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11 **Nutrient and arsenic biogeochemistry of *Sargassum* in the western Atlantic**
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The oceanographic ecology of pelagic *Sargassum*, and the means by which these floating macroalgae thrive in the nutrient-poor waters of the open ocean, have been studied for decades. Beginning in 2011, the Great Atlantic *Sargassum* Belt (GASB) emerged, with *Sargassum* proliferating in the tropical Atlantic and Caribbean where it had not previously been abundant. Here we show that the nutritional status of *Sargassum* in the GASB is distinct, with higher nitrogen and phosphorus content than populations residing in its Sargasso Sea habitat. Moreover, we find that variations in arsenic content of *Sargassum* reflect phosphorus limitation, following a hyperbolic relationship predicted from Michaelis-Menten nutrient uptake kinetics. Although the sources of nutrients fueling the GASB are not yet clear, our results suggest that nitrogen and phosphorus content of *Sargassum*, together with its isotopic composition, can be used to identify those sources, whether they be atmospheric, oceanic, or riverine in origin.

The floating macroalgae *Sargassum* spp. serves as a habitat for more than 200 types of organisms, including 10 endemic species¹⁻³ and provides habitat for fish nursery, spawning and foraging^{4,5}. Neonate and juvenile sea turtles use *Sargassum* habitat for feeding as well as protection from predators^{6,7}, and several species of seabirds forage over *Sargassum*^{8,9}. In contrast to these traditionally beneficial ecological impacts, the GASB's unprecedented inundations of *Sargassum* on Caribbean and Florida coastlines have had deleterious effects on near-shore seagrass and coral reef ecosystems¹⁰⁻¹³, and have led to declines in turtle hatchling survival¹⁴. The GASB has also presented challenges to regional economies, particularly those that rely heavily on tourism^{15,16}. *Sargassum* decay on coastal margins can cause respiratory and other human health issues¹⁷, and the presence of arsenic in *Sargassum* tissue¹⁸⁻²⁰ puts significant constraints on utilization of the biomass that washes ashore²¹⁻²³.

A complex set of interconnected hypotheses have been offered to explain dynamics of the GASB²⁴⁻²⁶. Anomalous wind patterns in 2009-2010 are thought to have introduced *Sargassum* from its habitat in the Sargasso Sea into the eastern North Atlantic where it was subsequently entrained into the equatorial current system²⁷. Since that time, *Sargassum* has increased dramatically in the tropical Atlantic, begging the question of nutrient supply. A variety of nutrient sources have been suggested²⁶⁻²⁹, including upwelling, vertical mixing, discharge from the Amazon and Congo rivers, and atmospheric deposition. However, the causes of the GASB and the mechanisms controlling its seasonal to interannual variability remain unknown. An underlying question is: is this massive abundance of *Sargassum* a result of higher nutrient availability in the GASB?

In this work we show that GASB *Sargassum* populations are enriched in both nitrogen and phosphorus content relative to its Sargasso Sea habitat, clearly identifying nutrient supply as a primary driver of this phenomenon. In addition, we demonstrate that *Sargassum*'s arsenic content varies with the degree of phosphorus limitation, linking our observations with a theoretical prediction based on nutrient uptake kinetics. Our results show that ascertaining the nutrient sources and their regulation is essential to understand the underlying causes of this basin-scale phenomenon—and only then will society have a conceptual basis on which to design potential strategies to mitigate the consequences of the GASB.

Results

Sargassum distributions and nutritional status

In order to address this question, *Sargassum* tissue samples were collected in spring 2021 along with hydrographic and nutrient measurements on two hydrographic sections in the western

Atlantic (Methods) that intersected the western portion of the GASB (Fig. 1). The samples were separated into two species *S. fluitans* and *S. natans* based on their morphology³⁰. *S. fluitans* and *S. natans* co-occurred in the southern portions of both A20 and A22. *S. natans* was more prevalent north of 24°N on A22, and north of 27°N on A20. Both species were present at 32°N on A20 as well as the farthest north sample, collected just south of the Gulf Stream on A22.

Sargassum elemental composition was similar between species (Fig. 2, Supplementary Table 1), a finding that is consistent with earlier studies²⁹. Our data reveal three distinct regimes within the sampling domain. In the Sargasso Sea, carbon content tends to be relatively high (particularly in the eastern transect A20), whereas nitrogen and phosphorus content tend to be low. Nutritional status in the GASB was much better, with nitrogen and phosphorus content of *Sargassum* in the Caribbean and western tropical Atlantic significantly higher than in the Sargasso Sea (Supplementary Fig. 1, Supplementary Table 2). Interestingly, nitrogen and phosphorus content were highest in the northern Sargasso Sea.

These trends are also evident in elemental ratios (Supplementary Fig. 2). As expected, C:N was high in the Sargasso Sea, driven by higher carbon content and lower nitrogen content (Fig. 2). These ratios are higher in A20 than in A22, particularly in *S. natans*. This zonal gradient with C:N increasing to the east is driven by both increasing carbon content and decreasing nitrogen content. C:P is also high in the Sargasso Sea, although the zonal gradient evident in C:N is not clear in C:P. N:P shows a pronounced maximum in the Sargasso Sea region of A22, which is driven by a combination of increased N content and decreased P content. Little meridional trend in N:P is evident in A20, and in aggregate N:P in the Sargasso Sea differs less from the surrounding regions than does C:N and C:P (Supplementary Fig. 1).

Based on the seasonal analysis conducted on prior data sets²⁹, the springtime samples described herein would be expected to be at their seasonal maxima of nitrogen and phosphorus content, and minima of their C:N and C:P ratios.

Nutrient sources

Because *Sargassum* is subject to both surface currents and wind, hydrodynamic transport plays a key role in its dynamics³¹⁻³³. In order to assess the recent history of our *Sargassum* samples, passive particles were inserted into a numerical ocean model hindcast at each collection site and tracked backward in time (Fig. 3; see Methods). The southernmost sample of A20 appears to have come from the southeast, whereas samples in the 10-30°N latitude band come primarily from the east. Exceptions to that pattern include an eddy-like flows from 25°N to 28°N on A22. Samples collected north of 30°N on A20 appear to have come from the north, consistent with a Gulf Stream origin. The northernmost sample on A22 was clearly under the influence of the Gulf Stream, although its point of entry into the Gulf Stream varied widely within the ensemble—ranging from the continental shelf north of Cape Hatteras to the South Atlantic Bight, with some in the core of the Gulf Stream as far south as 30°N.

This information, together with $\delta^{15}\text{N}$ values of the *Sargassum* tissue, facilitates some inferences about nitrogen sources. Specifically, *Sargassum* utilizing riverine nitrogen tend to have enriched (positive) $\delta^{15}\text{N}$ values, whereas those fueled by near-surface oceanic and atmospheric sources have lower (negative to slightly positive) $\delta^{15}\text{N}$ values²⁹. Nitrogen fixation typically results in a fractionation of -2‰³⁴.

Patterns in $\delta^{15}\text{N}$ from our survey reveal spatial coherence, with no systematic difference between *S. fluitans* and *S. natans* (Fig. 2). Depleted $\delta^{15}\text{N}$ values in the Sargasso Sea, Caribbean, and western tropical Atlantic could result from nitrogen fixation by epiphytic cyanobacteria^{35,36}

or perhaps atmospheric deposition³⁷. The highest $\delta^{15}\text{N}$ values occurred in the northern Sargasso Sea, with values of approximately +2‰ potentially reflecting riverine sources along the U.S. east coast (as indicated by spatial connectivity depicted in Fig. 3), or as distant as the Gulf of Mexico which has been identified as a source region for *Sargassum* in the western Atlantic³⁸. For example, a coherent plume emanating from the Mississippi River in summer of 2004 was entrained into the Loop Current, reaching the Straits of Florida in approximately 25 days, continuing northward in the Gulf Stream to be found in the South Atlantic Bight another 25 days after that³⁹. Our northern Sargasso Sea samples were collected another 600 nm farther downstream, so assuming a flow of 4 kt, they could have been influenced by Mississippi River water discharged as recently as 150 days before sampling. With end-member $\delta^{15}\text{N}$ values of +6-8‰ in northern Gulf of Mexico *Sargassum*²⁹, dilution to +2‰ would require several doublings of the population using oceanic sources of nitrogen—which is certainly possible based on observed growth rates^{36,40,41}. Alternatively, enrichment of $\delta^{15}\text{N}$ in samples from the northern Sargasso Sea could be caused by upwelling and/or vertical mixing, as values of +2‰ are characteristic of nitrate in the upper thermocline in that region^{42,43}.

Enriched $\delta^{15}\text{N}$ values were also found in the southernmost samples of the western tropical Atlantic (Fig. 2), under direct influence of the Amazon River plume (as evidenced by the salinity distribution in Fig. 1) which has been implicated as a nutrient source for the GASB^{26-29,44}. There was one station in the Caribbean interior (17°N, 67°W) where similarly high $\delta^{15}\text{N}$ values were measured, but the corresponding salinity (Fig. 1) does not bespeak riverine influence. Particle backtracking calculations suggest source waters to the east-southeast (Fig. 3), and given the cross-isohaline transport enabled by wind drag, Amazon River influence is plausible. However, it is noteworthy that neither the elemental composition (Fig. 2) nor nutrient ratios (Supplementary Fig. 2) in the high- $\delta^{15}\text{N}$ samples of the tropical Atlantic and Caribbean Sea show corresponding anomalies.

Hydrographic data from sections A20 and A22 provide environmental information with which to interpret the *Sargassum* observations. The nitracline and phosphocline are deepest in the warm and salty waters of the Sargasso Sea, and shallower in the warmer and fresher waters of the Caribbean and western tropical Atlantic (Supplementary Fig. 3). Both nutriclines are shallower in the colder and fresher waters of the northern Sargasso Sea. Near-surface nutrient concentrations are generally very low except for the northernmost portions of each transect where the nutriclines outcrop. Nitrate and phosphate are at or below the limit of detection in the surface waters Sargasso Sea (Supplementary Fig. 4). Nitrate is enhanced in the Caribbean, and less so in the western tropical Atlantic, where surface phosphate is elevated. The presence of detectable nitrate and phosphate in these areas is consistent with the enhanced nutritional status of *Sargassum* in the GASB.

Arsenic biogeochemistry

The fact that *Sargassum* bioaccumulates arsenic has generated considerable interest, particularly because the associated toxicity puts practical limitations on valorization of the biomass inundating coastal communities of the GASB. Our survey revealed regional scale variations in arsenic content (Fig. 2). Arsenic content was lowest in the GASB (Caribbean and Western Tropical Atlantic samples) and highest in the Sargasso Sea, particularly in the eastern transect A20. Other stations in A20 show modest enrichment, such as in the southernmost samples at 9°N, 52°W and the Northern Sargasso Sea samples at 31-33°N, 52°W. There are no

systematic differences in arsenic content between *S. fluitans* and *S. natans* (Supplementary Table 1), although interspecies variability is apparent at some stations (Fig. 2).

The high arsenic content of *Sargassum* in the subtropical gyre is accompanied by the lowest phosphorus content, which is consistent with the depression of the phosphocline (Supplementary Fig. 3) and surface dissolved phosphate concentrations generally below the limit of detection (Supplementary Fig. 4). Thus, the arsenic to phosphorus ratio of *Sargassum* of the subtropical gyre stands out as uniquely high in that region (Fig. 2), where *Sargassum* is known to be phosphorus limited⁴⁵.

Uptake of arsenate (AsO_4^{3-}) by aquatic plants occurs as a byproduct of phosphorus uptake, owing to its chemical similarity with the phosphate ion (PO_4^{3-})^{46,47}. Using the standard Michaelis-Menten form, uptake of dissolved phosphate and arsenate can be expressed as:

$$\rho_P = \mu_P \frac{[\text{PO}_4^{3-}]}{k_P + [\text{PO}_4^{3-}]} \quad \text{and} \quad \rho_{As} = \mu_{As} \frac{[\text{AsO}_4^{3-}]}{k_{As} + [\text{AsO}_4^{3-}]}$$

For low concentrations of phosphate and arsenate, uptake is approximately linear in concentration:

$$\rho_P \approx \mu_P \frac{[\text{PO}_4^{3-}]}{k_P} \quad \text{and} \quad \rho_{As} \approx \mu_{As} \frac{[\text{AsO}_4^{3-}]}{k_{As}}$$

The ratio of As to P uptake is therefore:

$$\frac{\rho_{As}}{\rho_P} = \frac{\mu_{As} k_P}{\mu_P k_{As}} \frac{[\text{AsO}_4^{3-}]}{[\text{PO}_4^{3-}]}$$

Surface arsenate concentrations in the tropical and subtropical Atlantic are relatively uniform in comparison with phosphate, and up to an order of magnitude lower⁴⁸. Moreover, surface concentrations of arsenate and phosphate are uncorrelated⁴⁹, so the ratio of As to P uptake can be simplified to:

$$\frac{\rho_{As}}{\rho_P} \sim \frac{1}{[\text{PO}_4^{3-}]}$$

Assuming that the tissue content of these two constituents reflects their proportionate uptake, one would expect that the ratio of arsenic to phosphorus in *Sargassum* would be a hyperbolic function of phosphorus content:

$$\frac{\%As}{\%P} \sim \frac{1}{\%P}$$

This prediction is qualitatively consistent with the present data as well as prior observations dating back to the 1980s (Fig. 4), although the dependence on phosphorus content varies as $\%P^{-1.3}$ rather than $\%P^{-1.0}$ predicted by the theory. The reason for this supra-hyperbolic dependence is not known, but it is statistically reliable with a p-value < 0.001 (Supplementary Note). This is a clear demonstration of arsenic content as a diagnostic of phosphorus limitation in a natural population of marine algae, and is consistent with laboratory studies^{50,51}, biogeochemical proxies based on dissolved As speciation in the ocean⁴⁹, and other recent field data⁵².

It could be argued that the As:P versus P relationship in Fig. 4 is a result of the intrinsic association among variables: for two random variables a and b, plotting the ratio a:b versus b will take on a hyperbolic form. However, the elemental composition of *Sargassum* is not random. For example, the As:C ratio does not show a hyperbolic dependence on carbon content (Supplementary Fig. 5). Interestingly, As:N varies hyperbolically with nitrogen content, which we attribute to covariation in nitrogen and phosphorus content.

Notwithstanding our theoretical prediction of the hyperbolic relationship of As:P and P content, one might also expect a negative correlation between As and P content as a symptom of phosphorus stress in *Sargassum*. Observations are also consistent with this expectation (Supplementary Fig. 6). A similar negative correlation is observed between arsenic and nitrogen content, which we again attribute to the correlation between nitrogen and phosphorus content. In contrast, As content is positively correlated with carbon content.

Discussion

Nutrient limitation of oceanic *Sargassum* populations in their native habitat was demonstrated decades ago^{45,53}, and enhanced nutrient availability has been advanced as a key factor in stimulating the GASB^{26,27,29}. We show clearly for the first time that *Sargassum* in the GASB is enhanced in both nitrogen and phosphorus, indicative of a healthy and thriving population. Stable nitrogen isotope values point to riverine sources in some circumstances, and are more equivocal in others. Distinguishing the various nutrient sources sustaining the GASB will require systematic snapshots of nutrient content and isotopic composition across its entire breadth. Presumably, the closer one gets to the source, the higher the nitrogen and / or phosphorus content of *Sargassum* should be. In that sense, basin-wide patterns in nitrogen and phosphorus elemental composition could provide the fingerprinting necessary to unequivocally determine the sources. However, given the strong seasonal to interannual variability intrinsic to the GASB, it will be essential that such snapshots be synoptic, which poses significant practical challenges for a phenomenon of this scale.

Our novel demonstration of arsenic content as an indicator of phosphorus stress in natural populations of *Sargassum* also has considerable implications. *Sargassum* inundating coastal areas of the GASB already contains arsenic concentrations that can exceed safe thresholds for consumption²¹⁻²³. If the phosphorus supply to the GASB were to wane relative to that of nitrogen, our findings would suggest that arsenic content of *Sargassum* in that area would rise even further, perhaps up to levels currently observed in the Sargasso Sea. This would have important implications for management if the nutrient sources turn out to be anthropogenic.

For all these reasons, expanded observational and modeling studies are needed to understand the GASB's physical, biological, and chemical drivers. Moreover, the societal need for scientific understanding is urgent: improved seasonal to interannual predictions would offer tremendous value for proactive planning and response, while quantification of the underlying causes could inform potential management actions to mitigate the problem.

Methods

Sampling was conducted on R/V *Thomas G. Thompson* voyages TN389 (16 March – 16 April 2021) and TN390 (20 April – 16 May 2021), occupying GO-SHIP lines A20⁵⁴ and A22⁵⁵, respectively.

Hydrography

Hydrographic profiles and water samples were collected with a standard Conductivity, Temperature, Depth (CTD) rosette system with Niskin bottles. Nutrient analyses were carried out at sea using a Seal Analytical continuous-flow AutoAnalyzer 3, consistent with the methods described in the GO-SHIP repeat hydrography manual⁵⁶.

Sargassum collection and identification

Sargassum spp. samples were collected with a dip net and sorted into the species and morphotypes, *S. natans* I and *S. fluitans* III per Parr³⁰. Recent literature has indicated the increasing presence of a previously rare form *S. natans* V III on the basis of both morphology²⁵ and genetics^{57,58}. Based on morphological similarity, any *S. natans* V III in our samples would have been classified as *S. fluitans* III.

Sargassum elemental analysis and isotopic composition

Samples for each morphotype were separated into up to three replicates as quantities allowed (6 to 10 thalli/species), rinsed briefly (3 to 5 s) in deionized water, cleaned of macroscopic epizoa and epiphytes, dried in a laboratory oven at 65 to 70°C for 48 h, and powdered with a mortar and pestle⁵³. The dried *Sargassum* samples were split in half and stored in plastic screw top vials. One half was used for arsenic analysis (see below), and the other half was shipped to the University of Georgia's Center for Applied Isotope Studies Stable Isotope Ecology Laboratory (UGA-SIEL; <https://cais.uga.edu/facilities/stable-isotope-ecology-laboratory/>) for analysis of $\delta^{15}\text{N}$ as well as %C and %N on a Thermo Delta V IRMS coupled to a Carlo Erba NA1500 CHN-Combustion Analyzer via a Thermo Conflo Interface. National Institute of Standards and Technology reference materials 8549, 8558, 8568, and 8569 were used to routinely calibrate working standards prepared in the laboratory. QA/QC results were incorporated into the raw data reports received by UGA-SIEL. The other part of this half sample was analyzed at UGA-SIEL for %P, where approximately 2 mg of dried tissue was weighed into crucibles, ashed at 500 °C for four hours and extracted with 0.2 mL of Aqua Regia acid^{59,60}. The acid extracts were then diluted 41:1 with deionized water for TP (as $\text{PO}_4\text{-P}$) analysis on an Alpkem 300 series analyzer.

Sargassum arsenic content

Arsenic content of *Sargassum* tissue was measured by the University of Missouri Soil and Plant Testing Laboratory (MU SPTL) using an Inductively Coupled Plasma Optical Emission Spectrometer (ICP-OES; Agilent 5800; $\lambda_{\text{As}} = 188.980$ nm). Subsamples of rinsed, dried, and powdered *Sargassum* tissue from the GO-SHIP A20/A22 expeditions were digested at MU SPTL in 2022 according to EPA method 3052. In brief, the powdered samples were digested with a combination of HNO_3 acid at 175°C for 15 minutes using a microwave-accelerated digestion system (CEM MARS Xpress). Samples collected prior to the 2021 surveys were retrieved from the B. Lapointe archives (1980-2018) at the Harbor Branch Oceanographic Institute, Florida Atlantic University. Prior to sending to the MU SPTL for ICP-OES analysis, this subset was digested at the National High Magnetic Field Laboratory at Florida State University (P. Morton) in 2020 following a two-step process. First, ~0.1 g aliquots of powdered sample were carefully weighed into 15-mL Teflon digestion beakers (Savillex), to which 3 mL of concentrated HNO_3 acid (Fisher Optima) were added. The beakers were tightly capped and left overnight (~12 hours) on a hotplate at 150°C. The beakers were then uncapped, and the digested sample taken to dryness (150°C, 2-4 hrs). The sample residue was then digested a second time (capped, 150°C,

overnight) using 3 mL concentrated HNO₃ (Fisher Optima) and 200 µL of concentrated HF (Fisher Optima). The samples were taken to dryness again (uncapped, 150°C) and the residue dissolved in 3.0 mL of 0.32 M HNO₃ (Fisher Optima).

All samples were analyzed at MU SPTL with ICAP-OES at a 1/100 dilution to bring the As concentrations into working range of the matrix-matched (0.16 M HNO₃) external standard calibration curve. Triplicate independent digestions and analyses of four *Sargassum* tissue samples were used to determine the representative reproducibility of the sample processing and instrumental analysis methods. For more details see <https://extension.missouri.edu/programs/soil-and-plant-testing-laboratory/spl-researchers>.

Backtracking of source waters

At each station where *Sargassum* was collected, the source waters were assessed by tracking particles backward in time for 60 days using a Lagrangian algorithm⁶¹. Surface currents were specified from the OSCAR 1/3° resolution analysis, described at <https://www.esr.org/research/oscar/oscar-surface-currents/> and available at https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg. A total of 100 particles were released at each location where *Sargassum* was found, with random walk diffusion applied each time step Δt with gaussian perturbations σ defined by $\sigma^2 = 4D\Delta t$. The horizontal diffusivity D was chosen to be 4000 m² s⁻¹ based on estimates for this region derived from Argo float observations⁶². In addition to being affected by surface currents, wind also influences *Sargassum* transport^{31,32}. Windage factors ranging from 0.5% and 3% produce the most accurate simulations of *Sargassum* trajectories^{63,64}, and a mid-point value of 2% was used here. Wind forcing was specified using daily NCEP/NCAR reanalysis⁶⁵ and validated with shipboard meteorological measurements made on R/V *Thomas G. Thompson* during voyages TN389 and TN390.

Satellite observations

Pelagic *Sargassum* distributions were derived from MODIS measurements using a floating algal index^{26,66,67}. MODIS data were obtained from the U.S. National Aeronautics and Space Administration (NASA) Goddard Space Flight Center (<https://oceancolor.gsfc.nasa.gov>). Surface salinity distributions were obtained from SMOS Earth Explorer mission and the data were accessed on <https://www.catds.fr/Products/Available-products-from-CPDC>.

Data availability

Sargassum tissue data are available as separate files in the Supplementary Information.

Shipboard hydrographic data:

<https://cchdo.ucsd.edu/cruise/325020210316> (TN389)

<https://cchdo.ucsd.edu/cruise/325020210420> (TN390)

Surface currents used for particle tracking:

https://podaac.jpl.nasa.gov/dataset/OSCAR_L4_OC_third-deg

Satellite-based surface salinity:

<https://www.catds.fr/Products/Available-products-from-CPDC>

Raw data for computation of satellite-based *Sargassum* distributions:

<https://oceancolor.gsfc.nasa.gov>

Sargassum density distribution maps:

<https://optics.marine.usf.edu/projects/saws.html>

Code availability

Particle tracking code: <https://doi.org/https://doi.org/10.5281/zenodo.3468524>

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569

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Author contributions

The following uses categories defined at: <https://www.elsevier.com/authors/policies-and-guidelines/credit-author-statement>

D.J.M. Conceptualization, methodology, formal analysis, investigation, writing-original draft, writing-reviewing and editing.

R.A.B. Data curation, writing - review and editing.

C.H. Investigation, writing - review and editing.

T.B.K. Investigation, writing - review and editing.

P.L.M. Investigation, resources, writing – review and editing.

A.R.S. Formal analysis, writing – review and editing.

B.E.L. Conceptualization, methodology, investigation, writing-reviewing and editing.

Competing Interests

The authors declare no competing interests.

Figures

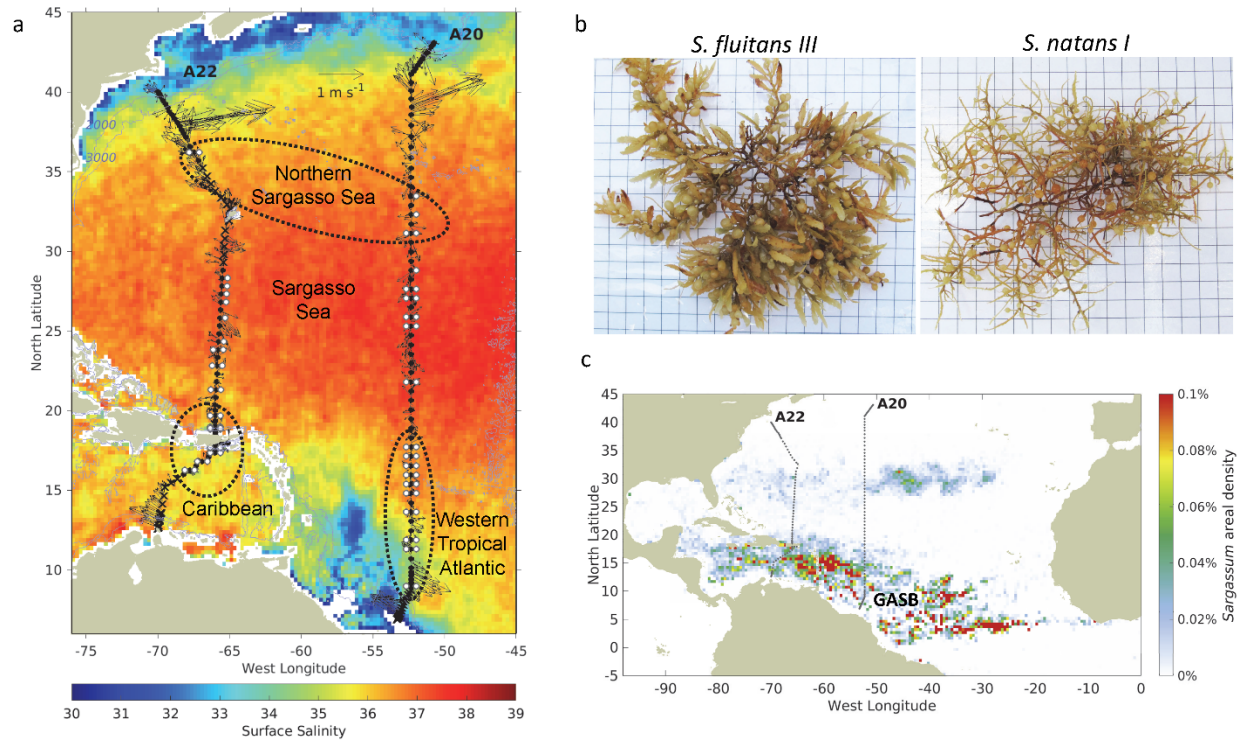


Fig. 1. *Sargassum* sampling on GO-SHIP lines A20 (16 March – 16 April 2021) and A22 (20 April – 16 May 2021). **a**, White circles indicate collection of *Sargassum* samples, with *S. fluitans III* shown to the left and *S. natans I* to the right of the station locations, which are indicated as black circles (where *Sargassum* sampling was possible), and black Xs (where *Sargassum* sampling was not possible). Dashed black lines indicate sample groupings in the northern Sargasso Sea, Sargasso Sea, western tropical Atlantic, and Caribbean. Velocity vectors are from the uppermost bin (centered at 29 m depth) of the ship's ADCP. The surface salinity field is comprised of a time-average of SMOS measurements for the cruise period (16 March – 16 May, 2021). **b**, Photographs of *S. fluitans III* and *S. natans I* samples on a 1 cm grid background. Photo credit: Amy Siuda and Jeffrey Schell, Sea Education Association. **c**, Location of GO-SHIP lines A20 and A22 relative to the GASB (contiguous area of *Sargassum* coverage surrounding the annotation) for the cruise period estimated from MODIS data. Blue lines are the 2000 m and 3000 m isobaths.

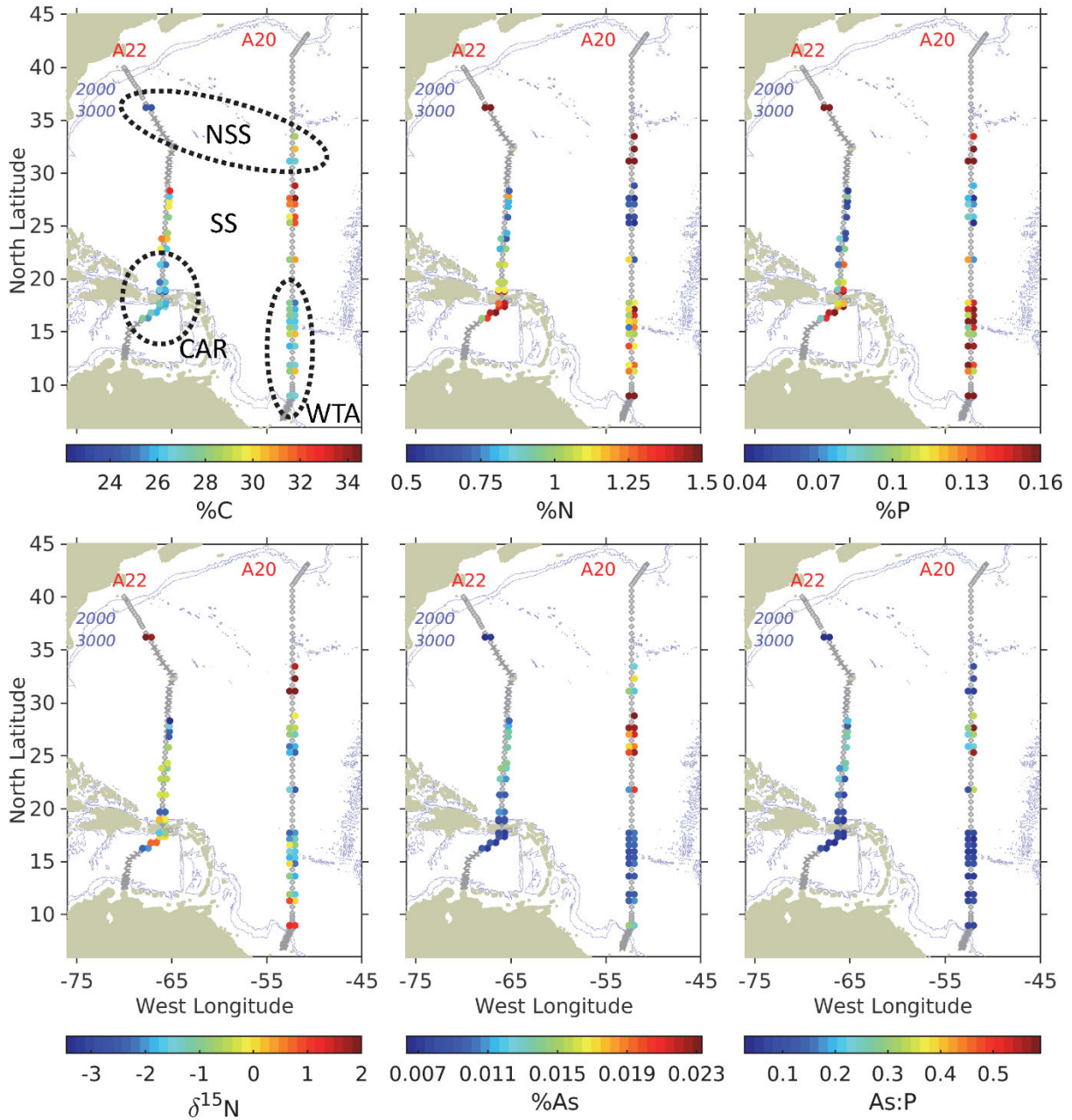


Fig. 2. *Sargassum* tissue data: Top row: carbon (left), nitrogen (middle), and phosphorus (right) content (% dry weight). Bottom row: $\delta^{15}\text{N}$ values, arsenic content, and arsenic to phosphorus ratio in *Sargassum* tissue. *S. fluitans* III is shown to the left of transects A20 and A22, and *S. natans* I to the right. Stations where no *Sargassum* was found are shown as circles, and stations where *Sargassum* sampling was not possible are shown as Xs. Dashed black lines in the upper left panel indicate sample groupings in Northern Sargassum Sea (NSS), Sargassum Sea (SS), Caribbean (CAR), and Western Tropical Atlantic (WTA), as in Fig. 1. Blue lines are the 2000 m and 3000 m isobaths.

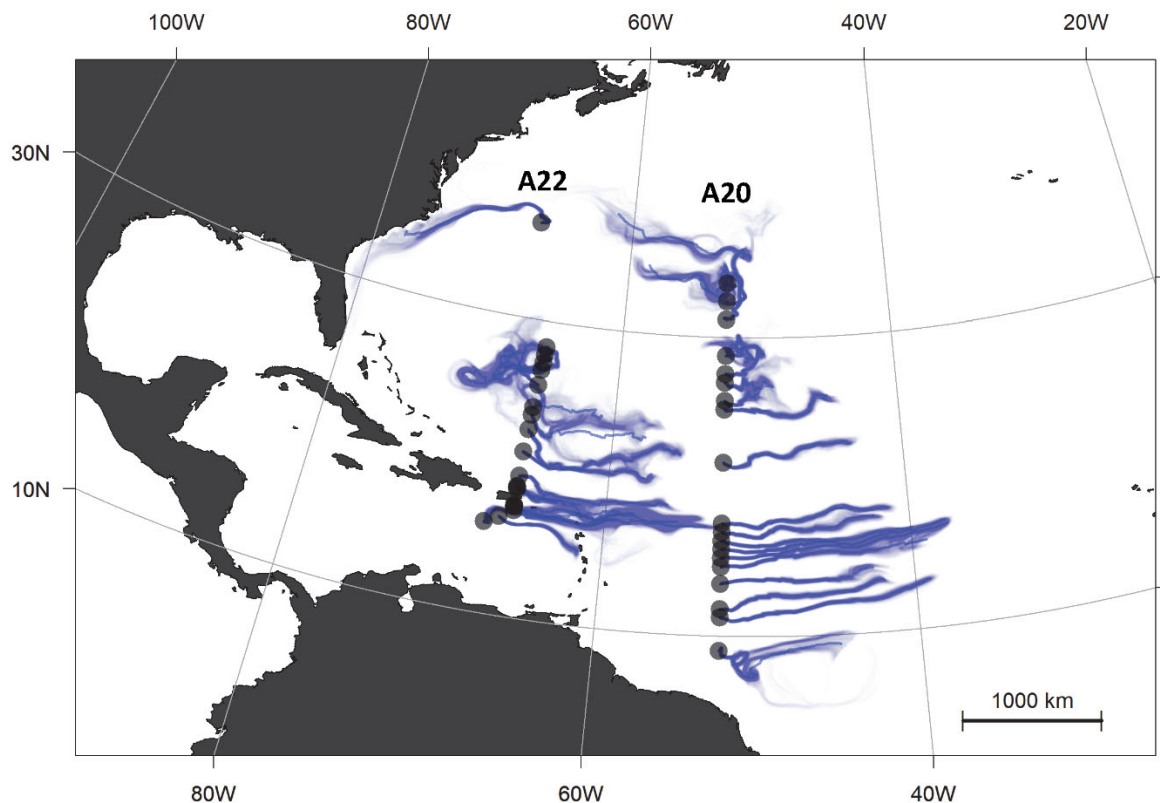


Fig. 3. Origins of *Sargassum* spp. samples from GO-SHIP lines A20 and A22. Surface particles deployed at sample collection sites (Figs. 1 and 2) were tracked back in time for 60 days. The centroid of the ensemble is shown as a bold blue line with individual trajectories shown in lighter blue.

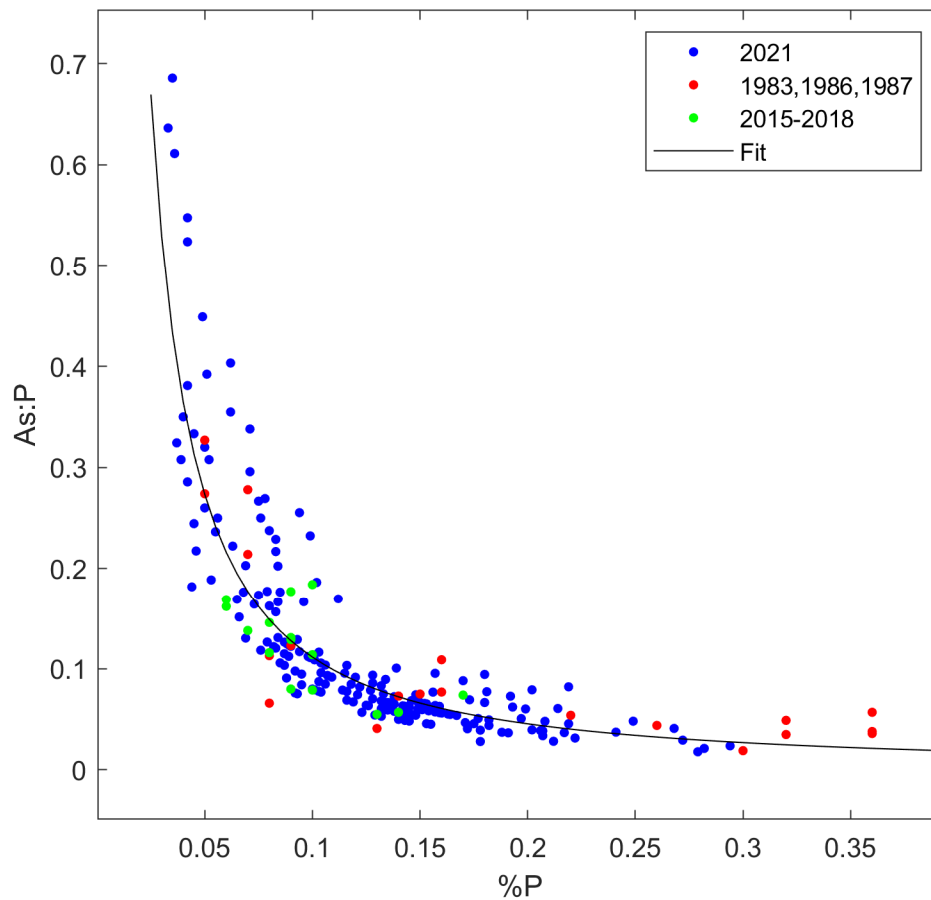


Fig. 4. Arsenic to phosphorus ratio as a function of phosphorus content in *Sargassum* tissue. Data from GO-SHIP lines A20 and A22 in 2021 are in blue (N=200), 1983-1987 in red (N=20), and 2015-2018 in green (N=21). Black line is the fit described in the Supplementary Note.

Supplementary Information

Supplementary Table 1. Subregional comparisons of elemental composition (% dry weight) and ratios, as well as stable isotope values (‰) for *S. fluitans* and *S. natans*. Mean and 95% confidence interval are indicated in each case. See Fig. 1 for geographic boundaries of the subregions.

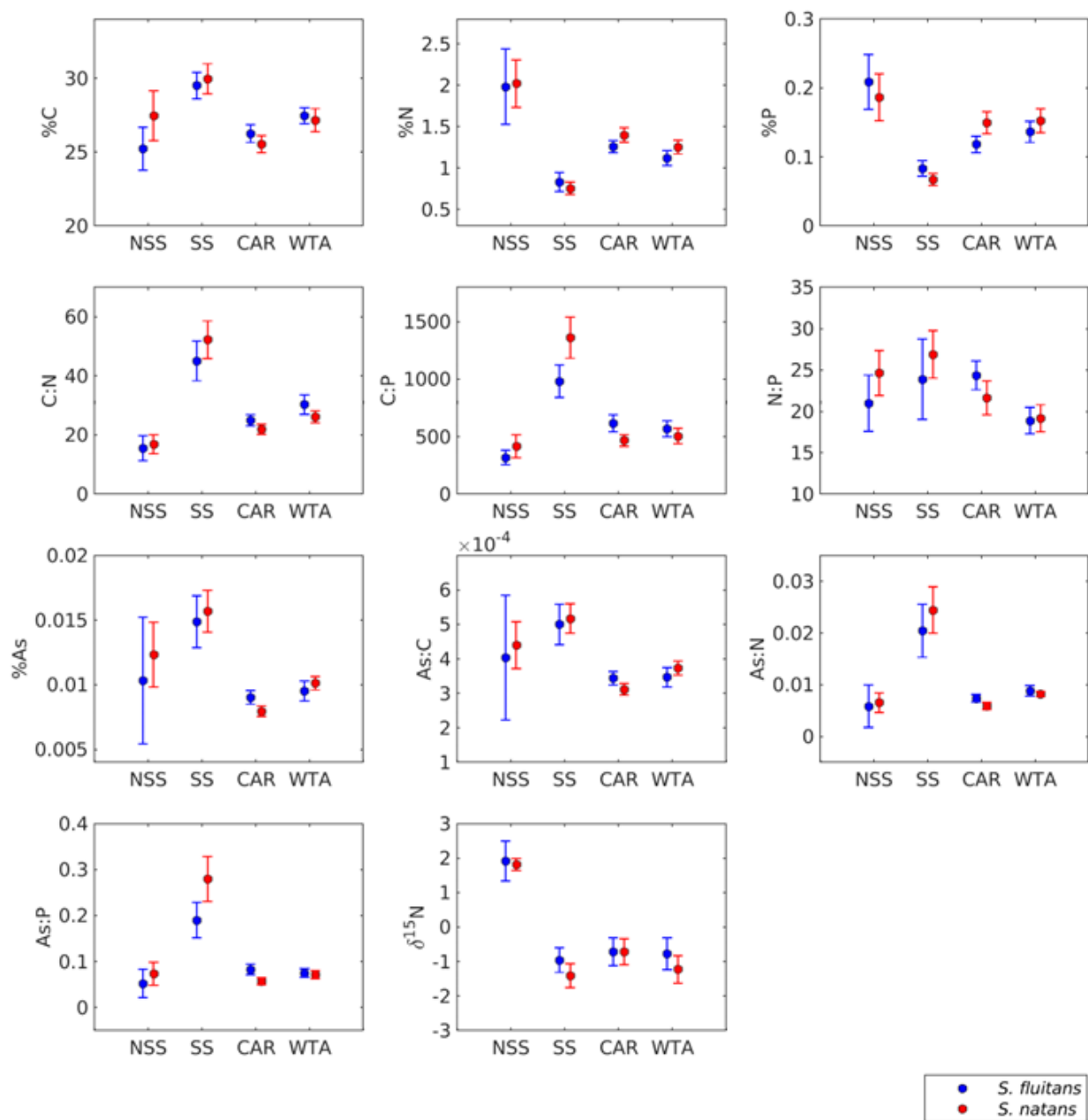
	Northern Sargasso Sea		Sargasso Sea		Caribbean		Western Tropical Atlantic	
	<i>S. fluitans</i>	<i>S. natans</i>	<i>S. fluitans</i>	<i>S. natans</i>	<i>S. fluitans</i>	<i>S. natans</i>	<i>S. fluitans</i>	<i>S. natans</i>
N	6	12	20	43	30	29	30	30
%C	25.2 ± 1.5	27.5 ± 1.7	29.5 ± 0.9	30.0 ± 1.0	26.3 ± 0.6	25.6 ± 0.6	27.5 ± 0.5	27.2 ± 0.8
%N	2.0 ± 0.5	2.0 ± 0.3	0.8 ± 0.1	0.8 ± 0.1	1.3 ± 0.1	1.4 ± 0.1	1.1 ± 0.1	1.3 ± 0.1
%P	0.21 ± 0.04	0.19 ± 0.03	0.08 ± 0.01	0.07 ± 0.01	0.12 ± 0.01	0.15 ± 0.02	0.14 ± 0.02	0.15 ± 0.02
C:N	15.6 ± 4.3	16.9 ± 3.2	45.1 ± 6.7	52.3 ± 6.4	25.1 ± 1.8	22.0 ± 1.7	30.4 ± 3.3	26.2 ± 2.0
C:P	320 ± 63	419 ± 100	984 ± 142	1363 ± 179	619 ± 74	469 ± 49	570 ± 71	506 ± 67
N:P	21.0 ± 3.4	24.7 ± 2.7	23.9 ± 4.8	26.9 ± 2.9	24.4 ± 1.7	21.6 ± 2.0	18.9 ± 1.6	19.2 ± 1.6
δ ¹⁵ N	1.93 ± 0.58	1.82 ± 0.18	-0.95 ± 0.36	-1.40 ± 0.34	-0.71 ± 0.41	-0.71 ± 0.37	-0.77 ± 0.46	-1.22 ± 0.40
%As	0.010 ± 0.005	0.012 ± 0.003	0.015 ± 0.002	0.016 ± 0.002	0.009 ± 0.001	0.008 ± 0.0004	0.010 ± 0.001	0.010 ± 0.001

Supplementary Table 2. Statistical significance (p-values of two-sided t-tests) for subregional comparisons of mean elemental composition, stoichiometry, and stable isotope values for the combined species *S. fluitans* and *S. natans*. Cells with p-values in excess of 0.05 are highlighted. See Fig. 1 for geographic boundaries of sample groupings in the Northern Sargasso Sea (NSS), Sargasso Sea (SS), Caribbean (CAR), and Western Tropical Atlantic (WTA).

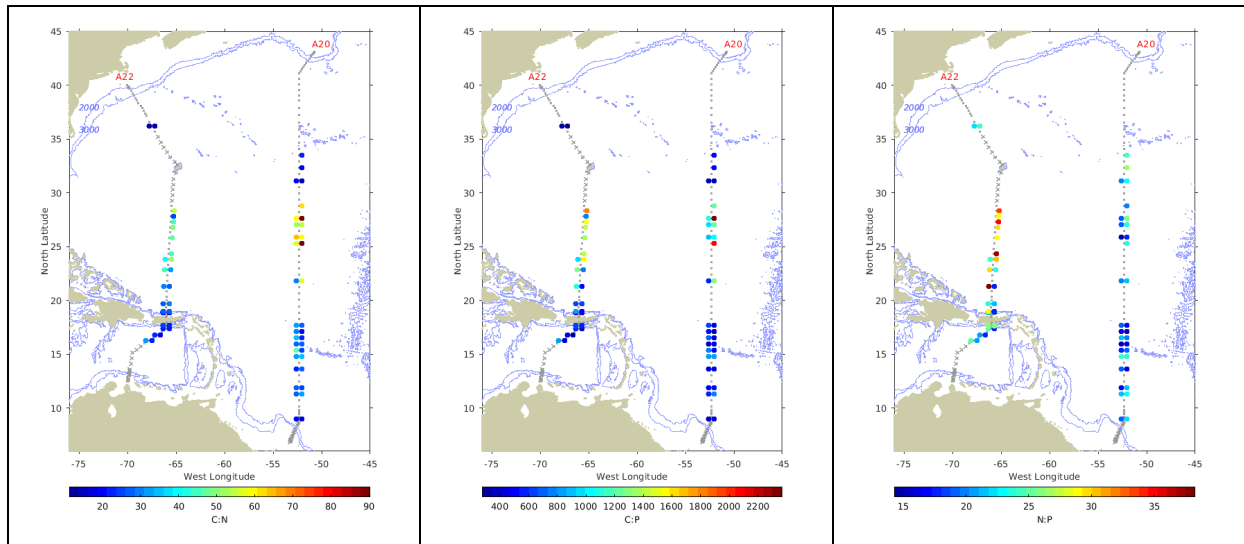
%C	SS	CAR	WTA	%N	SS	CAR	WTA	%P	SS	CAR	WTA
NSS	1.03e-04	0.21	0.36		2.40e-10	2.94e-06	1.79e-07		2.53e-09	7.82e-05	7.19e-04
SS		6.94e-15	1.08e-07			3.88e-25	4.20e-16			1.56e-16	2.91e-18
CAR			1.33e-05				9.80e-04				0.17
C:N				C:P				N:P			
NSS	1.10e-20	4.42e-06	2.31e-10		3.87e-18	3.55e-04	6.10e-04		0.11	0.74	6.72e-04
SS		2.65e-16	1.29e-12			7.24e-15	4.68e-15			0.04	1.46e-06
CAR			1.03e-04				0.83				1.24e-05
%As				As:C				As:N			
NSS	2.73e-03	5.38e-03	0.09		0.02	4.50e-03	0.04		1.12e-13	0.68	0.01
SS		1.27e-16	9.99e-13			4.01e-16	3.36e-12			6.11e-14	4.70e-12
CAR			9.62e-06				3.67e-03				4.03e-06
As:P				δ ¹⁵ N							
NSS	6.58e-14	0.74	0.48		2.74e-31	1.91e-25	1.59e-26				
SS		2.28e-14	4.74e-14			3.88e-03	0.19				
CAR			0.49				0.16				

Supplementary Table 3. Summary of least squares fits $y = ax + b$ for arsenic content as a function of phosphorus, nitrogen, and carbon content (% dry weight). Asterisk indicates p-values so low that they could not be distinguished from zero.

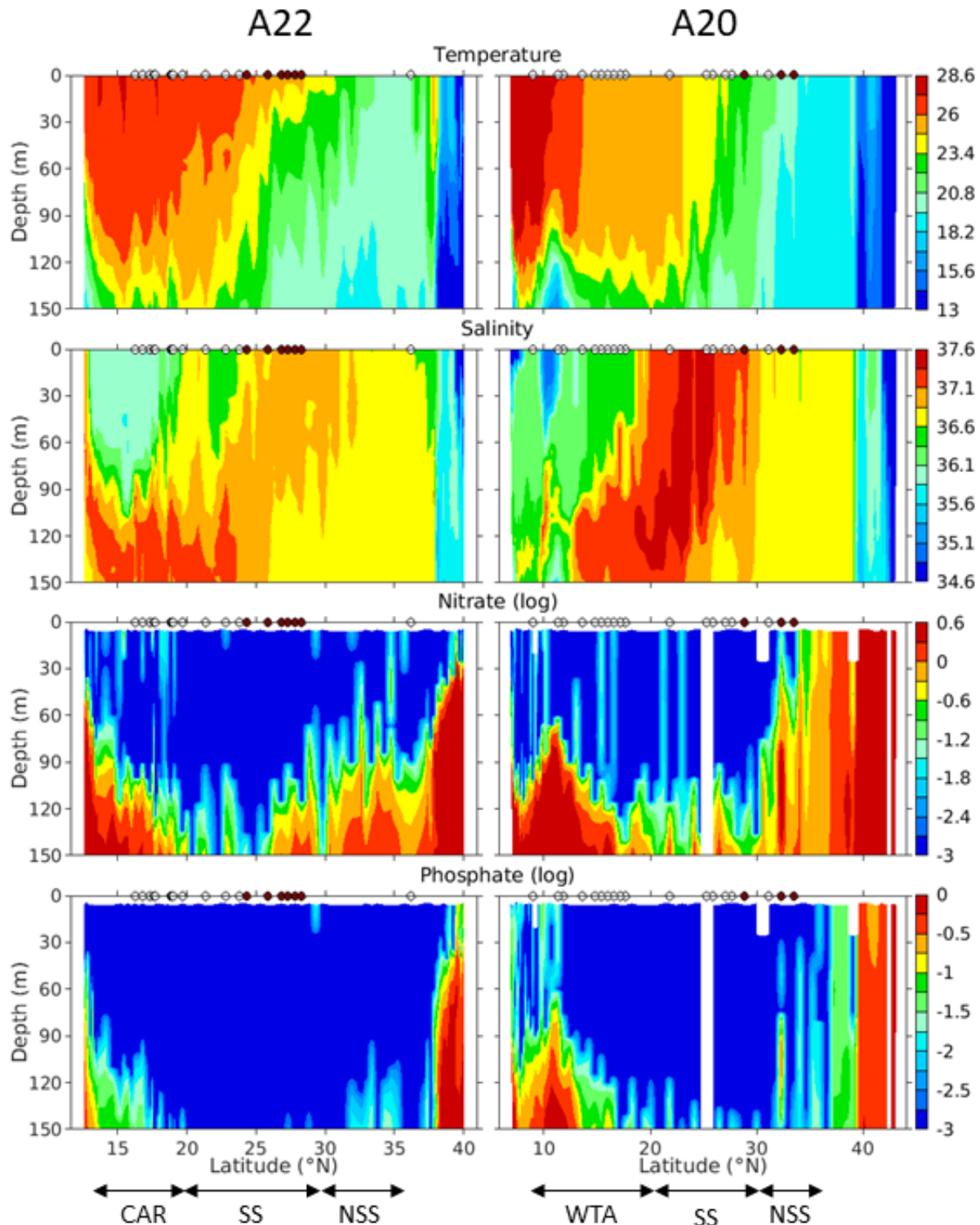
y	x	r ²	Intercept (b)	p	Slope (a)	p
As	P	0.23	1.60e-02	0.00e+00*	-3.79e-02	1.16e-12
As	N	0.27	1.75e-02	0.00e+00*	-5.25e-03	3.66e-15
As	C	0.50	-1.98e-02	3.33e-16	1.13e-03	0.00e+00*



669
670 Supplementary Fig. 1. Subregional comparisons (by species) of carbon, nitrogen, and
671 phosphorus content (top row), elemental ratios (middle row and bottom left), and stable isotope
672 values (bottom row, middle and right) for the Northern Sargasso Sea (NSS), Sargasso Sea (SS),
673 Caribbean (CAR), and Western Tropical Atlantic (WTA). Error bars are 95% confidence
674 intervals.

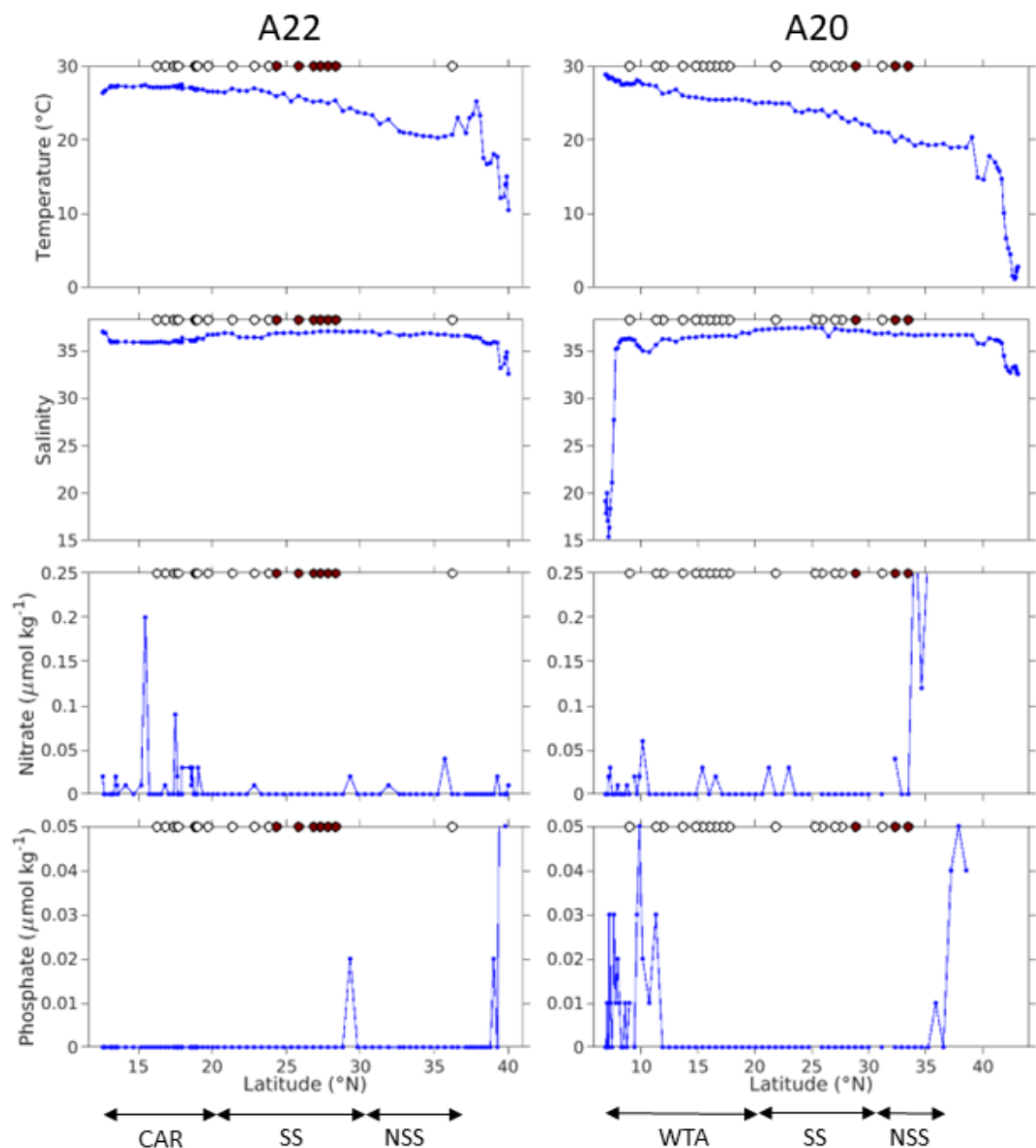


Supplementary Fig. 2. *Sargassum* elemental ratios: carbon to nitrogen (left), carbon to phosphorus (middle), and nitrogen to phosphorus (right). *S. fluitans III* is shown to the left of transects A20 and A22, and *S. natans I* to the right. Stations where no *Sargassum* was found are shown as circles, and stations where *Sargassum* sampling was not possible are shown as Xs. Blue lines are the 2000 m and 3000 m isobaths.



Supplementary Fig. 3. Vertical sections of temperature (°C), salinity, nitrate, and phosphate for A22 (left) and A20 (right). Nitrate and phosphate concentrations ($\mu\text{mol kg}^{-1}$) have been log transformed in order to better resolve gradients at low concentrations. Circles along the top of each plot indicate stations where *Sargassum* was collected: *S. fluitans* and *S. natans* (white) and *S. natans* only (brown). Northern Sargasso Sea (NSS), Sargasso Sea (SS), Caribbean (CAR), and Western Tropical Atlantic (WTA) regions are indicated.

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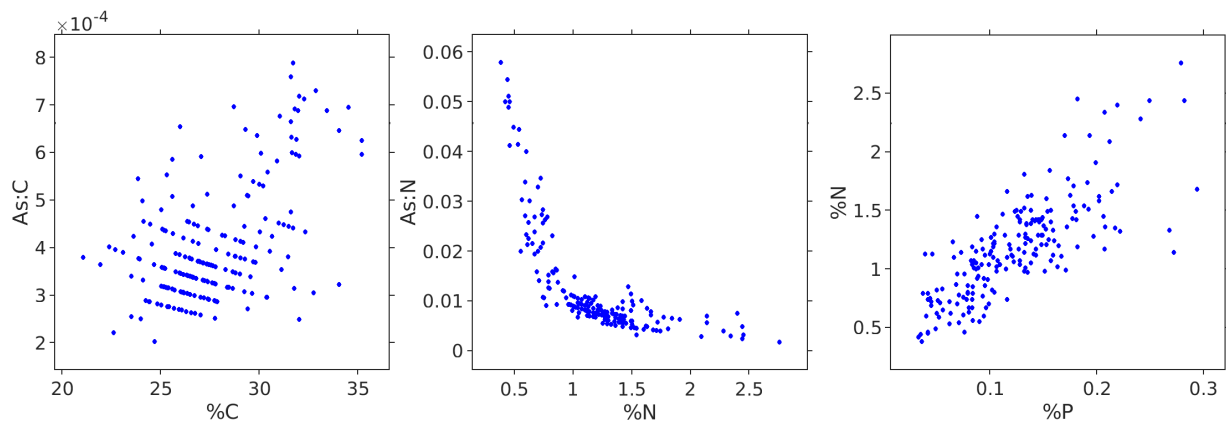
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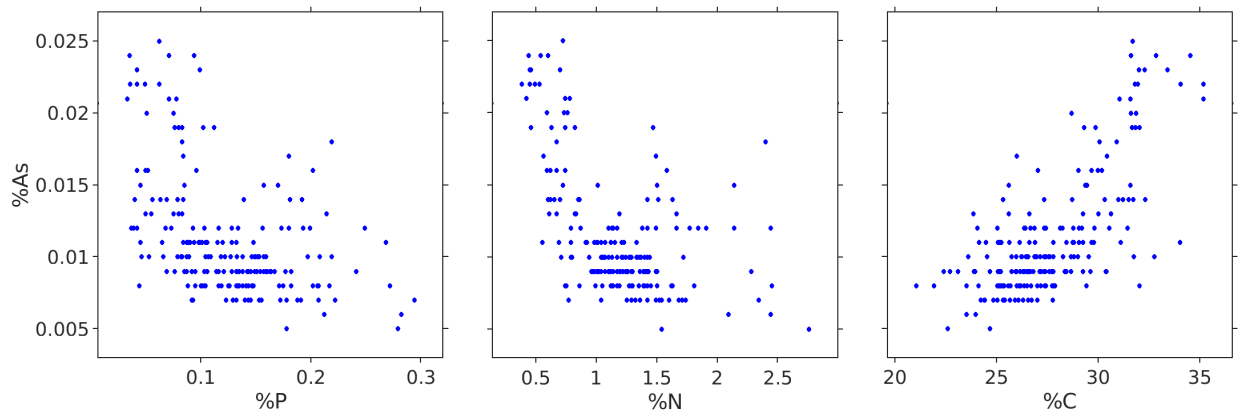
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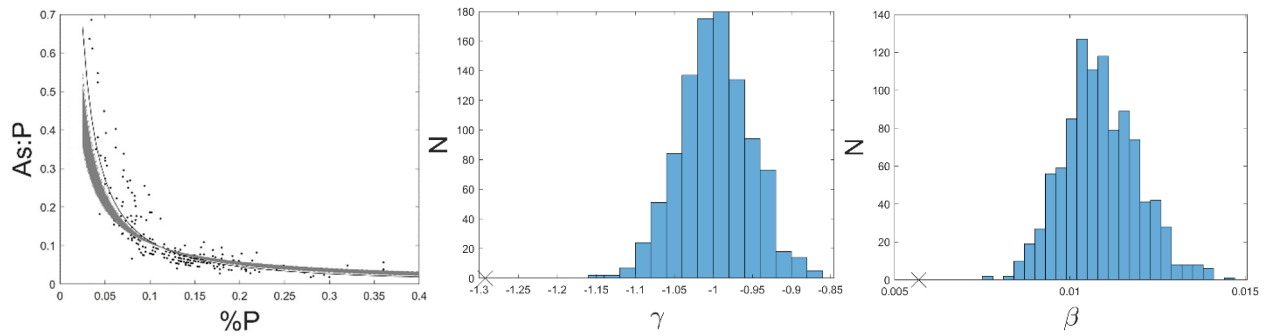
Supplementary Fig. 4. Surface temperature, salinity, nitrate, and phosphate for A22 (left) and A20 (right). Circles along the top of each plot indicate stations where *Sargassum* was collected: *S. fluitans* and *S. natans* (white) and *S. natans* only (brown). Northern Sargasso Sea (NSS), Sargasso Sea (SS), Caribbean (CAR), and Western Tropical Atlantic (WTA) regions are indicated.



Supplementary Fig. 5. Elemental ratios in *Sargassum* tissue. Left: arsenic to carbon ratio as a function of carbon content; middle: arsenic to nitrogen ratio as a function of nitrogen content; right: nitrogen content as a function of phosphorus content.



Supplementary Fig. 6. Arsenic in *Sargassum* tissue. Left: arsenic as a function of phosphorus content; middle: arsenic as a function of nitrogen content; right: arsenic content as a function of carbon content. Results of least squares fits are presented in Supplementary Table 3.



Supplementary Fig. 7. Left: Fits of the arsenic to phosphorus ratio in *Sargassum* ratio as a function of phosphorus content. Solid line is the fit to the data from Fig. 4 (black dots), and the gray lines are 1000 trials using the permuted phosphorus data as described in the Supplemental Note. Middle and left panels report the distribution of parameters γ and β for the permuted data (blue bars) and the actual data (X on the x-axes).

Supplementary Note

The general model relating observations i of arsenic and phosphorus content we wish to test is

$$\frac{As_i}{P_i} = \beta P_i^\gamma \quad (1)$$

Where $\gamma = -1$ would constitute the $\frac{1}{P}$ dependence predicted by the theory. This model can be recast as

$$\log(As_i) = c + (\gamma + 1)\log(P_i) \quad (2)$$

where $c = \log(\beta)$. The parameters c and γ were estimated by least squares, and it turns out that the dependence of As:P on P is supra-hyperbolic: $\gamma = -1.29 \pm 0.04$. We tested the statistical robustness of this finding by permuting the independent variable P_i in Equation (2) 1000 times, and the fit to the actual data falls outside that envelope (Supplementary Fig. 7). Thus, we conclude our result is robust with $p < 0.001$.

We note that recent observations suggest variation of As content among genotypes, with *S. natans VIII* having higher As content than *S. natans I* and *S. fluitans III*^{20,52}. Because our methods did not distinguish *S. natans VIII*, it would have been grouped together with *S. fluitans III* due to their morphological similarity. Our data do not indicate large variations in As content among the species we resolved (Supplementary Fig. 1, Supplementary Table 1), so this analysis was based on the As content of the combined species.

20 Cipolloni, O.-A. *et al.* Metals and metalloids concentrations in three genotypes of pelagic *Sargassum* from the Atlantic Ocean Basin-scale. *Marine Pollution Bulletin* **178**, 113564 (2022). <https://doi.org/10.1016/j.marpolbul.2022.113564>

52 Gobert, T. *et al.* Trace metal content from holopelagic *Sargassum* spp. sampled in the tropical North Atlantic Ocean: Emphasis on spatial variation of arsenic and phosphorus. *Chemosphere* **308**, 136186 (2022). <https://doi.org/10.1016/j.chemosphere.2022.136186>