and 2018 coinciding with cooler SST, while the non-bloom year of 2013 and relatively weak bloom year of 2016 coincided with warmer SST (Skliris et al., 2022). We note however, that these trends of interannual variability in sargassum blooming are also likely to be influenced by differences in nutrient availability. Several studies have shown that sargassum growth is significantly enhanced by increasing nutrient (N and P) concentrations, especially an increase in the ratio of P:N, given that availability of P is generally an important limiting factor for sargassum growth (Lapointe, 1986, 1995; Lapointe et al., 2014). As Skliris et al. (2022) point out, years with particularly large sargassum blooms appear to be linked to negative phases of the Atlantic Meridional Mode and positive phases of the Atlantic Niño. These events not only reduce SST but also result in enhanced nutrient upwelling.

5. Conclusion

The present study is the first to examine the growth of all three common morphotypes *in-situ*, and demonstrates that our simple, novel 'growth mesocosms' can be used successfully to assess the growth of pelagic sargassum.

Our results, together with those of previous studies, have a number of implications for managing sargassum influxes from the NERR source region. Confirmation of extremely fast growth of pelagic sargassum in the Tropical Atlantic (capable of doubling its biomass in less than two weeks) highlights the importance of incorporating growth rates into models used for medium and long-term forecasting of sargassum influxes. It also has important implications for informing innovative applications considering carbon sequestration and/or aquaculture of pelagic sargassum.

Firstly, we recognize that the growth rate variation among morphotypes, now confirmed for Tropical Atlantic sargassum, will make parameterizing forecast and yield models highly complex, requiring explicit modelling of growth for each of the sargassum morphotypes and consideration of their relative abundance (morphotype composition). This is especially so, since morphotype composition of sargassum rafts varies over space and time. The task will be further complicated by the reported differential growth responses of morphotypes to variations in the abiotic environment that they will experience along their transport pathways from the NERR source region to their beaching locations. Furthermore, current discrepancies in the results reported across different studies, will add to the uncertainties for model parameterization. As such, there is a clear need for studies to further explore and clarify how pelagic sargassum growth is influenced by morphotype physiology, variable environmental conditions and changes in nutrient demand and tissue reserves (e.g. Magaña-Gallegos et al., 2023a) before growth parameters can be usefully incorporated into medium and long-term forecast models to improve their accuracy.

Secondly, as management efforts are directed towards finding beneficial uses of sargassum there is increasing interest in the potential role of sargassum in climate mitigation through large-scale carbon fixation and sequestration (Gouvêa et al., 2020; Paraguay-Delgado et al., 2020; Hu et al., 2021; Gray et al., 2021). Climate mitigation projects seeking to actively culture and sink sargassum in the deep ocean (e.g., Reid and Rowlett, 2022) could be better informed by the variable morphotype growth rates revealed in this study. Likewise, the growth rate data will also be valuable to projects considering sargassum aquaculture for various valorisation applications (e.g., Sherman et al., 2018).

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CRedit authorship contribution statement

Makeda Corbin: Conceptualization, Investigation, Formal analysis, and Writing – original draft preparation. **Hazel A. Oxenford:** Conceptualization, Supervision and Writing – review & editing.

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.2023.103654](https://doi.org/10.1016/j.aquabot.2023.103654).

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