

Surface *Sargassum* and Pollution Observations in the Sargasso Sea over Five Decades (1974–2024)

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A Report Submitted to the Sargasso Sea Commission



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Cover photo: Sea Education Association's research vessel, the SSV *Corwith Cramer*, sailing in the Sargasso Sea with holopelagic *Sargassum*. Photo credit: S. Zankl.

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The Sargasso Sea Commission works to “encourage and facilitate voluntary collaboration toward the conservation of the Sargasso Sea.” The Hamilton Declaration on Collaboration for the Conservation of the Sargasso Sea, established in 2014, provides a framework for voluntary collaboration between ten signatory governments and a Commission of scientific experts operating in their independent capacities for the conservation of the Sargasso Sea.

This work is an underlying report to the Socio-Ecosystem Diagnostic Analysis (SEDA) for the Sargasso Sea—the first analysis of its kind of a high seas ecosystem.

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A full version of this report and of the reports commissioned by the SSC are available for download on the website at www.sargassoseacommission.org

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CHAPTER 1

Introduction

1.1 Sea Education Association

Sea Education Association (SEA; www.sea.edu) is a global teaching, learning, and research community dedicated to the exploration, understanding, and stewardship of marine and maritime environments. For over 50 years, SEA has empowered students with life-changing sea voyages aboard tall ships and coastal community interactions focused on scientific and cultural discovery, academic rigor, and personal growth. All SEA programs feature an interdisciplinary curriculum and dynamic leadership-development experiences.

Through week- to semester-long offerings, SEA educates and inspires ocean scholars, stewards, and leaders. The organization fosters and enhances knowledge about the state of oceans and coastal communities. It also helps shape public dialogue and policy through long-term environmental research, global partnerships, and the continued impact of students, faculty, and alumni worldwide. SEA programs are learning communities focused on addressing critical issues such as climate change, sustainability, biodiversity, human impacts on the ocean, and environmental justice. Acknowledging that human actions underlie environmental change, these issues must be approached from multiple disciplines across ocean sciences and blue humanities.

A core principle of SEA's academic approach is 'learning by doing.' Students explore the marine environment by conducting independent scientific research. SEA's ships are equipped with state-of-the-art oceanographic labs and participating students deploy equipment, process samples, collect data, and contribute to what we know about the world's oceans. While over the decades many research topics have been explored, from the earliest days of the institution SEA students documented the presence of floating plastic, tar, and *Sargassum* alongside zooplankton community composition and hydrographic conditions (Carpenter, 2022). The results presented in this report were generated during SEA Semester program voyages.

1.2 The Sargasso Sea

The Sargasso Sea is the western subregion of the North Atlantic Subtropical Gyre, bounded by clockwise-flowing

currents and defined by a combination of ecological and oceanographic characteristics. The Gulf Stream establishes the Sargasso Sea's western boundary, the North Atlantic Drift demarks the northern edge, and the Antilles Current flows along the south; over time, the eastern extent of the region has been drawn at a variety of longitudes (Winge, 1923; Laffoley et al., 2011) and remains the least certain aspect of its definition. Light and variable winds dominate under the Bermuda High, and properties such as sea surface temperature, salinity, primary productivity, and a unique pelagic ecosystem distinguish the Sargasso Sea from its surrounding North Atlantic marine regions. As early as Columbus's voyage in 1492, the distinctive and fascinating floating *Sargassum* macroalgae was recognized as a key feature of the surface ocean environment and used to delimit its boundaries (Winge, 1923). Bermuda and its associated Exclusive Economic Zone fall within the Sargasso Sea but the vast majority of the region lies beyond national jurisdiction in the high seas, presenting challenges for conservation and management. Subject to a diversity of human impacts—commercial fishing, international shipping traffic, and pollution among others—the Sargasso Sea nonetheless provides resources and ecosystem services that benefit nations throughout the Atlantic basin (Laffoley et al., 2011).

SEA's regular voyages between Woods Hole, MA, USA and the Caribbean Sea result in consistent transits of and sampling within the Sargasso Sea region during fall, winter, and spring seasons. Occasionally, summertime cruises from New England crossed the Gulf Stream into the North Sargasso Sea. Early voyages between 1977–1981 found *Sargassum* in 76% of Sargasso Sea neuston net tows (Stoner, 1983). Similarly, microplastics were collected in 100% of North Sargasso tows from 1984–87 and 67% of those conducted in the South Sargasso Sea (Wilbur, 1987). Floating tar was also documented in >81% of surface net tows between 1982–1996 (Joyce, 1998).

Surface neuston net tow data from SEA's autumn and spring cruises through the Sargasso Sea during the organization's first three decades (1977–2010) were summarized by Siuda (2011) in a commissioned report for the Sargasso Sea Alliance supporting the scientific case for the

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region's global importance. The present report is both an extension and update of Siuda (2011), broadening the summarized data sets, comparing the most recent period to historical records, and offering an assessment of ecological change over time. This synthesis of SEA marine plastics, floating tar, holopelagic *Sargassum*, and

Sargassum-associated ecology data was requested by the Sargasso Sea Commission as part of the UNESCO Global Environment Facility Council Areas Beyond National Jurisdiction program's "Strengthening the stewardship of an economically and biologically significant high seas area—the Sargasso Sea" project initiated in 2024.

CHAPTER 2

Sea Education Association Field and Laboratory Methods

Most data summarized in this report were collected from SEA's sailing oceanographic research vessels, the *SSVs Westward* and *Corwith Cramer*, during annually-repeated cruises of opportunity through the North Atlantic. Voyages were not designed specifically for scientific monitoring but rather to optimize weather and sailing conditions; the majority of Sargasso Sea cruises were carried out within the SEA Semester program.

Unless otherwise specified, graphs and summary statistics herein utilize only data from the Sargasso Sea Geographical Area of Collaboration (Laffoley et al., 2011) including waters within the Bermuda Exclusive Economic Zone. For consistency with Siuda's (2011) report and because they offer the greatest annual suite of observations, autumn/spring cruises transiting the region were the focus; exceptions are noted in section introductions and figure captions. For temporal analyses, data were organized by 'ecological year' (the period from October in the previous year through May in the current year) to align with the known seasonal cycle of holopelagic *Sargassum* growth, transport, and senescence. Sampling stations were designated as in the North or South Sargasso Sea region based on Ullman et al.'s (2007) autumn/spring subtropical convergence zone position.

2.1 Neuston Net Tow Field Protocols

Microplastics, tar, *Sargassum*, and biological samples were collected with a surface skimming rectangular neuston net (1 m wide x 0.5 m high, 333 μm mesh) towed at the air-sea interface (Figure 2.1) for approximately 1 nautical mile at a target ship speed of 2 knots. Tow distances (m) were determined based on speed/time (1973-1992), from a mechanical taffrail log deployed off the ship's stern that measured distance travelled through the water (1992-2007), or using GPS positions recorded every minute during the tow (2008-2024). Tow distance was used to compute the ocean surface area sampled by the net (tow distance x 1 m net width = tow area in m^2). While current (2008-present) protocols call for 1200 and 0000 neuston net tows each day the vessel is underway, earlier cruises may not have followed the same schedule. Neuston sampling through 1986 was conducted using a 500 μm mesh net, which should result in lower densities

of small zooplankton but not impact densities of nekton, microplastics, tar, or *Sargassum*.

Following each tow, net contents were processed as soon as possible following SEA's standard procedure that has remained consistent over time. Organisms >2 cm (nekton) and floating material (anthropogenic and biological) were first removed, a 1 mL sample of remaining zooplankton biomass was set aside for microscope-aided community composition analysis, and total zooplankton biomass was determined via volume displacement. Nekton were categorized taxonomically and enumerated, often including migrating mesopelagic fish, juvenile pelagic fish, larval eels, spiny lobster larvae, stomatopod larvae, gelatinous organisms, and occasionally larger endemic *Sargassum* fauna. Specimens of the marine insect *Halobates* were also enumerated and removed from the zooplankton biomass.

Qualitative comments related to community composition of marine fauna >2 cm were available for the majority of neuston tows. A lack of qualitative record may either indicate that no nekton were collected or that the information was not recorded on the datasheet. Even when qualitative comments were recorded on a datasheet, the list of organisms may not be comprehensive. In some cases, numbers and/or biovolumes of nekton were recorded, but this practice was not consistent throughout the early portion of the archive. Species-level visual identification was possible for many taxa though not all.

All plastic particles visible to the naked eye (typically millimeters in size) were hand-picked out of the neuston net sample, rinsed, enumerated, air-dried, and archived for future analysis. Industrial resin pellets, which are easily identifiable by visual appearance, were counted separately from other particles. Plastic density was computed as the total number of pieces collected (pellets plus particles) divided by tow area, reported in units of pieces km^{-2} . Where encountered, pelagic tar balls were removed from neuston tow contents, rinsed, enumerated, and archived for future analysis.

Every piece of *Sargassum* caught in the neuston net was counted and bulk weight (g) measured using a spring scale. Prior to 1990, only total *Sargassum* was recorded. Since then, however, all collected *Sargassum* has been

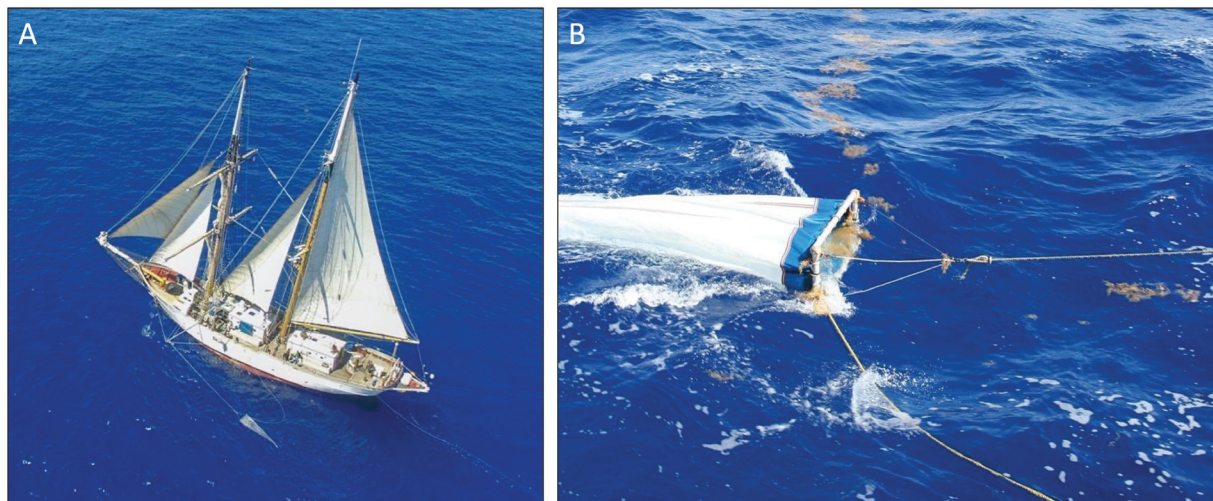


FIGURE 2.1. Neuston net A) towing along the port side of Sea Education Association’s sailing research vessel SSV *Corwith Cramer*, and B) sampling *Sargassum* as well as other floating material and organisms at the air-sea interface. Photo credits: C. Nolan (a) and J. Schell (b).

identified to species and variety on the basis of morphological characteristics and weight of each type recorded separately (Winge, 1923; Parr, 1939; Schell et al., 2015; Siuda et al., 2024). Total and variety-specific *Sargassum* densities were calculated as weight divided by tow area, reported in units of g m^{-2} . Because nets were towed from vessels under sail, neuston sampling was conducted perpendicular to the direction of the wind and therefore perpendicular to any *Sargassum* windrows encountered; densities are not biased by towing only between or along windrows.

SEA has conducted more than 9,200 neuston net tows in the North Atlantic over the past five decades (autumn/spring Sargasso Sea subset shown in Figure 2.2). In this report and related scientific publications, the total number of neuston tows analyzed for different parameters varies based on when within SEA’s history data collection started and mixed consistency of sampling focus in early years.

2.2 Hourly Observation Field Protocols

Visual field surveys have been conducted during most daylight hours since 2011 (Figure 2.3), yielding a highly spatiotemporally resolved (hourly and every 10 km) dataset. Each daytime observation occurred near the top of the hour for a 6-minute period ($1/10^{\text{th}}$ of an hour) and were systematic regardless of wildlife, marine debris, or macroalgal presence. Standing on the SSV *Corwith Cramer*’s quarterdeck at approximately 4 m height of eye, observers documented the presence and quantity of any

megafauna (seabirds, fish, sea turtles, marine mammals) within the entire field of view and any isolated target floaters (debris, *Sargassum*, other vegetation) alongside the port side of the ship. From the deck of the ship, no taxonomic differentiation of *Sargassum* spp. was possible. The date, time, GPS position, Beaufort Force, visibility, and relevant notes about key sightings were captured as metadata with each hourly observation.

Sargassum was recorded in multiple categories reflecting its general abundance in the region and different states of aggregation: fragments, clumps, windrows, and mats. Fragments and clumps were recorded when within 5 m of the ship. Windrows were counted when they passed perpendicular to the observer or within 50 m of the ship. Large mats were recorded when seen, typically within 100 m of the ship but occasionally at greater distance during calm conditions. *Sargassum* aggregation states were ranked (fragments/clumps < windrows < mats) and each observation assigned the highest aggregation state recorded during that period. Additional details of field and analytical methods for hourly observations available in Goodwin et al. (2022).

2.3 Dip Net Field Protocols

Discrete *Sargassum* clumps were collected by hand-held dip net for studies of associated motile epifauna (Martin et al., 2021), genetics (Dibner et al., 2021), and morphology (Siuda et al., 2024). The dip net (mouth dimensions 0.45 x 0.35 m, 333 μm mesh) was deployed from the vessel’s mid- or quarterdeck area only during calm sea

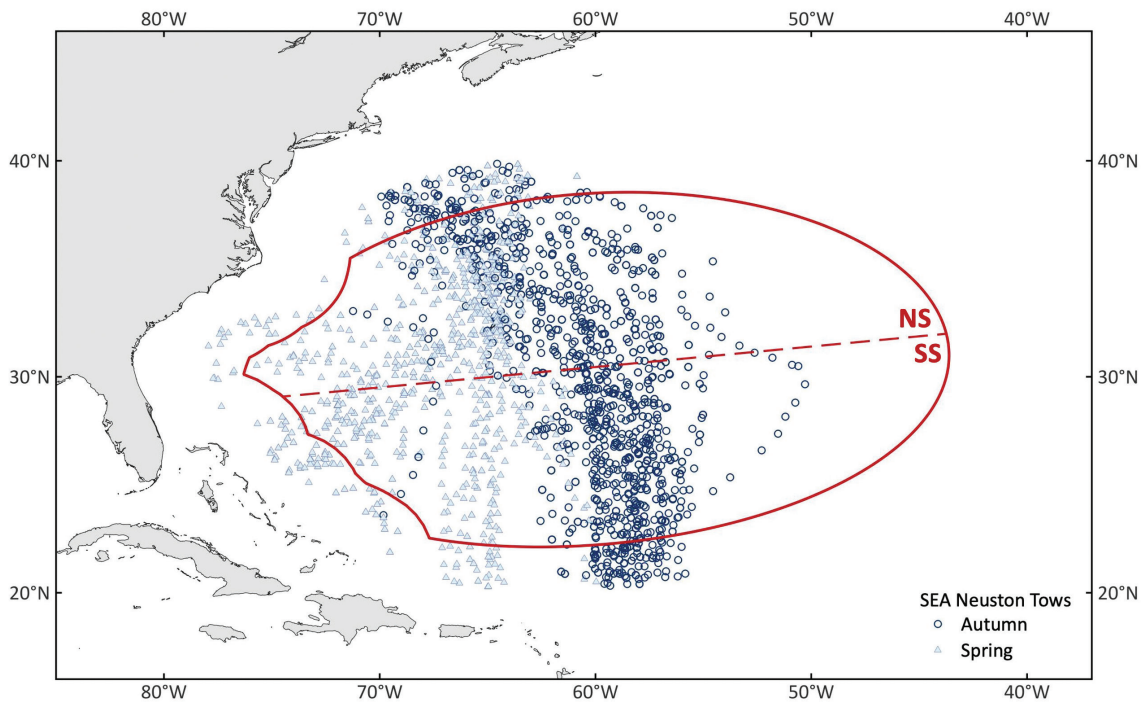


FIGURE 2.2. Locations of SEA surface neuston net tows conducted between 1973–2024 during autumn (dark blue circles) and spring (light blue triangles) research voyages. Stations in the Sargasso Sea Geographical Area of Collaboration (red line) and within a 2 degree (120 nm) buffer are shown to illustrate connectivity with surrounding oceanographic regions. North (NS) and South (SS) Sargasso Seas delineated based on the autumn/spring subtropical convergence zone position (dashed red line).

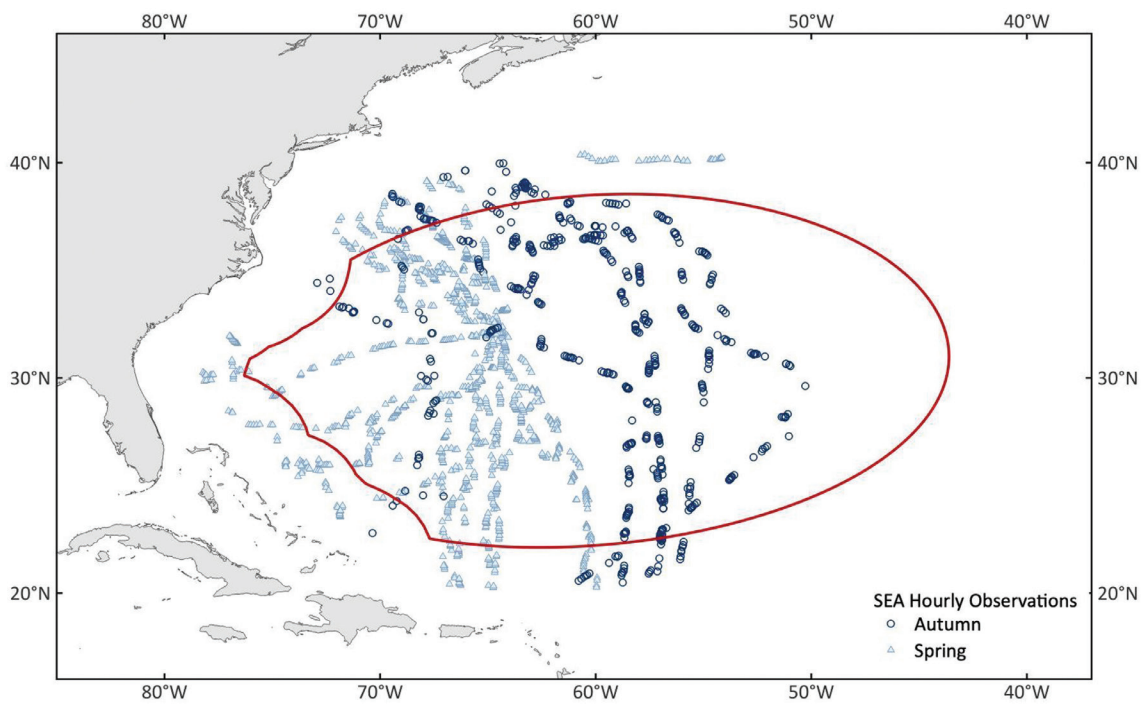


FIGURE 2.3. Locations of SEA hourly observations conducted between 2011–2024 during autumn (dark blue circles) and spring (light blue triangles) research voyages. Visual surveys in the Sargasso Sea Geographical Area of Collaboration (red line) and within a 2 degree (120 nm) buffer are shown to illustrate connectivity with surrounding oceanographic regions.



FIGURE 2.4. SEA students, crew, and faculty prepare to dip net a clump of *Sargassum* floating at the sea surface. Photo credit: J. Schell.

conditions (Figure 2.4). Individual samples were placed into plastic buckets containing seawater and the full net mesh was carefully examined, with particular focus along the seams and corners, to ensure that all collected fauna were transferred to the bucket.

In the ship's lab, fauna were separated from their

Sargassum substrate by rinsing with freshwater and funneling organisms into a jar for preservation. *Sargassum* samples were meticulously examined and forceps were used to remove any clinging organisms not dislodged by freshwater flushing. Post-voyage, fauna were visually identified to the lowest taxon possible using Morris and Mogelberg (1973). Additional details of field and analytical methods for dip net samples available in Martin et al. (2021).

2.4 Experimental Methods

To examine *Sargassum* growth rates and environmental tolerances, a controlled experiment was conducted in the greenhouse at Eckerd College (St. Petersburg, FL, USA) during spring 2023 (Schell et al., 2024). Healthy (i.e., blades and vesicles light yellow in color) *Sargassum* specimens of all available species and varieties were collected from the ocean surface via hand-held dip net. Approximately 60 mm lengths of the healthiest apical tips were cut from the clumps and placed in individual glass jars. For the greenhouse experiment, 10 replicates of each variety were exposed to seven unique treatments for 21 days (Figure 2.5).

Treatments reflected the wide range of temperature (20-30°C) and salinity (28-40 psu) conditions *Sargassum* may encounter throughout its extensive geographic range and across all seasons, seeking to examine how environmental conditions support or limit the distribution



FIGURE 2.5. Growth and environmental tolerance experimental setup in the Eckerd College greenhouse. Individual *Sargassum* specimens in glass jars containing salinity treatment were submerged in circulating water baths with regulated temperatures. Photo credit: J. Schell.

and seasonality of different varieties in the North Atlantic basin. Large water-filled basins were regulated near target treatment temperatures with recirculating heaters and chillers; upside-down incubation jars containing target salinity conditions and marine nutrient solution were submerged within the basins (Figure 2.5). Overhead bulbs on a 12:12 hr light:dark cycle provided broad spectral coverage, including ultra-violet and red wavelengths, to supplement ambient light in the greenhouse.

All specimens were inspected, weighed, and photographed prior to initial treatment exposure and daily during the experiment, prior to water change and returned to treatment conditions. Wet mass (g) was obtained after blotting dry with paper towels. Growth rates, expressed as doublings day⁻¹, were calculated for each replicate. Additional details of field and analytical methods for growth rate and environmental tolerance experiments available in Schell et al. (2024).

CHAPTER 3

Marine Pollution

3.1 Microplastics

Section 3.1 builds on the research findings published in Law et al. (2010), which utilized a 1986-2008 dataset of floating microplastics collected by SEA neuston net tow throughout the western North Atlantic and Caribbean Sea. For this report, observations from 2009-2024 were added, data were subset to just autumn/spring to align with other sections, and an updated map and time series were generated. Years were here defined ecologically as the period from October in the previous year through May in the current year. Graphs in this report show results for presence/absence data within the Sargasso Sea Geographical Area of Collaboration only, while broader patterns and driving mechanisms in microplastic concentration were described in the original publication. A more complex statistical consideration of temporal trends was offered in Wilcox et al. (2019).

Marine debris of any material and size may be carried to the sea in terrestrial runoff and wind deposition, or enter directly from beaches, ships, or mismanaged waste. Although “young” and unfragmented debris items are concentrated in coastal waters and near population centers, the most remote areas of all subtropical gyres contain the world’s highest concentrations of floating plastics, including particles that have drifted for decades (Egger et al., 2021; Law et al., 2024; ten Hietbrink et al., 2025). The Sargasso Sea Geographical Area of Collaboration comprises the core of the western North Atlantic Subtropical Gyre and is a well-known accumulation area for floating marine plastics (Law et al., 2010).

Microplastics, by definition smaller than 5 mm in length, are the focus of SEA’s neuston tow dataset (Figure 3.1). Small plastic particles in the marine environment have either fragmented from larger pieces or are manufactured that size. Exposure to UV light, wave motion, chemical changes, and accumulation of bacteria and rafting organisms all contribute to floating plastic fragmentation (Tekman et al., 2022). Polymer type, size, and time in the environment impact the rate of breakdown.

Floating microplastics may take different morphologies, such as foam, film, line, pellet, and fragment. Each reflects specific sources and/or weathering history; buoyancy and polymer type also vary by form (DiBenedetto et



FIGURE 3.1. Microplastics hand-picked from a SEA surface net tow conducted in the subtropical gyre. Plastic particles are also visible in the background, all comparable in size to simultaneously-collected zooplankton. Photo credit: Sea Education Association.

al., 2023). For example, foam and film typically result from breakdown of packaging materials, whereas microplastic line has likely shed from fishing gear such as ropes or nets. Pre-industrial resin pellets have relatively consistent size and shape while fragments, the most commonly observed category, are irregular in all characteristics (Figure 3.1; Moret-Ferguson et al., 2010).

In laboratory analyses on a subset of microplastics collected in SEA neuston nets from the western North Atlantic (748 tows from 1991-2007), including the Sargasso Sea, Moret-Ferguson et al. (2010) found that 69% of particles were 2-6 mm in size, with 88% under 10 mm. Particle size decreased and dominant form changed over the examined time period, and smaller plastics were collected in the subtropical gyre than outside it. Microplastics composed of polypropylene as well as high- and low-density polyethylene, all less dense than seawater, were most often found in surface net tows (Moret-Ferguson et al., 2010). Sargasso Sea samples contained >75% fragments, with pellets, line, and film present at <10%.

Between 1986 and 2024, SEA conducted 1,651 surface neuston net tows in the Sargasso Sea Geographical Area of Collaboration where plastics data were recorded. 92.2% (1,523) of tows contained buoyant microplastics (Figure 3.2); observed plastics were broadly distributed throughout the Sargasso Sea, although concentrations

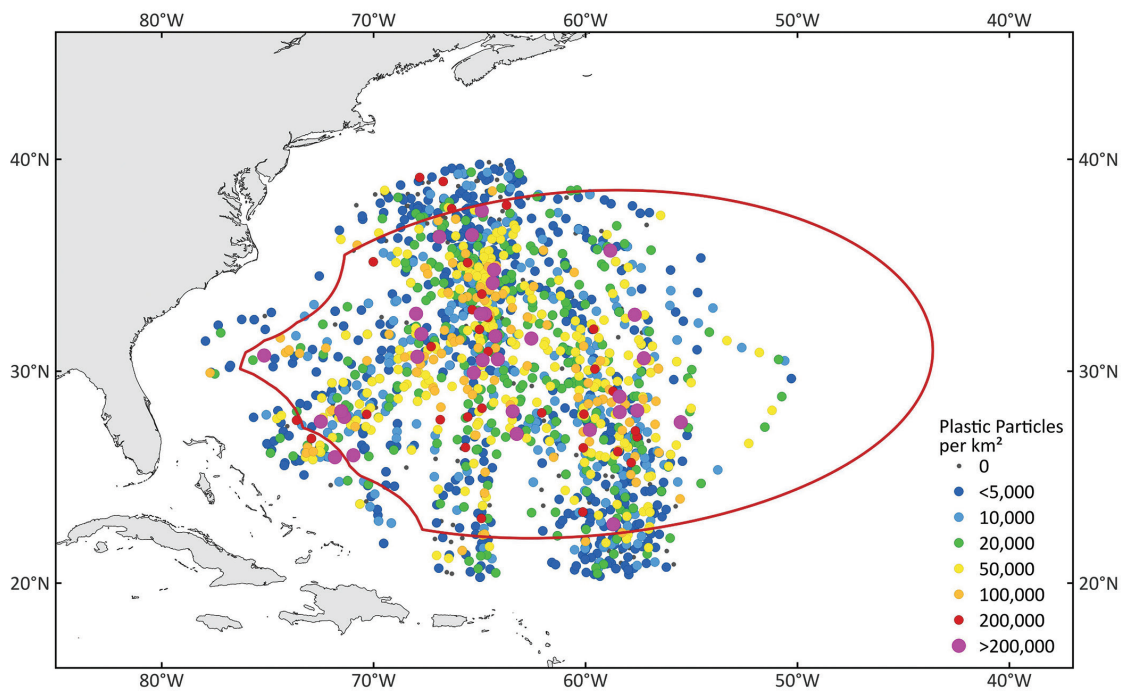


FIGURE 3.2. Locations of SEA autumn/spring surface neuston net tows conducted between 1986–2024 with density of floating microplastics (particles km^{-2}). Small gray dots indicate tows without microplastics. Stations in the Sargasso Sea Geographical Area of Collaboration (red line) and within a 2 degree (120 nm) buffer are shown to illustrate connectivity with surrounding oceanographic regions.

$>200,000$ particles km^{-2} were more frequently collected north of 28°N or near the subtropical convergence zone. Note that SEA sampling does not extend into the Geographical Area of Collaboration’s eastern sector. Mean overall density was 26,204 particles km^{-2} , with quantities about twice as high, on average, in middle latitudes ($\sim 25\text{--}35^{\circ}\text{N}$) than the perimeter of the region (Figure 3.2). Accumulation of plastic debris in subtropical gyres around the world is driven by basin-scale convergence in surface currents driven by Ekman and geostrophic processes (Law et al., 2010).

Most open ocean plastic field studies and modeling efforts have focused on surface concentrations, inherently underestimating total global quantities (albeit submerged debris amounts and distribution are poorly understood). Within the near-surface water column, when wind speeds are low and minimal turbulent mixing occurs, few plastics are carried below the air-sea interface sampled by a neuston net (Kukulka et al., 2012; DiBenedetto et al., 2023). However, in most locations and under most wind conditions vertical mixing affects the depth and concentration of buoyant plastic particles (Kukulka et al., 2012); the data presented here have not been corrected for wind impacts.

Over a 37-year record of annually-repeated cruise

tracks through the Sargasso Sea, both interannual variability and temporal patterns can be seen (Figure 3.3). The lowest yearly mean densities were recorded in 2024 (3,961 particles km^{-2} , SE 1,696; note only 6 tows conducted this year amidst stormy conditions) and 2004 (7,416 particles km^{-2} , SE 2,407); highest concentrations were found in 2021 (90,666 particles km^{-2} , SE 49,898) and 2016 (69,127 particles km^{-2} , SE 23,060). Natural patchiness in microplastic distribution (Figure 3.2) results in within-cruise variability, and extremely high-density outlier tows can skew mean values; their influence can be inferred from higher standard errors (Figure 3.3). Overall, variability increases with density and appears greater across nearly all observed densities since ~ 2012 .

Within the Sargasso Sea Geographical Area of Collaboration, the greatest microplastics concentration that SEA has recorded to date was 1,330,953 particles/ km^2 at 28.1°N , -57.6°W – that’s 3,280 plastic fragments hand-picked out of a single 30-minute net tow. Of the 10 highest yearly densities, eight have occurred since 2012; the mean concentration of these top years was 53,052 particles km^{-2} . In contrast, the 10 lowest yearly densities (mean concentration of these years 9,329 particles km^{-2}) were spread out in time.

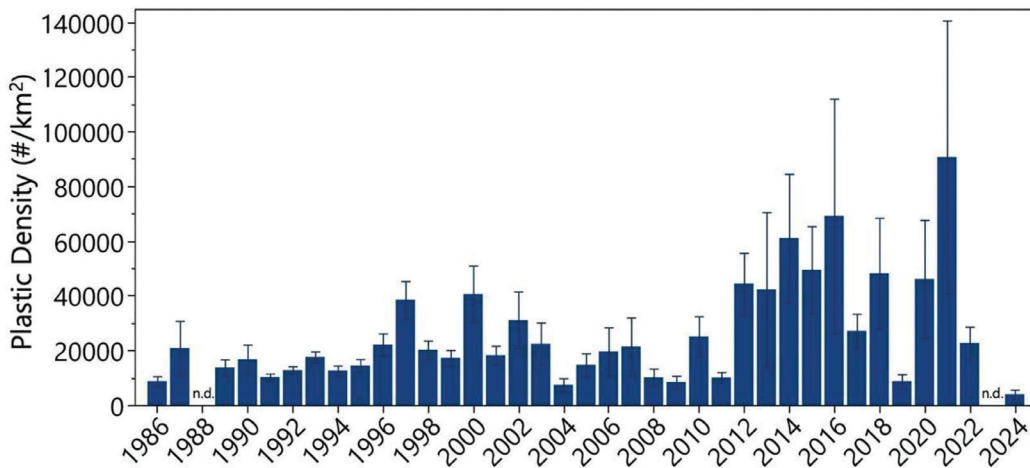


FIGURE 3.3. Mean densities (particles km⁻²) of floating microplastics in SEA autumn/spring surface neuston net tows conducted within the Sargasso Sea Geographical Area of Collaboration during each ecological year. Number of tows where plastics data was recorded ranged from 6 (2024) to 121 (1989 and 1992), with a mean of 46 tows per year. n.d. indicates no sampling in the region that year. Error bars show standard error.

Wilcox et al. (2019) modeled temporal trends in North Atlantic plastic concentrations leveraging SEA's neuston tow dataset with corrections for wind mixing, tow duration, and time of day. Their analysis suggested that higher concentrations observed in recent years (Figure 3.3) could result from plastics' long residence time in the marine environment, with processes removing particles from the surface ocean (sinking, ingestion, beach stranding, etc.) occurring at much lower rates than inputs. Cumulative global plastics production was strongly related to decadal patterns, suggesting influxes of marine debris have not meaningfully decreased over time and waste management efforts do not presently balance the ongoing rise in production (Wilcox et al., 2019).

Ecologically, floating plastic fragments may be ingested by a wide array of organisms, entering the food web and posing potential physical and chemical threats that are not comprehensively understood (Tekman et al., 2022). Many species inhabit debris objects in rafting communities, while other zooplankton and nekton taxa co-exist with microplastics in subtropical gyre surface waters, making removal and ecological mitigation strategies especially complex and challenging (Egger et al., 2021; Helm, 2021).

3.2 Tar

Section 3.2 summarizes the research findings published in Peters & Siuda (2015), which utilized a 1977-2012 dataset of floating tar collected by neuston net tow during autumn

in the Sargasso Sea region. For this report, observations from spring tows and 2013-2024 were added and an updated time series was generated. Years were here defined ecologically as the period from October in the previous year through May in the current year. Graphs in this report show results for presence/absence data within the Sargasso Sea Geographical Area of Collaboration only, while broader patterns and statistical results on historic tar mass are available in the original publication and Joyce (1998).

Tar balls are lumps of solid or semi-solid tar resulting from the weathering of oil in the marine environment. They are irregularly shaped and range from <1 mm to tens of centimeters across (Joyce, 1998). Some tar balls float at the ocean's surface and thus may be transported long distances by prevailing currents before washing ashore. Many marine organisms, from zooplankton to juvenile sea turtles to seabirds, can ingest these buoyant tar balls; other taxa form a rafting community on larger pieces that serve as basin-wide dispersal vectors.

Oil enters the sea naturally through seeps or anthropogenically through activities of the on- and offshore petroleum industries (drilling, extraction, processing, shipping, vessel spills, etc.). Depending on their source, hydrocarbon composition, floating time, and other processes, the appearance and density of tar balls varies. Chemical analyses of floating tar provide unique signatures that can, for example, differentiate whole crude oil from natural seep sources.

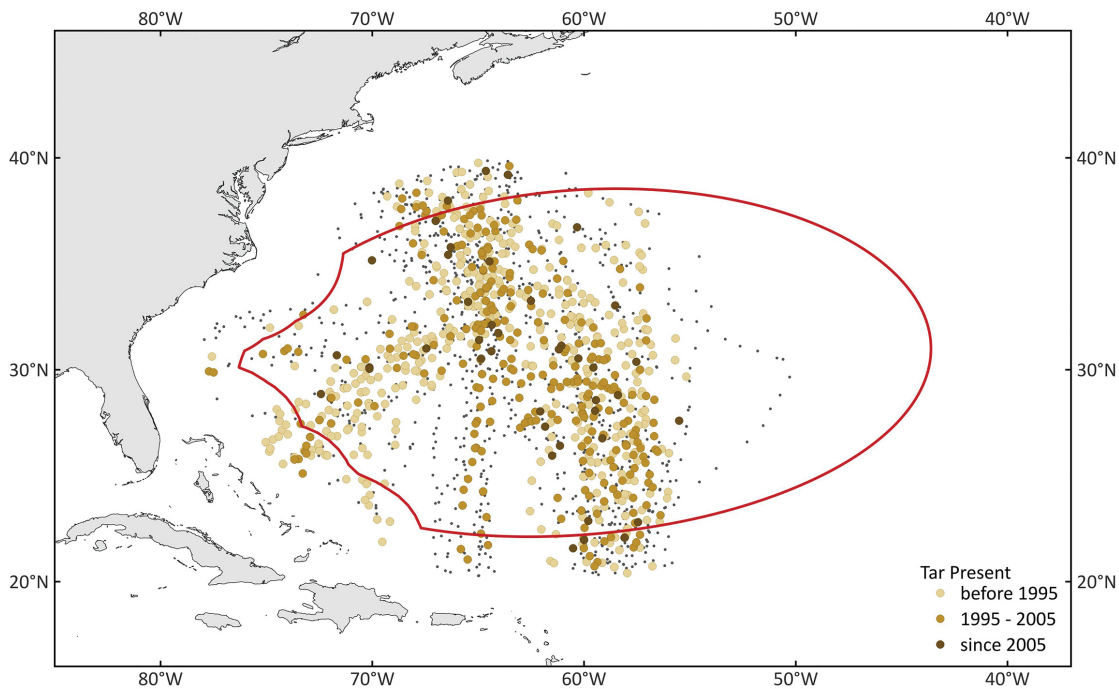


FIGURE 3.4. Locations of SEA autumn/spring surface neuston net tows conducted between 1978–2024 with temporal presence of floating tar. Small gray dots indicate tows without tar. Stations in the Sargasso Sea Geographical Area of Collaboration (red line) and within a 2 degree (120 nm) buffer are shown to illustrate connectivity with surrounding oceanographic regions.

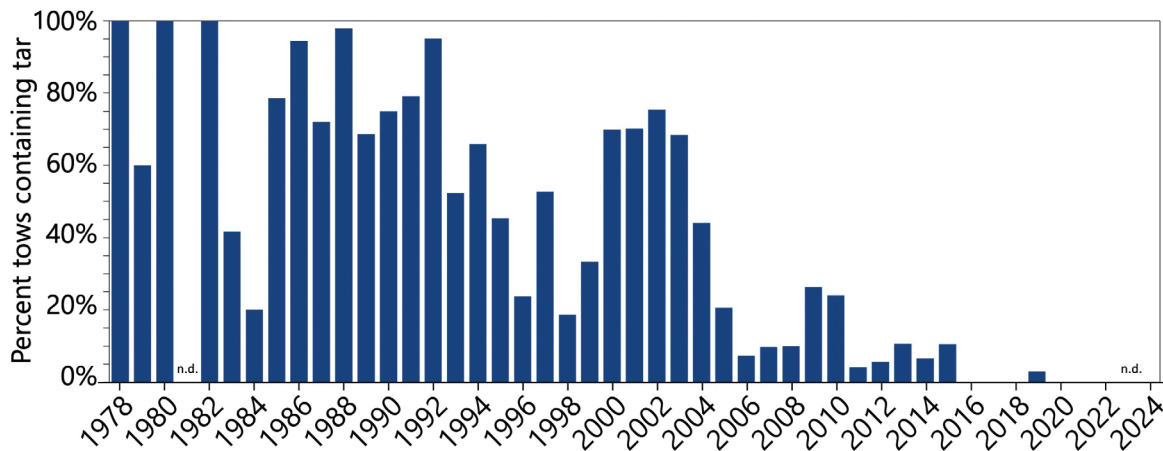


FIGURE 3.5. Floating tar frequencies of occurrence (%) in SEA autumn/spring surface neuston net tows conducted within the Sargasso Sea Geographical Area of Collaboration during each ecological year. Number of tows where tar data was recorded ranged from 5 (1984) to 121 (1989 and 1992), with a mean of 41 tows/year. n.d. indicates no sampling in the region that year.

For many years, buoyant tar has been collected in SEA’s neuston net tows and quantified, either by mass (earlier records) or count (later records; Joyce, 1998; Peters & Siuda, 2015). Out of 1,853 tows in the Sargasso Sea Geographical Area of Collaboration since 1978, tar was present in 864 with patchy distribution and highly

variable concentrations (Figure 3.4). Joyce (1998) noted that in the 1980s and 1990s the North Sargasso Sea contained the highest concentrations of surface tar compared to the South Sargasso Sea, Gulf Stream, Caribbean Sea, and continental shelf waters. At that time, densities were greatest near Bermuda and northwest to the Gulf Stream.

International policies were enacted in the early 1980s to reduce petroleum pollution from ships, particularly focused on discharge of wastewater from oil tanker cargo hold cleaning as well as decreasing vessel accidents and spills in the coastal zone. Concentrations of tar balls in SEA neuston tows declined as a result, but did not disappear altogether (Peters & Siuda, 2015; Figure 3.5). The highest annual frequency of occurrence was 100% of tows containing tar (1978, 1980, 1982), with percent presence above 80% documented in six years, all before 1993. In contrast, in seven years zero tar was collected and 14 years

had frequencies of occurrence below 10%, all since 2005 and especially since 2015 (Figure 3.5). Average percent presence before 2000 was 65% and after 19%. In the last decade, only six tows out of 273 collected floating tar.

Events contributing petroleum to the ocean still occur, and floating tar remains present and broadly dispersed in the Sargasso Sea. Discussions of tar residence time, transport via ocean currents around the North Atlantic basin, ecological impacts both positive and negative, and additional key references are offered in Peters & Siuda (2015).

CHAPTER 4

Sargassum Macroalgae

Chapter 4 summarizes research findings published in a series of articles and presentations by SEA faculty scientists and collaborators from the early 1980s to 2024. Over 45 years of SEA neuston net tows throughout the North Atlantic and Caribbean Sea provide an unequalled dataset on holopelagic *Sargassum* abundance, distribution, and spatiotemporal variability. Utilizing *Sargassum* specimens collected by surface tow and dip net, additional morphological and genetic studies have been conducted to extend our understanding of macroalgal taxonomy. For this report, observations from 2020–2024 were added, data were subset to just autumn/spring to align with other sections, and analyses were updated. Years were here defined ecologically as the period from October in the previous year through May in the current year. Graphs in this report show data within the Sargasso Sea Geographical Area of Collaboration only, while broader geographic patterns in *Sargassum* density were described in cited publications. While briefly mentioned here, detailed holopelagic species and variety-specific information is presented in Chapter 6, including long-term changes in their respective distributions and environmental tolerances.

Sargassum, a genus of brown macroalgae in class Phaeophyceae, is distributed globally from temperate to tropical ocean waters. Of more than 350 recognized species, two lack holdfasts and are uniquely holopelagic: *Sargassum fluitans* (Børgesen) Børgesen and *S. natans* (Linnaeus) Gaillon (Taylor, 1960; Guiry & Guiry, 2025). Distinct varieties have long been noted for each species (Parr, 1939) and both morphology and genetic analyses strongly sup-

port delineation of the three most common types as no intermediate characteristics have been observed (Siuda et al., 2024): *S. fluitans* var. *fluitans* (formerly *S. fluitans* III, abbreviated Sf), *S. natans* var. *natans* (formerly *S. natans* I, abbreviated Sn_n), and *S. natans* var. *wingei* (formerly *S. natans* VIII, abbreviated Sn_w).

Sf has thorny stems, broad blades, oblong bladders, and no spine on the bladders. Sn_n exhibits smooth stems, spherical bladders, long thin blades, and apical spines on the bladders (Parr, 1939). Sn_w is distinguished by smooth stems, spherical bladders, long broad blades, and only rarely spines on the bladders (Schell et al., 2015). At first glance or without examination of the stems, Sn_w is easily misidentified as Sf (Siuda et al., 2024). These three varieties also display different degrees of branching and foliation, resulting in a range of architectural complexity with habitat quality and ecological implications (Figure 4.1; Martin et al., 2021). See Parr (1939), Figure 1 in Schell et al. (2015), and Figure 4 plus the taxonomic key in Siuda et al. (2024) for more detailed guidance on holopelagic *Sargassum* morphological differentiation and identification.

Initial examinations of full-length mitogenomes indicated a closer proximity between Sn_n and Sn_w (0.02%) than either when compared to Sf (0.03%; Amaral-Zettler et al., 2017). In a more extended temporal and geographic analysis, targeting mitochondrial gene segments each with multiple polymorphisms, genetic distances among holopelagic varieties were in the range of those between pelagic and benthic species and on the same order as

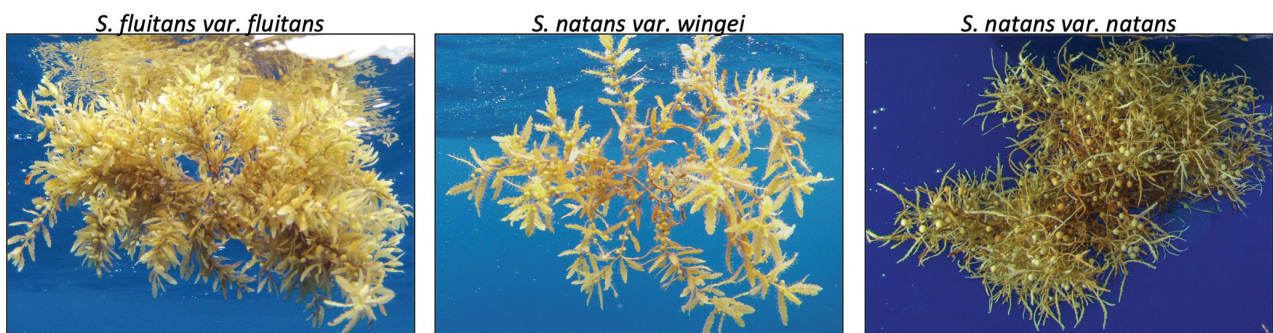


FIGURE 4.1. Floating clumps of the three common holopelagic *Sargassum* varieties showing different blade dimensions, branching structure, and spatial character. Photo credits: J. Schell (left, center) and S. Zankl (right). Figure from Martin et al. (2021).

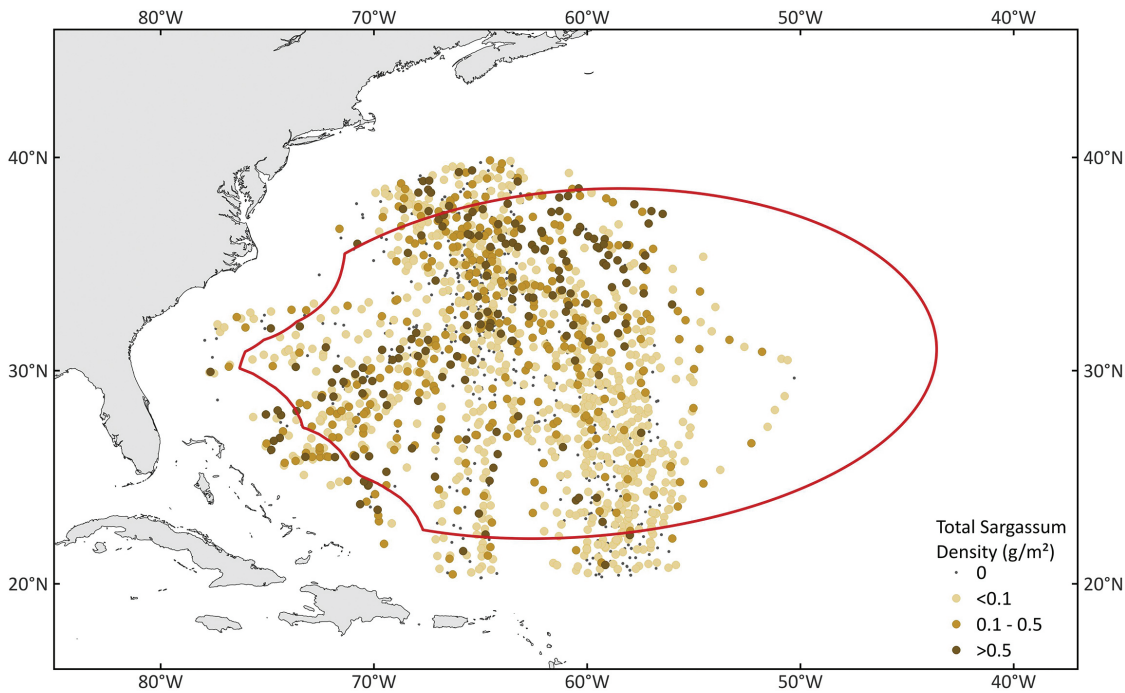


FIGURE 4.2. Locations of SEA autumn/spring surface neuston net tows conducted between 1978-2024 with density of holopelagic *Sargassum* (g m^{-2}). Small gray dots indicate tows without *Sargassum*. Stations in the Sargasso Sea Geographical Area of Collaboration (red line) and within a 2 degree (120 nm) buffer are shown to illustrate connectivity with surrounding oceanographic regions.

TABLE 4.1. Observations of mean total holopelagic *Sargassum* density

	<i>Sargassum</i> density (g m^{-2})	n tows
Spring	0.158 (SE 0.018)	676
Autumn	0.184 (SE 0.016)	1,047
North Sargasso Sea	0.247 (SE 0.021)	936
South Sargasso Sea	0.085 (SE 0.008)	828
North Sargasso Sea - Spring	0.146 (SE 0.027)	403
North Sargasso Sea - Autumn	0.342 (SE 0.031)	499
South Sargasso Sea - Spring	0.176 (SE 0.021)	273
South Sargasso Sea - Autumn	0.039 (SE 0.005)	548

Note: Mean total density (g m^{-2}) and standard error calculated for any observed *Sargassum* variety as a function of season, region, and region-season across 1,764 neuston net tows conducted in the Sargasso Sea Geographical Area of Collaboration from 1978-2024 where *Sargassum* data was recorded.

divergence among some benthic species (Dibner et al., 2021; Siuda et al., 2024). Future efforts aim to propose *Sn_w* as a new species.

During SEA research voyages, *Sargassum* species and variety identification and wet weight measurements were consistently recorded beginning in 1990. In order to examine the full available temporal record of *Sargassum* distribution and abundance, total densities (g of all collected types, whether or not identified to species,

divided by tow area in m^2) were utilized. Between 1978 and 2024, 1,764 surface neuston tows provided *Sargassum* information in the Sargasso Sea Geographical Area of Collaboration (Figure 4.2); three years had no observations and one extremely high-density outlier from 1986 was removed. On average, 42 tows were conducted per year in this region, with a maximum of 121 (1989 and 1992) and minimum of 5 (1984). Sampling was spatially and temporally well-dispersed (Table 4.1).

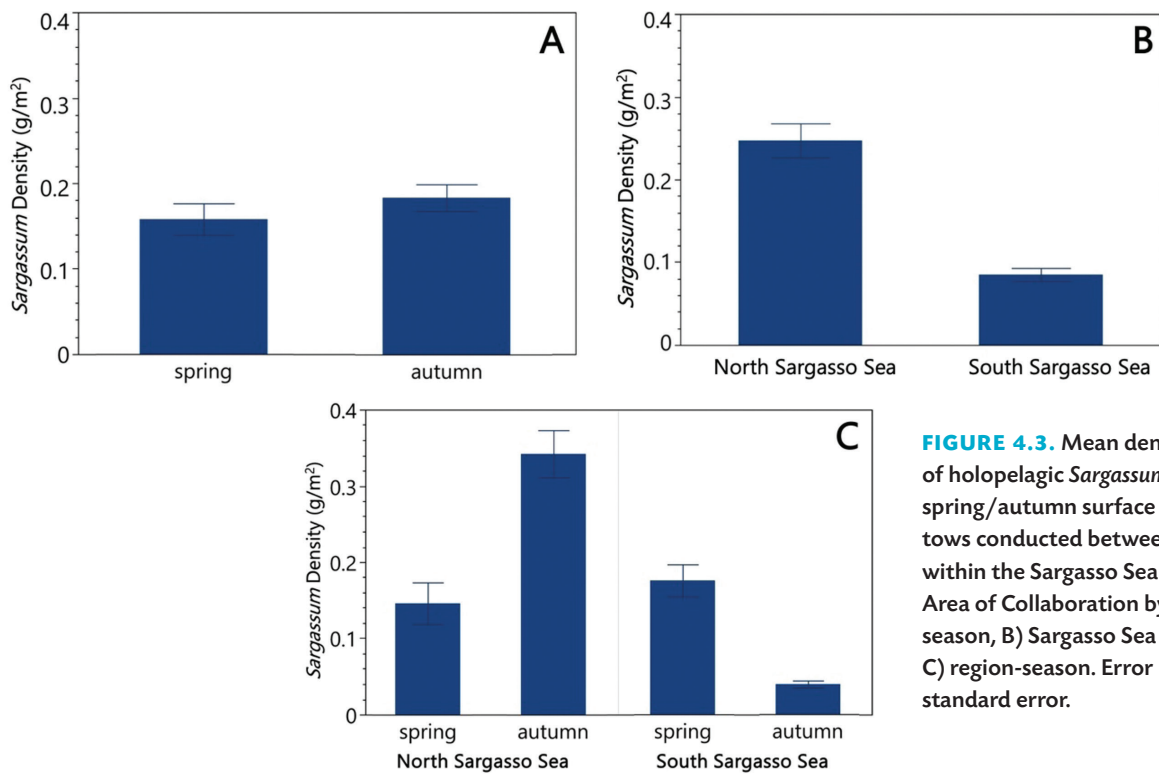


FIGURE 4.3. Mean density (g m^{-2}) of holopelagic *Sargassum* in SEA spring/autumn surface neuston net tows conducted between 1978–2024 within the Sargasso Sea Geographical Area of Collaboration by A) sampling season, B) Sargasso Sea region, and C) region-season. Error bars show standard error.

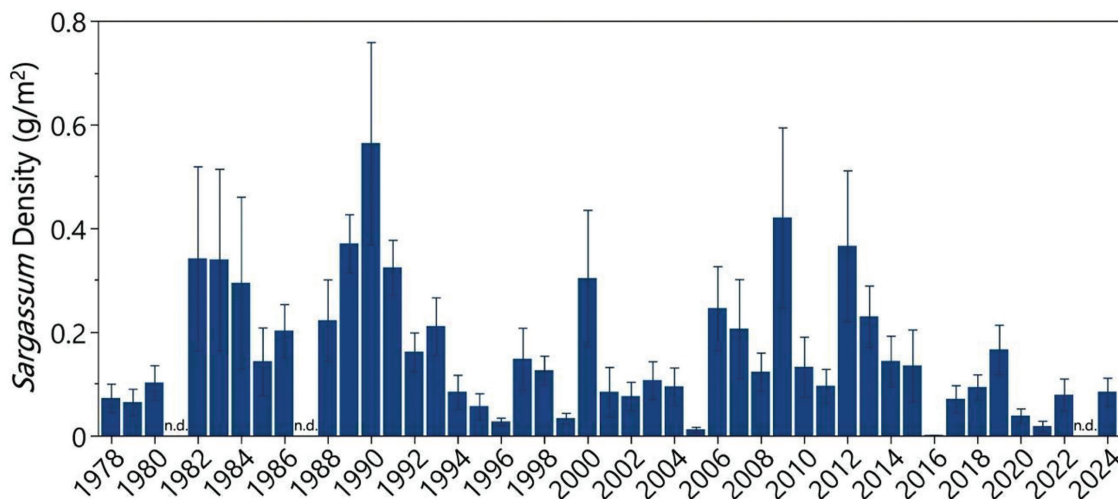


FIGURE 4.4. Mean densities (g m^{-2}) of holopelagic *Sargassum* in SEA autumn/spring surface neuston net tows conducted within the Sargasso Sea Geographical Area of Collaboration during each ecological year. Number of tows where *Sargassum* data was recorded ranged from 5 (1984) to 121 (1989 and 1992), with a mean of 41 tows per year. n.d. indicates no sampling in the region that year. Error bars show standard error.

For the entire data archive (all years, all locations), 72% of tows contained *Sargassum* and the overall mean total density was 0.164 g m^{-2} (SE 0.060). Although seasonal differences were present, aligning with the yearly cycle of *Sargassum* presence and movement in the western North Atlantic described by remote sensing observations (Gower & King, 2011), autumn and spring mean densities

and standard errors were similar when calculated for the full Sargasso Sea (Table 4.1; Figure 4.3A). Regionally, nearly three times more *Sargassum* was collected in the North Sargasso across all sampling months compared to the South (Figure 4.3B); the South Sargasso Sea reliably exhibited lower variability (Table 4.1) though the regional ratio fluctuated modestly from year to year. Stark

differences between seasons were noted within each region: autumn North Sargasso density was over double that of spring, and spring South Sargasso density was 4.5 times greater than autumn levels (Figure 4.3C). These spatial patterns track the historic annual distribution cycle for holopelagic *Sargassum* (Gower & King, 2011) but may be shifting with the recent onset of the Great Atlantic *Sargassum* Belt (Wang et al., 2019).

SEA has a strong history of annually-repeated autumn and spring cruise tracks through the western North Atlantic and Sargasso Sea from 1978 to 2014 and 2017 to 2024 (in 2014-2016, the SSV *Corwith Cramer* sailed to Europe during the summer and returned via the tropics to the Caribbean in late autumn). Multiple decades of geographically consistent sampling provide an unparalleled time series of *Sargassum* abundance (Figure 4.4). Across the entire Sargasso Sea, the lowest annual densities were recorded in 2016 (0.0009 g m^{-2}) and 2005 (0.012 g m^{-2}); highest concentrations were found in 1990 (0.564 g m^{-2}) and 2009 (0.421 g m^{-2}). While natural patchiness in *Sargassum* distribution and aggregation (Section 5.1) results in interannual and within-cruise variability, extremely high-density outliers that would skew mean values were rare. A decadal cycle in *Sargassum* abundance was evident in the nearly 50-year record, importantly not tied to the existence or behavior of the Great Atlantic *Sargassum* Belt (GASB) because the cyclical pattern predates GASB onset in 2011 (Stoner, 1983; Wang et al., 2019). Both the ~1982-1992 and ~2006-2013 intervals had higher quantities of macroalgae while ~1978-1980, ~1994-2005, and ~2014-2024 were lower but on par with each other when examined across the full Sargasso Sea (Figure 4.4). Variability (standard error) also fluctuates in magnitude over time and appears to increase with density. Potential drivers of these decadal patterns in *Sargassum* density have not been investigated.

While the three most common *Sargassum* varieties presently co-occur across broad geographic range and oceanic conditions, each exhibits distinct source regions and environmental tolerances (Goodwin et al., 2020; Schell et al., 2024). Based on Parr (1939), historically *Sargassum* density in the Sargasso Sea was four times greater than in the Gulf of Mexico and 40 times greater than in the Caribbean Sea, with regional differences in species and variety distribution. S_{n_n} dominated the Sargasso Sea and Gulf of Mexico with S_f accounting for the remainder, while in contrast the western Caribbean hosted more S_f and low proportions of S_{n_n} and S_{n_w} (Parr, 1939). Sampling during the 1970s and 1980s confirmed patterns consistent with the 1930s (Butler et al., 1983; Butler & Stoner, 1984). Interestingly, SEA data from the 1990s and early 2000s found greater amounts of S_f than S_{n_n} in the Gulf of Mexico, Gulf Stream and North Sargasso Sea, although in the most recent decade S_{n_n} again dominates within the Sargasso Sea.

Since 2011, coastlines on both sides of the tropical Atlantic have experienced unprecedented and near-yearly *Sargassum* inundations (Wang et al., 2019). Initially, these events were dominated by the previously rare S_{n_w} but now include a seasonally- and interannually-variable mix of all three varieties (Alleyne et al., 2023; Torres-Conde et al., 2023). The presence of substantial S_{n_n} in the tropics and Caribbean Sea since 2018 is novel within SEA's long-term dataset. Despite this shift to overlapping ranges, physical and molecular differences between varieties are conserved (Dibner et al., 2021; Siuda et al., 2024) and differences in nutrient biogeochemistry and chemical markers have recently been discovered (McGillicuddy et al., 2023; Kergosien et al., 2024). See Section 6 for further discussion of these changes in variety-specific holopelagic *Sargassum* abundance and distribution as well as potential implications for the Sargasso Sea.

CHAPTER 5

The *Sargassum* Ecosystem

Holopelagic *Sargassum* drifts at the water's surface creating a unique and ecologically-significant floating marine ecosystem in the oligotrophic open ocean (Haney, 1986; Wells & Rooker, 2004). Presently, two species and multiple varieties of *Sargassum* are recognized and distributed throughout the equatorial and western North Atlantic Ocean (Section 4; Parr, 1939; Butler et al., 1983; Goodwin et al., 2020; Dibner et al., 2021; Siuda et al., 2024).

The ecological role of holopelagic *Sargassum* is particularly important in nutrient-poor subtropical and tropical waters (Laffoley et al., 2011; de Boer & Saulino, 2020). It serves as critical nursery, spawning, foraging, roosting, and protective habitat for a diversity of invertebrate, fish, sea turtle, marine mammal, and seabird species (Dooley, 1972; Morris & Mogelberg, 1973). Faunal associates of pelagic *Sargassum* include over a hundred species from diverse phyla ranging in size, age class, and ecological function, all within a complex food web (Butler et al., 1983).

Rarely is living *Sargassum* substrate a food source for the fauna it supports (Turner & Rooker, 2006). Sessile filter-feeding fauna living attached to stipes, branches, and blades (e.g., colonial hydroids, encrusting bryozoans, barnacles, anemones, and tunicates) represent prey for

motile consumers, while invertebrates (e.g., crabs, shrimp, amphipods, isopods, snails, nudibranch, polychaetes, and flatworms) as well as fish occupy higher trophic levels (Figure 5.1; Morris & Mogelberg, 1973; Coston-Clements et al., 1991). Ten species are considered endemic to holopelagic *Sargassum* (Figure 5.1; Hemphill, 2005), exhibiting specialized coloration and morphology to camouflage with their macroalgal habitat.

Many larger, migratory species, including larval American and European eels (Kracht & Tesch, 1981; Siuda, 2011), mahi mahi and flying fish (Beardsley, 1967; Bortone et al., 1977; Casazza and Ross, 2008), juvenile sea turtles (Carr & Meylan, 1980; Witherington et al., 2012), and seabirds (Haney, 1986; Moser & Lee, 2012) temporarily visit aggregated windrows and mats to feed on motile epifauna, find shelter, and spawn. Their presence confirms the trophic, ecological, and commercial value of the holopelagic *Sargassum* ecosystem, which has been the focus of regional (NMFS, 2003) and international conservation efforts (Laffoley et al., 2011).

5.1 Aggregation State

Section 5.1 summarizes the research findings published in Goodwin et al. (2022), which utilized a 2011–2020 dataset

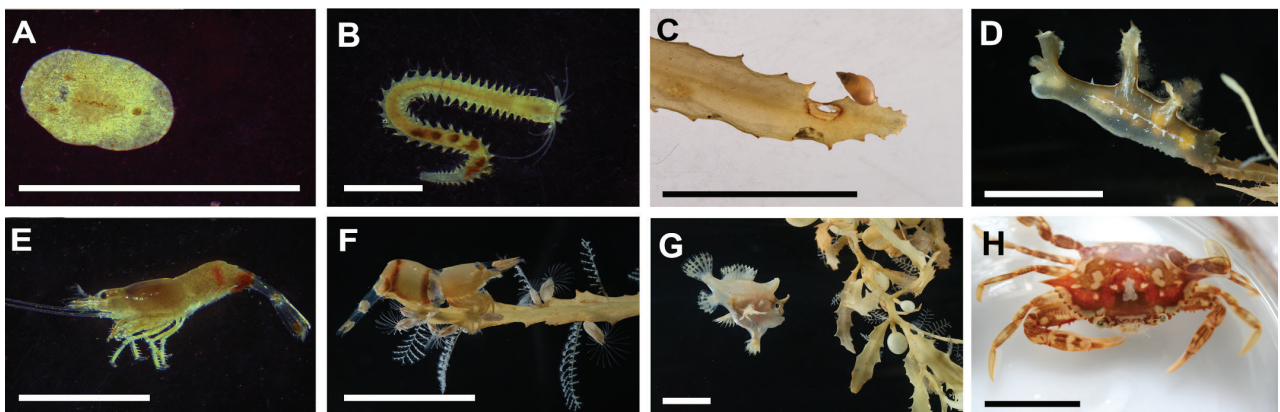


FIGURE 5.1. An assortment of cryptically colored, motile epifauna species commonly associated with *Sargassum*: (a) flatworm, (b) polychaete (*Platynereis dumerilii*), (c) snail (*Litiopa melanostoma**), (d) *Sargassum* nudibranch (*Scyllaea pelagica**), (e) slender *Sargassum* shrimp (*Latreutes fucorum**), (f) a second shrimp (*Leander tenuicornis*), (g) *Sargassum* anglerfish (*Histrio histrio**), and (h) *Sargassum* crab (*Portunus sayi*). Epifauna are shown in order of increasing trophic level; representative known endemics indicated with asterisks. Each scale bar indicates 1 cm. Photo credits: J. Schell (a, b, e, h), S. Zankl (d, f, and g), and J. Bering (c). Figure from Martin et al. (2021).

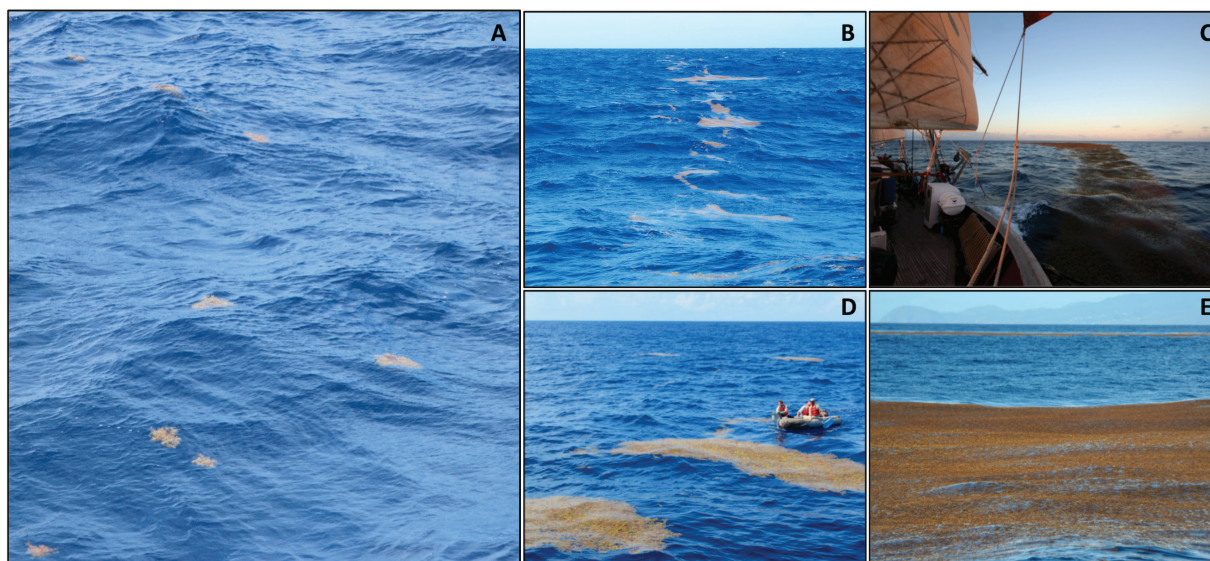


FIGURE 5.2. *Sargassum* offshore aggregation states. (A) Dispersed clumps and fragments (0.1 m diameter clumps; Caribbean, winter 2021). (B) Narrow windrow (0.5-1.5 m across; Tropical Atlantic, fall 2015). (C) Wide windrow (3-4 m across; Caribbean, winter 2015). (D) Small mats (3x9 m mat near small boat; Sargasso Sea, fall 2014). (E) Large mats (50x100 m; near Guadeloupe, Caribbean, spring 2015). Photo credits: J. Schell (a, c, e), A. Siuda (b), and C. Morrall (d). Figure from Goodwin et al. (2022).

of daytime hourly visual surveys spanning the entire North Atlantic basin. For this report, observations from 2021-2024 were added and several reanalyses were conducted. Holopelagic *Sargassum* aggregation states were ranked from small dispersed pieces to cohesive structures with defined boundaries (fragments/clumps < windrows < mats); each observation was assigned the highest aggregation state recorded during that period. Years were here defined ecologically as the period from October in the previous year through May in the current year; all available data from these months were included in temporal analyses. Graphs in this report show results for data within the Sargasso Sea Geographical Area of Collaboration only, while broader patterns, regional comparisons, and statistical results are available in the original publication.

Pelagic *Sargassum* may be observed in multiple aggregation patterns at the <1 to 100s of meters spatial scale (Figure 5.2; Parr, 1939; Butler et al., 1983; Marmorino et al., 2011; Ody et al., 2019), which underpin its ecological value, availability of highly localized prey biomass within and beneath the algae, and remote sensing detection capabilities (Moser & Lee, 2012; Wang & Hu, 2017; Wang et al., 2019).

Fragments are short fronds <20 cm in length, broken off a clump (Figure 5.2A). Individual clumps are spherical or oblong in shape when afloat, with >20 cm frond length or clump diameter. Both fragments and clumps are

stand-alone units of holopelagic *Sargassum* and can be found dispersed or aggregated (Butler et al., 1983; Ody et al., 2019). Windrows are aggregations of many fragments and/or clumps in a line generally parallel to the wind direction (Figure 5.2B-C); they may extend for multiple km distance and range in width from <0.5 m to several m (Woodcock, 1950). Mats are densely-packed fragments and/or clumps with a clear edge, irregular to round shape, and 5 to 100s m distance across. Often mats are observed associated with a windrow (Figure 5.2D-E; Marmorino et al., 2011; Ody et al., 2019) but under calm conditions, mats may be completely independent features.

The processes controlling formation and dissipation of *Sargassum* windrows and mats as well as the timescale of transitions between aggregation states remain poorly understood. Parr (1939) noted large mats appeared during periods of low wind, suggesting increased aggregation under calm conditions. However, Woodcock (1950) documented windrows at wind speeds from 1 to 17 m sec⁻¹ and wind-induced Langmuir cells, potentially reaching many km in length, are positively correlated in both horizontal and vertical dimensions with greater wind speeds (Langmuir, 1938; Faller & Woodcock, 1964). The local abundance of *Sargassum* strongly influences the observed level of aggregation. At low densities, clumps/fragments may appear dispersed when actually arranged in a diffuse windrow.

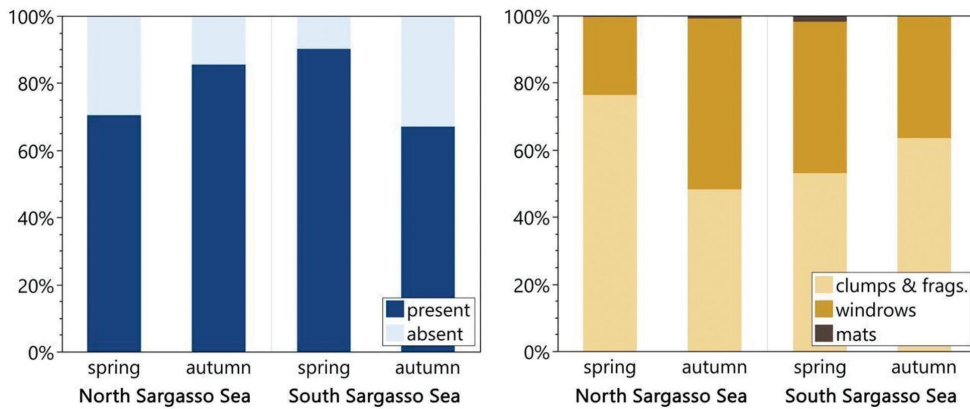


FIGURE 5.3. Holopelagic *Sargassum* proportional presence/absence in hourly observations across seasons (left) and proportion of highest ranked aggregation state (right) in observations where *Sargassum* was present.

Goodwin et al. (2022) leveraged visual surveys to describe *Sargassum* presence and aggregation state at spatial scales below those detectable using remote sensing; summary statistics below extend that work by three additional years. Holopelagic *Sargassum* was present in 1,126 (79%) of 1,424 total observations in the Sargasso Sea. Dispersed fragments/clumps were most common (in 99% of positive *Sargassum* observations) while aggregated windrows (39%) and mats (1%) were recorded less often. When *Sargassum* was present, <1% of observations included all three aggregation states, 39% included two aggregation states (99% of those were windrows concurrent with dispersed fragments/clumps), and 61% of observations included a single aggregation state (99% of those were dispersed fragments/clumps).

Examined both seasonally (autumn/spring) and regionally (North/South Sargasso Sea), *Sargassum* percent presence was consistently over 60% (Figure 5.3 left panel). Dispersed fragments/clumps alone comprised 49 – 76% of observations, and windrows, typically accompanied by fragments/clumps, were present in 23 – 50% of observations (Figure 5.3 right panel). Seasonal variability was evident, tracking the recognized annual cycle of holopelagic *Sargassum* movement between North and South regions (Gower & King, 2011). Mats were rarely documented in the Sargasso Sea, although within the geographically broader dataset the leeward sides of large islands in the Eastern Caribbean (e.g., Dominica and Guadeloupe) and the Windward Passage’s combination of local currents, winds, and bathymetry reliably produced substantial mats (Goodwin et al., 2022).

In the open Sargasso Sea, dispersed fragments/clumps were more abundant than windrows across all wind conditions (Figure 4 in Goodwin et al., 2022). At moderate Beaufort Forces, the proportion of windrow observations increased significantly; nonetheless, under

high wind conditions aggregations may have been broken apart by larger waves or more difficult to discern as algal material was carried below the sea surface (Woodcock, 1993). Location and macroscale weather did not drive observed patterns, but rather the instantaneous physical forces underlying Langmuir Circulation (Leibovich, 1983) and local *Sargassum* abundance determined windrow aggregation.

Temporal patterns of *Sargassum* presence and aggregation state were also explored. The Sargasso Sea exhibited consistently high percent presence, with *Sargassum* recorded in >80% of observations in 8 of 11 years; the minimum, in 2016, was 33% (Figure 5.4 left panel). In most years, dispersed fragments/clumps alone were equally or more commonly observed than aggregations; windrows were observed in all but one year (2016, when overall abundance was notably low) and mats were documented in four years (Figure 5.4 right panel).

When examined regionally, both exhibited considerable interannual variability in the proportion of observations with *Sargassum* present (Figure 5.5 left panels). While 2016 and 2020 were lower than typical for both the North and South Sargasso Sea, 2021 differed markedly between locations. More years with >90% presence occurred in the South Sargasso, with a lower overall range of percent present (65.9%) compared to in the North (73.6%). In most years in the North Sargasso Sea, dispersed fragments/clumps alone were more commonly observed than aggregated *Sargassum* whereas windrows in the South Sargasso Sea usually formed >50% of noted macroalgae (Figure 5.5 right panels). Interestingly, the three lowest percent presence years in the South Sargasso had zero windrows but North Sargasso low windrow years (2015–2018, 2024) varied considerably in their corresponding percent presence. Mats were recorded more often in the South Sargasso Sea.

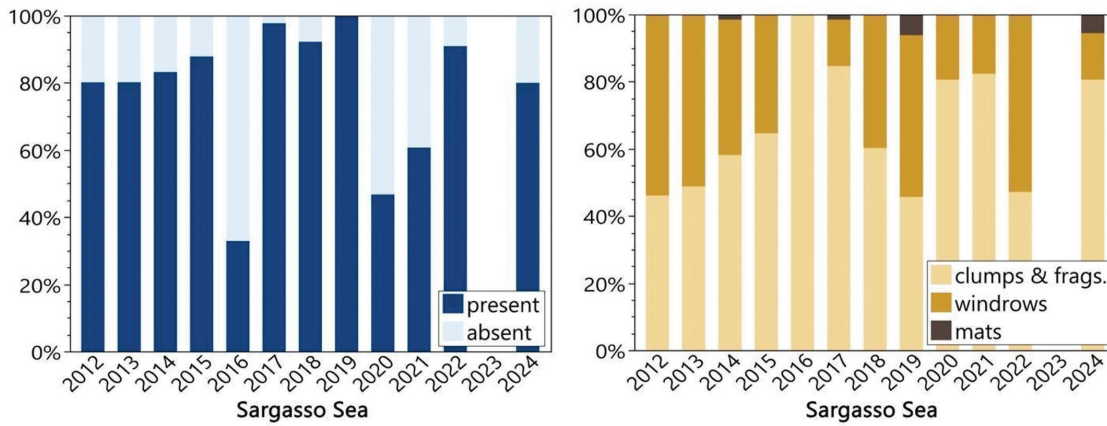


FIGURE 5.4. Holopelagic *Sargassum* proportional presence/absence across all Sargasso Sea hourly observations (left) and annual proportion of highest ranked aggregation state (right) in observations where *Sargassum* was present. Proportions calculated on an ecological year (October through May) basis. No data were collected in the Sargasso Sea during 2023.

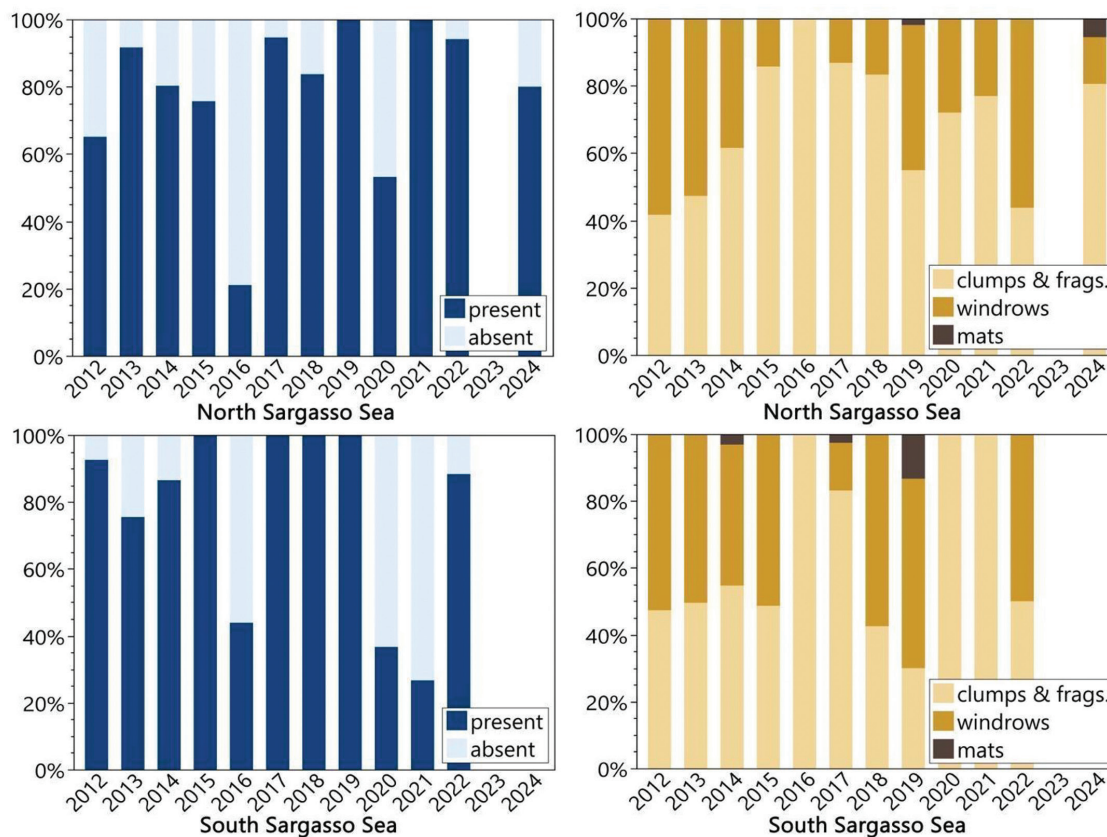


FIGURE 5.5. Holopelagic *Sargassum* proportional presence/absence across all North and South Sargasso Sea hourly observations (left) and annual proportion of highest ranked aggregation state (right) in observations where *Sargassum* was present. Proportions calculated on an ecological year (October through May) basis. No data were collected in the North Sargasso during 2023 or the South Sargasso in 2023 or 2024.

With the desire to predict and prepare for beaching events as well as understand basin-scale dynamics, communities and scientists have started using satellite-derived estimates of floating *Sargassum* distribution and abundance (Hu et al., 2016; Marechal et al., 2017; Trinanés et al., 2021). In practice, remote sensing provides a synoptic view that cannot be matched in geographic scale by field observations. The AFAI algorithm provides a good approximation of *Sargassum* distribution and abundance for areas and times when drifting macroalgae is abundant and concentrated (Wang & Hu, 2016). However, the dispersed *Sargassum* clumps as well as narrow or diffuse windrows so commonly recorded in Goodwin et al.'s (2022) extensive surveys are undetectable at coarse (1 km²) resolution (Wang & Hu, 2021). Furthermore, remote sensing cannot differentiate between healthy, actively-growing material and that in a state of senescence or decay. A measure of caution in interpretation is required as satellite-derived *Sargassum* biomass may not always reflect an active macroalgal bloom nor the total present ecologically-meaningful habitat.

5.2 Megafauna Associates

Section 5.2 summarizes the research findings published in Goodwin et al. (2022), which utilized a 2011–2020 dataset of daytime hourly visual surveys spanning the entire North Atlantic basin. For this report, observations from October through May of 2021–2024 were added and several reanalyses were conducted. Here graphs show results for data within the Sargasso Sea Geographical Area of Collaboration only, while broader patterns, regional comparisons, and statistical results are available in the original publication.

Megafauna presence/absence was recorded during 99.7% of hourly observations in the Sargasso Sea. A total of 896 fish, 184 seabirds, and 113 marine mammals were documented; no sea turtles were seen. When identification was possible, flying fish, mahi mahi, and tuna were the most common fish noted, while boobies, jaegers, petrels, gulls, terns, shearwaters, and tropicbirds dominated seabird observations. Occurrences of marine mammals

(typically groups of dolphins) were too infrequent to reveal patterns of association with holopelagic *Sargassum*.

Greater numbers of fishes were observed with *Sargassum* present relative to absent, and greater numbers near aggregated windrows and mats than dispersed fragments/clumps (Table 5.1). Past studies found similar patterns, with enhanced fish abundance and species diversity amongst floating *Sargassum* compared to open water; significant relationships between fish quantity and algal wet weight have also been noted, though aggregation states were not recorded (Wells & Rooker, 2004; Casazza & Ross, 2008). Small fishes live within and immediately proximate to *Sargassum* of any density, relying upon the architecturally-complex habitat for protection, associated epibiont and motile epifauna prey resources, and as a nursery (Rooker et al., 2006). Larger predators school deeper beneath windrows and mats to capitalize on congregated prey (Moser et al., 1998).

In the Sargasso Sea, seabirds were also found more frequently when *Sargassum* was present (Table 5.1), although the opposite pattern was documented in the Caribbean Sea and Tropical Atlantic regions (Goodwin et al., 2022). Where seabirds were observed with *Sargassum*, they were associated with dispersed fragments/ clumps more often than windrows and mats (Table 5.1). de Boer & Saulino (2020) and Haney (1986) likewise reported enhanced seabird abundances with *Sargassum* present, over 30 times greater around mats. Although not examined to such detail in this data, in previous work some seabird species (tropicbirds, boobies, terns) exhibited a preference for larger macroalgal aggregations to target flying fish prey and employ plunge-diving and aerial-dipping foraging strategies (Haney 1986; Moser & Lee, 2012). Smaller birds and those picking invertebrate prey from within the *Sargassum* (phalaropes, shearwaters) were more common near small patches and dispersed clumps. When comparing surveys in loose versus densely aggregated *Sargassum*, the former attracted larger groups of foraging seabirds as suitable prey was more visible and accessible (de Boer & Saulino, 2020).

Despite not being observed in these Sargasso Sea

TABLE 5.1. Observations of Megafauna

Holopelagic <i>Sargassum</i>	Fish presence	Seabirds presence
Absent	10.8%	6.4%
Present	15.2%	10.9%
Fragments and Clumps	12.3%	11.6%
Windrows and Mats	19.6%	9.9%

Note: Percent presence for fish or seabirds as a function of Sargassum absence/presence (top rows) across all hourly observations and as a function of ranked aggregation state (bottom rows) for the subset when Sargassum was present.

visual surveys, aggregated *Sargassum* is a documented biodiversity hotspot supporting higher abundances of juvenile sea turtles than neighboring open waters (de Boer & Saulino, 2020). Four species of sea turtles (loggerhead, green, hawksbill, and Kemp's ridley) exhibited strong dependence on *Sargassum* at the early-juvenile stage, during which mats provided shelter as well as ready access to their primary diet of associated invertebrate fauna (Witherington et al., 2012).

While the ecological value of *Sargassum* scales with clump and aggregation size (Stoner & Greening, 1984; Martin et al., 2021), even dispersed fragments/clumps offer important niches within the open ocean environment, a resource consistently underestimated by remote sensing methods. In this geographically and temporally expansive dataset, dispersed clumps and windrows were far more common than mats (Section 5.1); both provide excellent habitat for transient and resident megafauna regardless of their ever-changing, wind-driven aggregation status. Species requiring persistent aggregated *Sargassum* for survival at certain life stages may be challenged by the dominance of dispersed clumps. As aggregation is intricately tied to macroalgal abundance, in years and/or regions with lower overall *Sargassum* biomass (Figure 5.4), large mats may never form or be sustained because insufficient material is available on a local scale. Different *Sargassum* varieties host invertebrate communities of mixed abundance, diversity, and value as a food resource (Martin et al., 2021); hourly observations reported here did not attempt to identify *Sargassum* clumps or aggregations to species or variety, but this detail may inform interpretation of future megafauna studies.

5.3 Nekton Associates

Section 5.3 builds on the dataset summary published in Siuda (2011), which utilized neuston net tows from 1973-2010 autumn and spring cruises through the Sargasso Sea. For this report, the 2011-2024 neuston tows were added and several reanalyses were conducted. During net processing, qualitative comments were recorded about community composition of organisms >2 cm in size. A lack of qualitative comment for a given tow may either indicate that no organisms >2 cm were collected, or that a nekton description was not recorded by the lab team. It should also be noted that even when qualitative comments were present on a datasheet, the list of organisms may not be comprehensive. Report graphs below show cumulative results over the full time period for autumn/spring net tows within the Sargasso Sea Geographical Area of Collaboration only; additional patterns and statistics for the early record are available

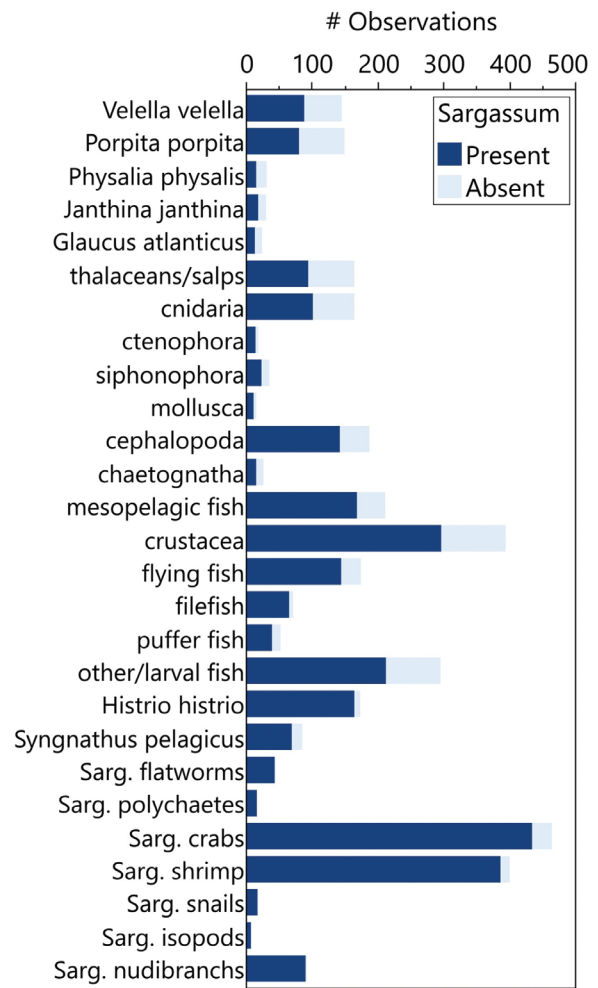


FIGURE 5.6. Frequency of collection for nekton (zooplankton >2 cm in size) during 1,593 SEA surface neuston net tows conducted between 1973-2024 in the Sargasso Sea Geographical Area of Collaboration. Colors indicate whether holopelagic *Sargassum* was present/absent in the net tow.

in the original publication. Anguillid (eel) larvae are discussed separately in Section 5.5.

A total of 1,593 neuston net tows from the Sargasso Sea offered qualitative comments about the collected nekton assemblage. Of those, 1,201 (75%) tow samples contained holopelagic *Sargassum* and 392 did not. Tows were reasonably evenly split geographically (880 in North Sargasso, 713 in South Sargasso) and seasonally (763 in autumn, 830 in spring), allowing robust spatiotemporal comparisons.

Sargassum crabs, *Sargassum* shrimp, other crustaceans, and other fish were most frequently observed (Figure 5.6). For the majority of recorded taxa, a greater

number of occurrences had co-located *Sargassum* than not, although the proportions varied markedly.

For the purposes of regional and seasonal analysis, nekton were placed into five ecologically-based groups:

- juvenile fish (filefish, puffer fish, flying fish, other/ unidentified larval fish)
- *Sargassum* endemics (*Histrio histrio*, *Syngnathus pelagicus*, *Sargassum* flatworm, *Sargassum* polychaete, *Sargassum* crab, *Sargassum* shrimp, *Sargassum* snail, *Sargassum* isopod, *Sargassum* nudibranch)
- non-*Sargassum* crustaceans (spiny lobster larvae (phyllosoma), mantis shrimp larvae (stomatopods), euphausiids, juvenile lobsters, etc.)
- mesopelagic taxa that undergo diel vertical migration (salps, cnidaria, ctenophores, siphonophores, mollusks, cephalopods, chaetognaths, mesopelagic fish)
- obligate neuston (*Velevella velevella*, *Porpita porpita*, *Physalia physalis*, *Janthina janthina*, *Glaucus atlanticus*)

Clumps and aggregations of holopelagic *Sargassum* are known nurseries for larval fish and transient habitat for juvenile and older fish, all in diverse assemblages (Bortone et al., 1977; Moser et al., 1998; Casazza & Ross, 2008). 77% of juvenile fish collected in neuston tows were observed when *Sargassum* was present (Figure 5.7). This proportion was higher in autumn than spring (87% vs 69%; Figure 5.8) and varied only slightly between regions (75% North Sargasso and 80% South Sargasso; Figure 5.9). As expected, members of the endemic *Sargassum* community (Butler et al., 1983; Coston-Clements et al., 1991) exhibited the highest frequency of occurrence with *Sargassum*, from 88% in spring to 97% in autumn and consistently >90% when examined regionally. At times, *Sargassum* was caught on the net frame, towed for a distance, then released outside of the net mouth. As a result, some *Sargassum* community organisms were found in

tows that did not collect macroalgae; this was most often the case for *Sargassum* crabs that are known to capably swim between clumps or algal rafts.

A wide array of non-*Sargassum*-endemic crustaceans, gelatinous organisms, and mesopelagic fish were recorded within the nekton community. Most of these taxa have patchy distributions and undergo diel vertical migration (Angel & Pugh, 2000). They occupy deeper waters during the day and migrate to/towards the surface at dusk, stimulated by a change in light intensity. Vertical migrators usually, but not always, feed actively at night while near the surface; simultaneously, they must avoid predation, thus crustaceans and mesopelagic fish appear to leverage both the food resources and protection offered by holopelagic *Sargassum* when it is present (Figure 5.7). Across seasons and regions, crustaceans were observed on average 73% of the time with *Sargassum* and mesopelagic taxa 71%, with greater variability between autumn and spring than location (Figures 5.8 and 5.9). However, these organisms are not reliant upon macroalgae at any scale for survival, shelter, breeding, or to locate prey, and all were commonly observed in open ocean waters throughout the surveyed area.

Obligate neuston comprise nekton that, by structure or physiology, cannot swim or survive beneath the ocean surface (Helm, 2021). The same wind and circulation forces transport microplastics, drifting *Sargassum*, and obligate neuston taxa, therefore all aggregate in the Sargasso Sea gyre (Chong et al., 2023). No direct preference or action on the part of these four gelatinous species and one nudibranch has been documented to indicate a need for or benefit conferred by proximity to *Sargassum*; indeed, the same obligate neuston thrive in the North Pacific subtropical gyre (Helm, 2021; Chong et al., 2023). In neuston net tows, just 54 – 64% of obligate neuston observations had co-located *Sargassum*, the lowest proportion of all recorded nekton.

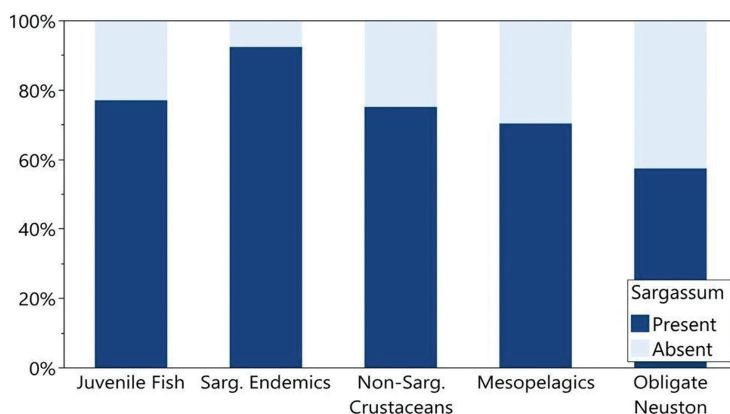


FIGURE 5.7. Nekton proportional occurrence when holopelagic *Sargassum* was present/absent in SEA autumn/spring surface neuston net tows conducted between 1973–2024 within the Sargasso Sea Geographical Area of Collaboration. Proportions calculated based on tows where each ecological group of taxa was present.

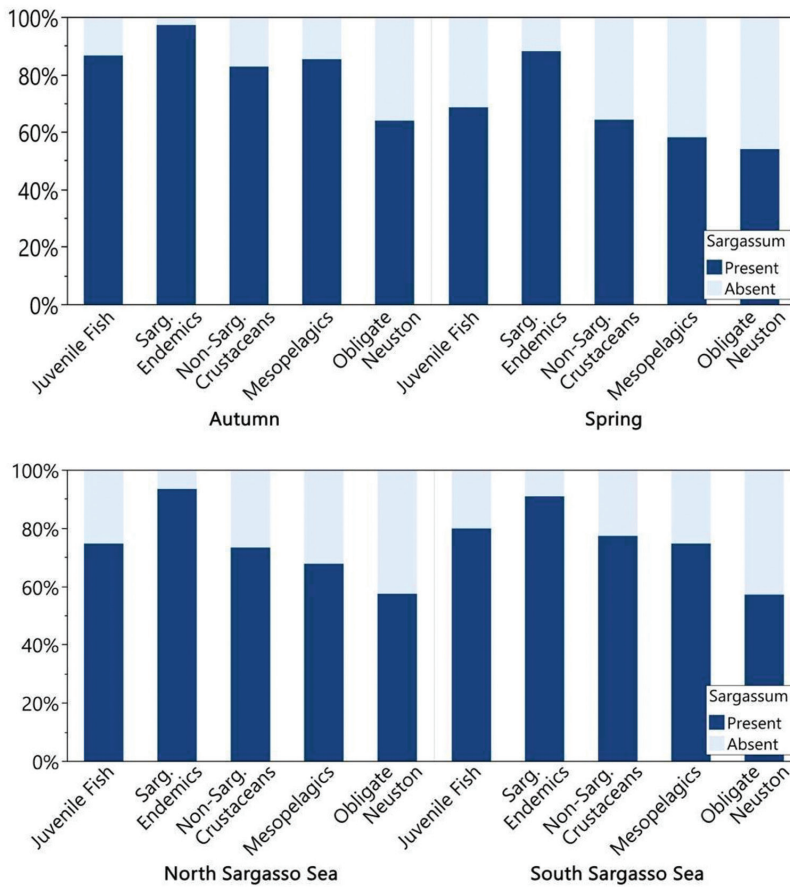


FIGURE 5.8. Nekton proportional occurrence when holopelagic *Sargassum* was present/absent in SEA surface neuston net tows conducted between 1973-2024 within the Sargasso Sea Geographical Area of Collaboration. Proportions calculated based on tows where each ecological group of taxa was present. Data were divided seasonally into autumn (left) and spring (right) based on sampling date.

FIGURE 5.9. Nekton proportional occurrence when holopelagic *Sargassum* was present/absent in SEA surface neuston net tows conducted between 1973-2024 within the Sargasso Sea Geographical Area of Collaboration. Proportions calculated based on tows where each ecological group of taxa was present. Data were divided geographically into North (left) and South (right) Sargasso Sea regions based on sampling location.

One additional obligate neuston taxa, too small to classify as nekton, are *Halobates* (data not shown). These marine water striders (insects) lay their eggs on a variety of floating substrates, including microplastics and *Sargassum* (Dias & Lopes, 2009; Goldstein et al., 2012; Mahadik et al., 2019). Within the Sargasso Sea, the role of *Sargassum* abundance, variety, aggregation, and seasonality on *Halobates* population dynamics has not been formally studied. Nonetheless, SEA neuston tows found *Halobates* present with *Sargassum* 66% (South Sargasso Sea) to 74% (North Sargasso Sea) of the time, with similar proportions when examined seasonally (61% spring – 71% autumn tows).

5.4 Motile Epifauna Community

Section 5.4 summarizes the research findings published in Martin et al. (2021), which examined holopelagic *Sargassum* motile epifauna from over 370 dip net samples collected at 66 unique locations in the Gulf of Mexico, Gulf Stream, Caribbean Sea, Sargasso Sea, and Tropical Atlantic. A total of 20,975 individual motile epifauna were collected, representing 32 taxa (species and groups of related species) and typically <2 cm in size. For this report, no additional data were added or analyses

conducted; detailed patterns noted in the complete dataset and statistical results are available in the original publication.

Holopelagic *Sargassum* offers a complex habitat supporting high biological diversity in comparison to the surrounding water (Figure 5.1). *Sargassum*-associated motile epifauna density and community composition was known to vary between the Gulf Stream and Sargasso Sea (Fine, 1970; Stoner & Greening, 1984), seasonally (Butler et al., 1983; Monroy-Velázquez et al., 2019), and with clump age (Stoner & Greening, 1984). However, epifauna assemblage differences between structurally-distinct holopelagic *Sargassum* varieties had not been rigorously explored prior to Martin et al. (2021).

Finely-structured macroalgae support higher density and diversity of epifaunal associates than simple and open morphologies (Cacabelos et al., 2010; Gutow et al., 2015). With greater niche availability, complex architecture provides a balance of refuge for prey (Vandendriessche et al., 2007; Ware et al., 2019), perches for sit-and-wait predators (Klecka & Boukal, 2014), and surface area for consumers of sessile epifauna (Chemello & Milazzo, 2002). The most influential *Sargassum* characteristics

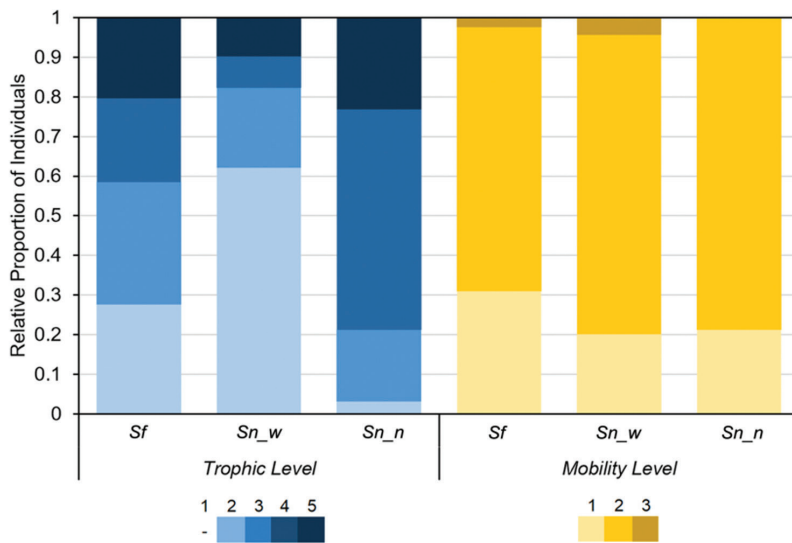


FIGURE 5.10. Proportion of individuals from non-dominant motile epifauna taxa in trophic and mobility levels by holopelagic *Sargassum* variety. Trophic levels (2–5) assigned using Butler et al. (1983); no true herbivores (1) were found. Mobility levels assigned to taxa that require physical contact with the substrate to move (1), cling with limited swimming ability (2), and free-swimming (3). Figure from Martin et al. (2021); assigned trophic and mobility levels for all taxa are listed in their Supplemental Table 1.

are distance between blades and vesicles (together, foliation), branching frequency, blade surface area, and the resulting three-dimensional interstitial spaces (Leite et al., 2007; Ware et al., 2019; Stelling-Wood et al., 2020). *Sn_w* foliation distance is nearly double that of both *Sn_n* and *Sf*, meaning fewer branches present overall; its blades are generally twice as long and wide as those of *Sf* and equal in length but almost five times the width of *Sn_n* (Figure 4.1). Together, *Sn_w*'s features yield lower surface area-to-volume ratio, fewer interstitial spaces, and a less intricate architecture. *Sf* provides enhanced habitat complexity and shelter from predation, and *Sn_n*'s long, narrow blades create a comparatively open structure.

Sargassum sample mass led to increased abundance of motile epifauna individuals and taxon richness for all three varieties (Figure 6 in Martin et al., 2021). At any mass, *Sf* supported significantly higher abundance and richness than *Sn_n* and *Sn_w*. This finding is consistent with rafting ecology (Hobday, 2000; Abé et al., 2013) and earlier *Sargassum* studies (Fine 1970; Butler et al., 1983; Stoner & Greening, 1984) as increased sample/raft size confers increased branching, dimensionality, range of algal growth stages, and architectural space for habitat, refuge, and foraging. Few regional differences were observed.

The most common (percent presence across all samples) and abundant (average number of individuals per sample per gram) residents of the *Sargassum* motile epifauna community, respectively, were the shrimp *Latreutes fucorum* and the snail *Litiopa melanostoma*. *L. fucorum* occurred on >85% and *L. melanostoma* on 55–63% of samples for each pelagic *Sargassum* variety (Table 2 in Martin et al., 2021). The third most abundant species was the isopod

Carpas minutus, which favored *Sn_w*. Comparatively, all other taxa were less frequently observed.

Sargassum species and variety influenced epifaunal assemblage (Table 2 in Martin et al., 2021). For example, the shrimp *Leander tenuicornis* and crab *Portunus sayi* were more common on *Sf* but the shrimp *Hippolyte coerulescens* and crab *Planes minutus* were found mostly on *Sn_n*. Polychaetes and flatworms were more often on *Sf* and *Sn_w*. Unique fish assemblages were documented on *Sf* and *Sn_w*, with fish absent on *Sn_n*. The Gulf of Mexico hosted highest fish diversity and density, perhaps due to its proximity to broad, shallow shelf waters and valuable nursery habitat compared to environments further offshore (Dooley, 1972; Wells & Rooker, 2004). Community composition was 86% dissimilar between *Sf* and *Sn_n*, 38% between *Sf* and *Sn_w*, and 78% dissimilar between *Sn_n* and *Sn_w*.

Functional structure analyses, conducted without the dominant *L. fucorum* and *L. melanostoma*, showed the average motile epifauna trophic level on architecturally complex *Sf* was 3.3 (abundances of shrimp, crabs, and fish; near-equal distribution across trophic levels), while *Sn_w* averaged 2.6 (higher proportion of amphipods and isopods; Figure 5.10). The community trophic level for *Sn_n* (4.0) was notably greater, with increased higher-predator taxa (crabs, nudibranchs, and pycnogonids). With an open structure, *Sn_w* was home to organisms with higher mobility (1.84) compared to *Sf* (1.71 average, with more clinging taxa that require the surface area provided by densely-packed, broad blades; Figure 5.10). The moderately open *Sn_n* (1.79 average mobility) supported a similar proportion of clinging taxa as *Sn_w*, however no free-swimming species were observed.

In combination, community- and taxa-level observations demonstrate that morphological differences influence the ecological value of holopelagic *Sargassum*, both to its faunal associates and the wider marine ecosystem. Motile epifauna provide a food source for higher trophic levels, particularly important fish species (NMFS, 2003). Over the past decade, influx of the previously rare and less morphologically complex *Sn_w* to tropical and western North Atlantic waters has shifted the balance of *Sargassum* variety abundances and their respective geographic distributions. As *Sn_w* continues to move into areas where the more ecologically valuable *Sf* was historically dominant (Parr, 1939; Schell et al., 2015; Garcia-Sanchez et al., 2020; Alleyne et al., 2023), it alters available trophic resources, including the relative proportions of associated taxa, and may endanger already threatened species or commercially important stocks. At the same time, does the presence of more *Sargassum* distributed across a greater spatial extent, as a result of unprecedented blooms, offset the reduction in overall ecological value (Wernberg et al., 2004)? The balance between positive effects of increasing *Sargassum* presence and negative effects of decreasing motile epifauna density and richness where macroalgal varieties now co-occur is unknown. These ecosystem-level questions have important yet unexplored conservation and management implications.

Martin et al.'s (2021) study provides the most recent dataset in a multi-decadal sequence that documents temporal shifts in *Sargassum*-associated epifauna community composition (Stoner & Greening, 1984; Huffard et al., 2014). Modern motile assemblages differed in dominant taxa and evenness from those recorded during the 1960s and 1970s. Samples collected prior to 1975 included more flatworms, polychaetes, isopods, and amphipods

than other taxa; community structure was relatively even, with three to five species comprising the top 75% by abundance (Table 5.2; Fine, 1970; Butler et al., 1983). Over time, the shrimp *L. fucorum* has transitioned from <10% of the epifauna community to reach 60-80% in a majority of modern samples; the snail *L. melanostoma* dominated when *L. fucorum* did not (Table 5.2; Martin et al., 2021). Huffard et al. (2014) described their collected fauna as <15% similar to historic records for the Sargasso Sea, reflecting a decline in evenness and, in their assertion, a shift in overall composition.

Interestingly, the community of sessile epifauna living on *Sargassum* blades and branches has not experienced substantial changes over time (Butler et al., 1983; Calder, 1995), reducing the likelihood that motile epifauna assemblage shifts were driven by climate or bottom-up trophic mechanisms (as proposed by Huffard et al., 2014). These explanations do not address the rapid change in motile community composition from the mid-1970s to the early 1980s and available data do not permit a retrospective analysis. Since sampling occurred throughout the year in historical and modern studies, seasonality does not appear to influence the observed shift in community composition.

5.5 Larval Eels

The Sargasso Sea serves as spawning ground for many ecologically- and commercially-important fishes, including the American and European eels (*Anguilla rostrata* and *Anguilla anguilla*, respectively; Miller & McCleave, 2007). The larvae of these and other eel species, called leptocephali, circulate in the region until they migrate to their adult habitat and metamorphose (Bonhommeau et al., 2010). Fifteen families of marine eels are recognized, with

TABLE 5.2. Motile Epifauna Species Comprising Top ~75% of Total Abundance in the Sargasso Sea

Study	Most Common Species				
Fine (1970)	<i>Hemiaegina minuta</i> (38%)	<i>Carpas minutus</i> (27%)	<i>Sunampitoe pelagica</i> (11%)		
Butler et al. (1983)	<i>Platynereis dumerilii</i> (42%)	<i>Gnesioceros sargassicola</i> (27%)	<i>Litiopa melanostoma</i> (13%)	<i>Biancolina sp.</i> (7%)	<i>Carpas minutus</i> (7%)
Stoner & Greening (1984)	<i>Litiopa melanostoma</i> (25%)	<i>Latreutes fucorum</i> (22%)	<i>Planes minutus</i> (12%)		
Huffard et al. (2014)	<i>Latreutes fucorum</i> (87%)				
Martin et al. (2021)	<i>Latreutes fucorum</i> (50%)	<i>Litiopa melanostoma</i> (25%)			

Note: Table lists species comprising approximately the top 75% of total abundance in holopelagic *Sargassum*-associated community studies. Only frequencies of motile epifauna were of interest, hence values from investigations that included pelagic species like copepods were excluded. Studies are ordered by sample collection date (oldest first) and only records from Sargasso Sea samples are shown. Table modified from Martin et al. (2021) Table 3.

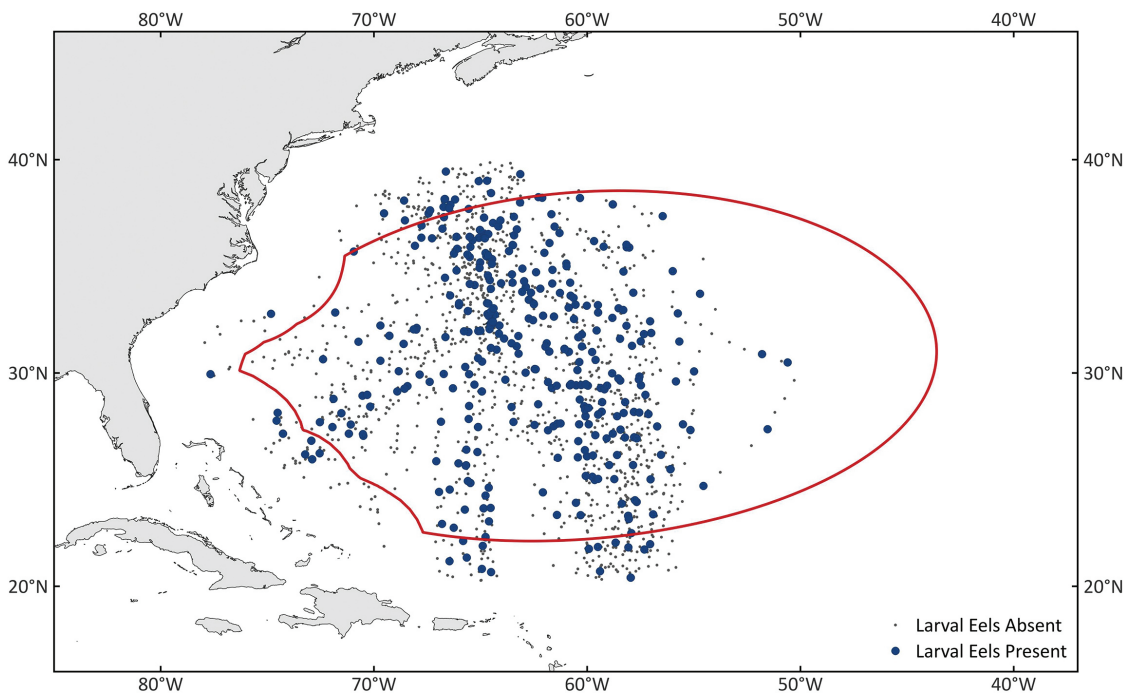


FIGURE 5.11. Locations of SEA autumn/spring surface neuston net tows conducted between 1979–2024 where eel data was recorded, with presence of larval eels (leptocephali) in blue dots. Small gray dots indicate tows without eels. Stations in the Sargasso Sea Geographical Area of Collaboration (red line) and within a 2 degree (120 nm) buffer are shown to illustrate connectivity with surrounding oceanographic regions.

TABLE 5.3. Surface Observations of Larval Eels

	Leptocephali presence
Holopelagic <i>Sargassum</i> Absent	23.3%
Holopelagic <i>Sargassum</i> Present	76.7%
Spring	27.1%
Autumn	72.9%
North Sargasso Sea	55.2%
South Sargasso Sea	44.8%
North Sargasso Sea - Spring	11.6%
North Sargasso Sea - Autumn	43.5%
South Sargasso Sea - Spring	15.6%
South Sargasso Sea - Autumn	29.4%

Note: Percent presence for larval eels (leptocephali) of any species as a function of *Sargassum* absence/presence, season, region, and region-season across 1,612 surface neuston net tows conducted in the Sargasso Sea Geographical Area of Collaboration from 1979–2024 where eel data was recorded. 354 total tows collected leptocephali.

14 fully marine and one catadromous (Anguillidae). Over 100 different species of leptocephali have been documented in the Sargasso Sea, in some cases representing geographically-distinct subpopulations maintained by timing differences in adult spawning cycles and ocean circulation processes (Miller, 2002; Miller & McCleave, 2007).

Leptocephali are laterally compressed transparent

fishes living in oligotrophic pelagic waters that feed mainly on detritus. They may use holopelagic *Sargassum* as nursery habitat during early life stages (Bonhommeau et al., 2010). Larval eels are known diel vertical migrators, swimming to greater depths during the day as a predator avoidance mechanism and returning to surface or near-surface waters at night to feed (Miller, 2002). This behavior influences at what depth and time of day net sampling methods encounter leptocephali.

In SEA data records, larval eels were collected in surface neuston net tows across all sampled regions of the Sargasso Sea, with greatest consistency in north-central waters (Figure 5.11). They were observed at significantly greater densities when *Sargassum* was present and far more often in the autumn than in the spring (Table 5.3). Regional differences were lower, though more distinct when considered as region-season (Table 5.3).

A laboratory study morphologically identified and measured the length of 2,293 preserved larval eels collected in 113 autumn/spring SEA surface neuston net tows between 1988–2012 (Schofield & Siuda, 2013). Over 99% were *Ariosoma balearicum* (family Congridae, the bandtooth conger eel). Of the remaining, 6 individuals were unidentifiable, 1 was family Anguillidae, and 6 other marine eel families were represented. Smaller (~60 mm

TABLE 5.4. Spring 2013-2016 Leptocephali Identifications

Family	Represented Species	# Individuals	% Total
Anguillidae	<i>Anguilla anguilla</i> * <i>Anguilla rostrata</i> *	15	2.1%
Chlopsidae	<i>Chilorhinus suensonii</i> * <i>Kaupichthys hyoprroides</i> *	22	3.1%
Congridae	<i>Ariosoma balearicum</i> * <i>Gnathophis bathytopos</i> * <i>Paraxenomystax bidentatus</i> <i>Bathyrcongler parvibranchialis</i> * <i>Urocongler syringinus</i>	425	60.6%
Derichthyidae	<i>Derichthys serpentinus</i> *	8	1.1%
Moringuidae	<i>Moringua edwardsi</i> *	20	2.9%
Muraenesocidae	<i>Synaphobranchus kaupii</i> *	1	0.1%
Muraenidae	<i>Anarchias yoshiae</i> <i>Gymnothorax moringa</i> * <i>Gymnothorax nigromarginatus</i> <i>Gymnothorax miliaris</i>	28	4.0%
Nemichthyidae	<i>Avocettina infans</i> <i>Nemichthys scolopaceus</i> * <i>Nemichthys curvirostris</i>	165	23.5%
Nettastomatidae	<i>Hoplunnis macrura</i>	3	0.4%
Ophichthidae	<i>Ahlia egmontis</i> <i>Myrophis punctatus</i>	7	1.0%
Serrivomeridae	<i>Serrivomer beanie</i> * <i>Serrivomer lanceolatoides</i> *	5	0.7%
Synaphobranchidae	-	2	0.3%

Note: Total number of individuals and percent presence for larval eels (leptocephali) of all morphologically identified species across 87 surface, shallow subsurface, and deep net tows conducted in the Sargasso Sea Geographical Area of Collaboration from 2013-2016. * indicates confirmed genetic identification.

length) individuals were found in the North Sargasso Sea during fall months while larger specimens (~80-90 mm) were collected in the spring (Scofield & Siuda, 2013). Mortality processes, altered vertical migration behavior and depth range, and the transition to juvenile stage contribute to the decreased population densities noted in spring sampling. Reliance on *Sargassum* aggregations for food resources and shelter may decline as eel larvae mature (Bonhommeau et al., 2010).

During four (2013-2016) spring Marine Biodiversity and Conservation program cruises, multifaceted investigations of larval eel biogeography were conducted. 701 leptocephali were collected (2013 – 50 eels, 2014 – 272, 2015 – 225, 2016 – 154) at approximately local midnight using a stacked array of nets: surface (0 m) neuston net, shallow (average depth range 5-17 m) subsurface 1-m ring net, and deep (average depth range 55-183 m) 2-m ring net. Leptocephali were found in all nets, with greater proportions in surface (37%) and deep (25-100 m: 49%; 166-207 m: 5%) tows than shallow subsurface samples (9%). Measured length ranged from 9-256 mm, with an

average length of 83 mm. All leptocephali from these four cruises were morphologically identified to at least the family level; focusing on less represented species, morphological identifications were confirmed for 22% of individuals using the cytochrome c oxidase I (Cox1) barcoding gene. Twelve families were represented across all samples and the greatest proportion (403, 57%) of leptocephali were *Ariosoma balearicum* (Table 5.4).

Fifteen *Anguilla* sp. individuals were collected, with 6 of these identifications confirmed via genetic sequencing as *Anguilla anguilla* (3 individuals) and *Anguilla rostrata* (3 individuals; Table 5.4). 14 of the 15 morphologically identified *Anguilla* sp. larvae were collected in deep net tows, demonstrating that surface-focused sampling for leptocephali population studies will not accurately represent the Sargasso Sea abundance or distribution for these species. Overall, *Anguilla* sp. comprised a very small portion of the larval eel community encountered in nearly two decades of SEA's daily, non-targeted net tows; these methods do not permit examination of temporal trends in eel, nor specifically *Anguilla* sp., populations.

CHAPTER 6

Ecological Connectivity and Long-term Change

6.1 *Sargassum* Variety Dynamics and Regional Connectivity

Section 6.1 summarizes research findings presented at the 2020 Ocean Sciences meeting (Goodwin et al., 2020) and published in Govindarajan et al. (2019). Since the early 1990s, any holopelagic *Sargassum* species and variety present in neuston net tows have been quantified separately, offering the only multidecadal record of their distribution and abundance throughout the North Atlantic. For this report, observations from 2020–2024 were added and analyses were updated. Years were here defined ecologically as the period from October in the previous year through September in the current year, and data from all seasons were included. The full geographic extent of SEA’s dataset was utilized to illustrate variety-specific basin-scale spatial patterns.

Holopelagic *Sargassum* sits at or just below the sea surface and drifts with prevailing currents. In the western North Atlantic, transport generally moves from east to west, across the tropics via the North Equatorial Current, between the islands of the Lesser Antilles and through the Caribbean Sea to the Yucatan Channel west of Cuba (Figure 6.1). The Florida Straits funnel the Gulf Stream as it leaves the Gulf of Mexico and travels north. The North and South Sargasso Seas form the core of the subtropical gyre, with gentle recirculation occurring between them. Finally, the Antilles Current is a continuation of tropical westward-flowing currents, carrying water past Puerto Rico and into the Bahamas before joining the Gulf Stream, with eddy mixing along the southern edge of the Sargasso Sea.

Historically (1993–2007), the Sargasso Sea contained both *Sf* and *Sn_n*, with greater quantities of the former (Figure 6.2). Over the last 15 years, *Sn_n* has become dominant here and *Sf* density significantly declined, while *Sn_w* has not been found consistently or in quantity. Samples collected outside the Sargasso Sea usually contained higher proportions of *Sf* in the early decades of this dataset; more recently, *Sn_w* was common and a mix of all three *Sargassum* varieties observed (Figure 6.2). Total (all varieties) *Sargassum* density outside the Sargasso Sea has increased during recent years when compared to prior decades. Biomass within the Sargasso Sea as a

whole has decreased overall, but not below historic levels (Figure 6.2).

In recent decades, holopelagic *Sargassum* is a recurring feature of open ocean pelagic environments well beyond the historic boundaries of the Sargasso Sea, extending throughout the equatorial Atlantic, Caribbean Sea, and Gulf of Mexico (Schell et al., 2015; Torres-Conde et al., 2023) where it is referred to as the Great Atlantic *Sargassum* Belt (GASB; Wang et al., 2019). There exist no historical records of analogous macroalgal inundations in these locations, reinforcing the scientific consensus that the GASB is a new phenomenon within multiple centuries of North Atlantic *Sargassum* documentation. Years of SEA field observations since GASB onset demonstrate that it is sustained independently of the Sargasso Sea. Potential causes of the GASB’s near-annual unprecedented and highly consequential tropical blooms since 2011 include warming and excess nutrients (Djakouré et al., 2017) and/or anomalous transport during a negative North Atlantic Oscillation event (Johns et al., 2020), ideas supported by modeling studies (Putman et al., 2018; Berline et al., 2020; Jouanno et al., 2025) but not fully confirmed. While major ocean currents appear unchanged during the recent GASB period, vast amounts of *Sargassum* now reach the Caribbean Sea and Antilles Current from the east via the North Equatorial Current (Franks et al., 2016; Wang et al., 2019). GASB-sourced *Sargassum* may enter the South Sargasso Sea through mixing along the subtropical gyre’s southern boundary with the Antilles Current near the Bahamas, or travel through the western Caribbean to the Florida Straits and Gulf Stream to eventually reach the North Sargasso Sea.

Temporal fluctuations in Sargasso Sea holopelagic *Sargassum* biomass from the 1930s to 1980s were discussed by Butler & Stoner (1984), who noted an order of magnitude decrease over several decades in the southwest sector but not near Bermuda. SEA neuston tow observations for total *Sargassum* through the present likewise capture significant continued biomass variability on approximately ten-year cycles (Figure 4.4), underlying mechanism as yet unstudied. When examined at the variety level and with the expanded geographic perspective of the full North Atlantic basin, however, patterns are

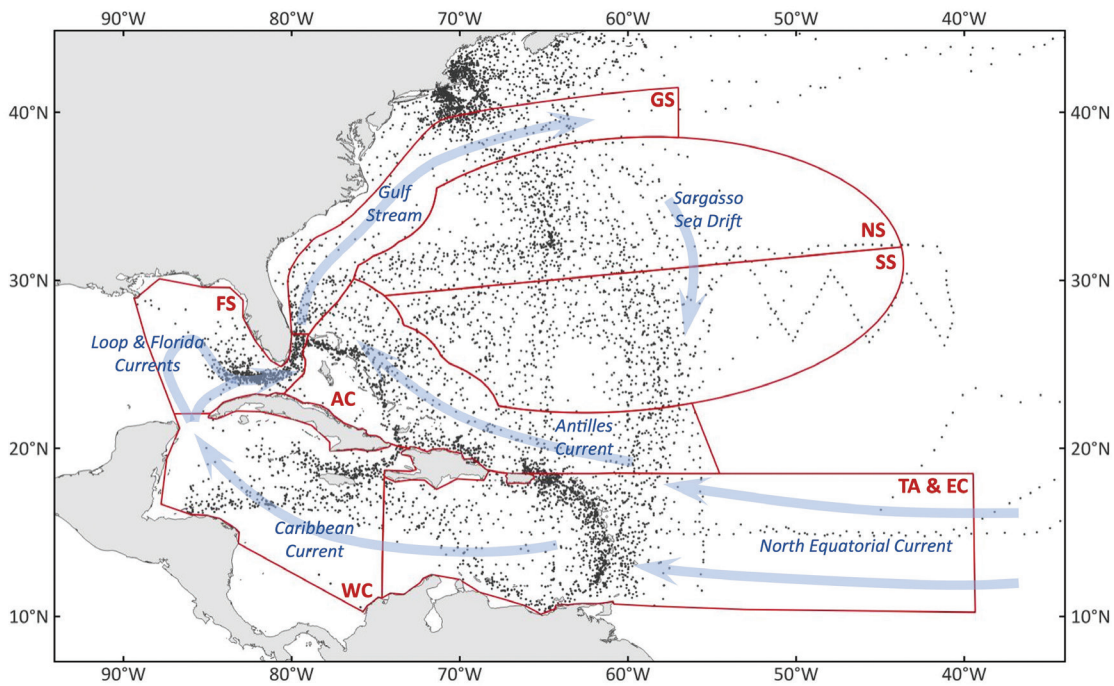


FIGURE 6.1. Locations of SEA surface neuston net tows conducted between 1993-2024 (all seasons) throughout the western North Atlantic where common holopelagic *Sargassum* species and variety data was recorded. Prevailing surface currents (blue arrows/labels) drive regional connectivity. Major regions (red lines/abbreviations) utilized in Section 6 analyses were defined on the basis of physical oceanographic boundaries: NS - North Sargasso Sea, SS - South Sargasso Sea, AC - Antilles Current, TA & EC - Tropical Atlantic and Eastern Caribbean, WC - Western Caribbean, FS - Florida Straits, GS - Gulf Stream. Voyages sampling the eastern North Atlantic, coastal European waters, the Mediterranean Sea, and from Madeira south to the Cape Verde Islands observed no *Sargassum* in any neuston tows and are not shown.

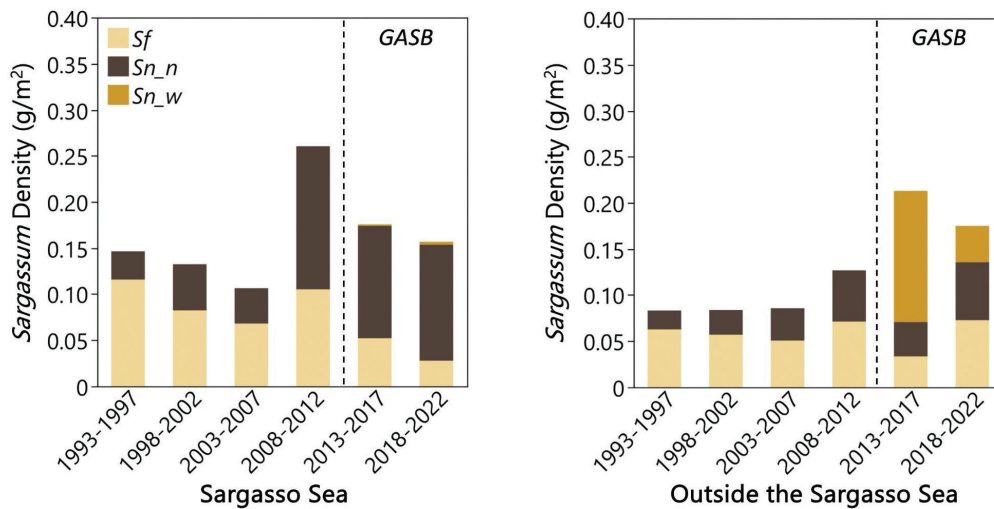


FIGURE 6.2. Weighted mean density (g m^{-2}) of holopelagic *Sargassum* in SEA surface neuston net tows conducted between 1993-2022 (all seasons) within the Sargasso Sea Geographical Area of Collaboration (left panel) and outside (tropical Atlantic, Antilles Current; eastern and western Caribbean, Florida Straits, and Gulf Stream; right panel). Data were divided into 5-year bins on an ecological year (October through September) basis. Years when the Great Atlantic *Sargassum* Belt (GASB) was present demarked with dashed line. Colors represent common varieties: *Sf* = *Sargassum fluitans* var. *fluitans*; *Sn_n* = *Sargassum natans* var. *natans*; *Sn_w* = *Sargassum natans* var. *wingei*.

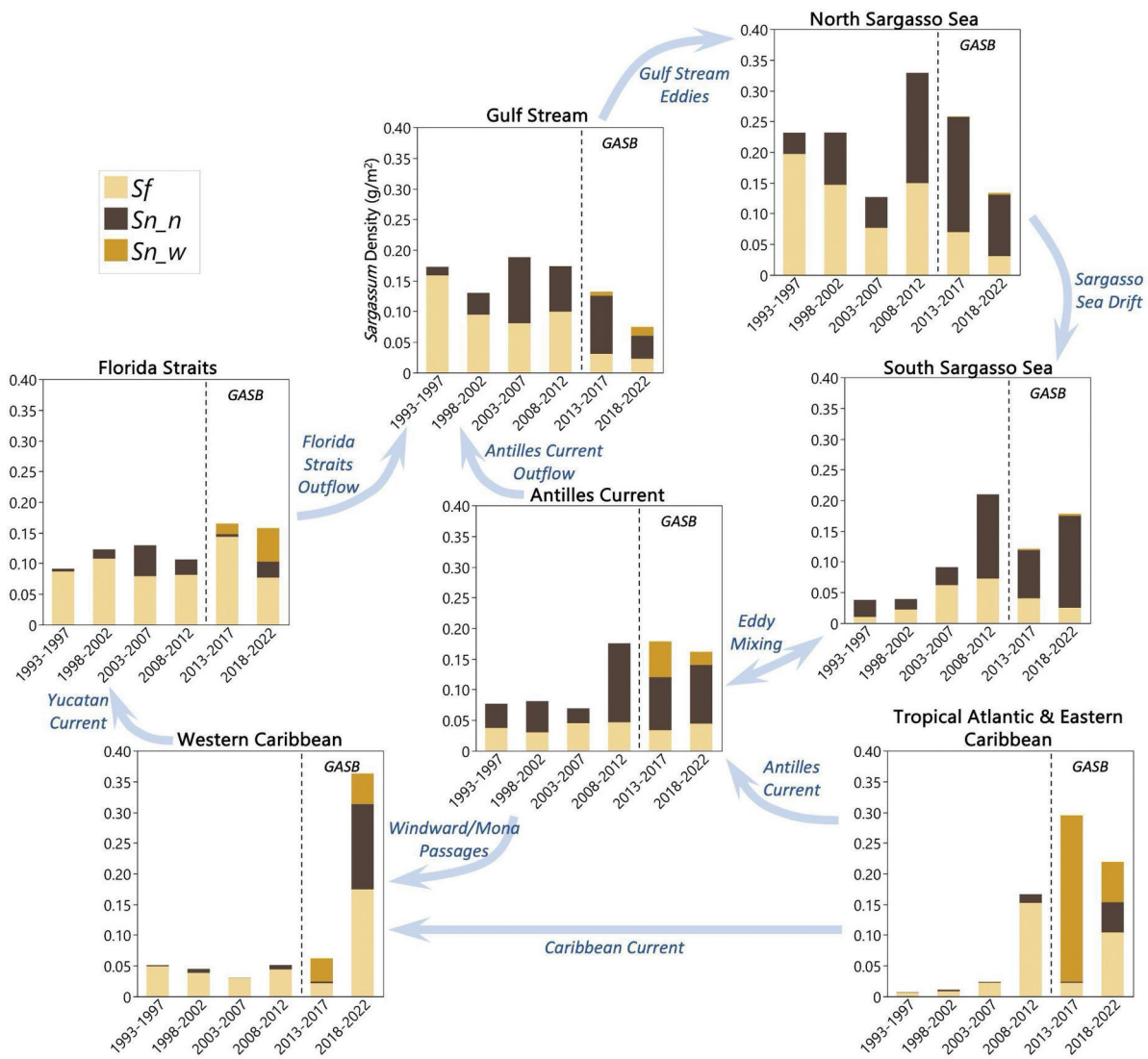


FIGURE 6.3. Weighted mean density (g m^{-2}) of holopelagic *Sargassum* in SEA surface neuston net tows conducted between 1993–2022 (all seasons) within major oceanographic regions of the western North Atlantic. Prevailing surface currents (blue arrows/labels) drive regional connectivity and *Sargassum* transport. Data were divided into 5-year bins on an ecological year (October through September) basis. Years when the Great Atlantic Sargassum Belt (GASB) was present demarked with dashed line. Colors represent common varieties: *Sf* = *Sargassum fluitans* var. *fluitans*; *Sn_n* = *Sargassum natans* var. *natans*; *Sn_w* = *Sargassum natans* var. *wingei*. Note most recent values in the western Caribbean skewed by three very high density tows in the Windward Passage.

more nuanced than depicted above (Figures 6.2 vs 6.3). In SEA's records since 1993, *Sf* was historically widespread and especially common in the Florida Straits, Gulf Stream, and North Sargasso Sea, with none observed in the tropical Atlantic and minimal quantities in the Caribbean Sea (Figure 6.3); this distribution differs from Parr's (1939) observations, wherein *Sf* was noted less frequently than *Sn_n*. High densities of new growth seen during spring in the Florida Straits reflect a Gulf of Mexico source region (the place where a variety blooms under optimal environmental conditions and from which it is transported).

Carried by the Gulf Stream, *Sf* then enters the North Sargasso Sea; a portion drifts into the South Sargasso Sea and disperses, fragmenting into smaller, older pieces as it declines.

Throughout the earliest decades of SEA's dataset, *Sn_n* was found in the Sargasso Sea and along its margins due to eddy mixing near the Bahamas feeding the Antilles Current and subsequently the Gulf Stream (Figure 6.3). Notably, *Sn_n* was not collected in the Caribbean Sea or tropical Atlantic at this time, supporting the Sargasso Sea as its source region where local environmental dynamics

drive biomass temporal patterns. In contrast, Parr (1939) recorded Sn_n more widespread than in the 1990s and 2000s, including dominant in the Gulf of Mexico – such gradual shifts in distribution and abundance of the two most common holopelagic *Sargassum* varieties reflect unexplored long-term natural variability. Sn_w was described as rare in texts containing the first North Atlantic species and variety distribution information (Parr, 1939), appeared in no Atlantic-focused publications since the 1930s, and was not found in SEA's records before 2012 (Figures 6.2 and 6.3). Onset of the GASB brought significant quantities of Sn_w from its North Equatorial source region to the western North Atlantic (Franks et al., 2016).

We hypothesize that distinct *Sargassum* variety-specific source regions were historically driven by their respective physiological tolerances for temperature, salinity, nutrients, and other environmental conditions (Schell et al., 2024; see Section 6.2). These requirements dictate when and where *Sargassum* might bloom, to what magnitude and at what rate, and where it will decline. Beyond SEA net tow observations, source region evidence was provided by a population genetics study of the hydroid *Aglaophenia latecarinata*, part of the sessile epifauna community on drifting *Sargassum* (Calder, 1995; Govindarajan et al., 2019). Abundant on both Sf and Sn_w , *A. latecarinata* forms colonies of interconnected polyps; lacking a medusa stage and thus with limited dispersal capability, the species releases planula larvae that settle onto the same or nearby *Sargassum* substrates and develop into new hydroids (Calder, 1995). Sequences of the 16S gene from 140 hydroid colonies collected at 47 stations across the North Atlantic between 2015-2018 from available

Sargassum varieties showed strong association between *A. latecarinata* haplotypes and their algal substrate (Figure 6.4; Govindarajan et al., 2019). This finding demonstrates hydroid colonization on *Sargassum* clumps that differ in geographic origin and maintain separate distributions through bloom seasonality, dispersal rate and timing, and other physical processes. If *Sargassum* varieties continue to co-occur in the tropical Atlantic as they have since ~2019, the hydroid population structure described here may shift, potentially blending into a singular population; parallel future changes to the broader sessile and motile epifauna communities might also take place, potentially enhancing the abundance and diversity of taxa hosted by Sn_w (Martin et al., 2021; Section 5.4)

Since 2011, shifts in holopelagic *Sargassum* variety distribution and abundance have been observed throughout the western North Atlantic, only some of which can be directly attributed to the onset and continued annual occurrence of the GASB. Sf concentrations have increased in the Caribbean Sea and tropical Atlantic while its relative proportion in the Gulf Stream and Sargasso Sea has declined in the past decade (Figure 6.3). Modest influxes of Sn_n to the western Caribbean have occurred through the Windward Passage (between Cuba and Haiti) and increased presence and concentration throughout the Antilles Current and eastern Caribbean were noted (Figure 6.3). Furthermore, Sn_n now holds a greater biomass proportion in the Sargasso Sea than Sf and, surprisingly, an increasing proportion in other regions. For more than a decade, Sn_w has been a strong, consistent component of GASB-sourced *Sargassum* in the tropical Atlantic, eastern Caribbean, and Antilles Current

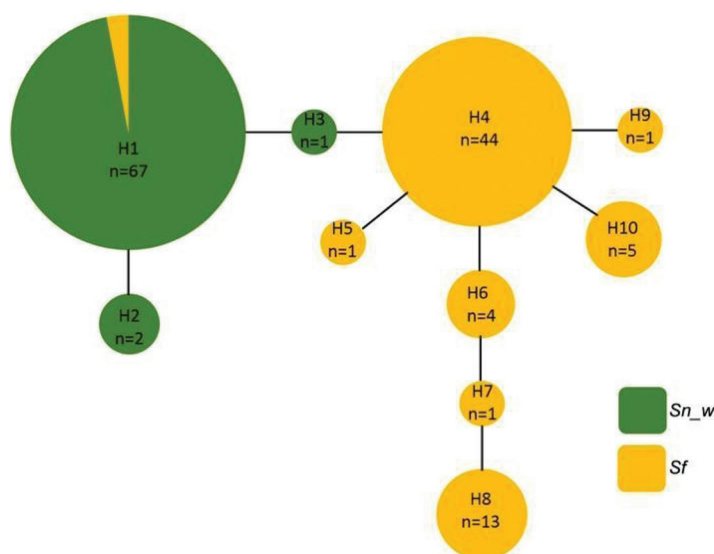


FIGURE 6.4. Haplotype network of *Aglaophenia latecarinata* 16s sequences. Circle size reflects the number of individuals possessing a given haplotype (n). Yellow indicates hydroids found on *S. fluitans* var. *fluitans* (Sf) and green indicates hydroids found on *S. natans* var. *wingei* (Sn_w). No colonies on Sn_w possessed an Sf haplotype. Figure from Govindarajan et al. (2019).

regions. Much of the arriving tropical *Sn_w* biomass is lost to beaches and bays along the eastern side of the Lesser Antilles (Alleyne et al., 2023), with equivalent quantities not transported further downstream to the western Caribbean and Gulf of Mexico (Figure 6.3). To date, it appears that *Sn_w* cannot thrive in the Gulf of Mexico or Sargasso Sea – if capable of establishing under local environmental conditions, many years of GASB inundations should have already provided sufficient biomass for this to happen.

Sargassum variety abundance and distribution across the North Atlantic basin have always varied temporally, reflecting local and regionally-linked dynamics (Parr, 1939; Butler et al., 1983). For example, the amount of *Sf* present in the North Sargasso Sea each year depends on the magnitude of its preceding Gulf of Mexico source region bloom, any residual biomass, and Gulf Stream transport and eddy variability. *Sn_n* fluctuations are more driven by year-to-year environmental conditions within the Sargasso Sea, quantity and health of the local seed population, and episodic events that prompt and/or sustain bloom events. The processes and factors underpinning equatorial bloom dynamics for *Sn_w* are not yet well-understood and with minimal *in situ* quantitative observations from the tropics at critical GASB phases are lacking. The greater Caribbean region has experienced multiple waves of *Sargassum* arriving on the North Equatorial Current, each year's GASB of different spatio-temporal extent and density (Wang et al., 2019). During 2014–2015, *Sn_w* accounted for over 85% of the GASB (Schell et al., 2015), however subsequent years have seen mixed assemblages with *Sargassum* variety proportions varying considerably (Figure 6.3; García-Sánchez et al., 2020; Alleyne et al., 2023). Despite unique source regions and distinct geographic ranges in the pre-GASB era, the distributions of *Sargassum* varieties have changed within the past decade to reach a state of substantial overlap (Figures 6.2 and 6.3). Spatial coincidence results in merging of ecological niches and faunal communities, creates opportunity for nutrient resource competition between varieties, and makes predicting *Sargassum* bloom and transport dynamics more complex.

6.2 *Sargassum* Variety Environmental Tolerances

Section 6.2 summarizes research findings presented at the 2024 Ocean Sciences meeting (Schell et al., 2024) and further analyzed in a forthcoming publication. A three-week experiment conducted in the Eckerd College (Florida) greenhouse during

April–May 2023 investigated the growth and tissue health responses of holopelagic *Sargassum* varieties under a range of temperature and salinity conditions. The project sought to identify environmental tolerance limits and determine the effects of suboptimal oceanographic conditions on *Sargassum* longevity and growth.

Environmental conditions influence growth rate, tissue health, photosynthetic processes, and raft longevity in macroalgae, with response timelines and magnitudes species- and location-dependent. Drifting *Sargassum* clumps experience variable temperature, salinity, light, and nutrient conditions due to seasonal changes as well as the dynamic oceanographic regions encountered over their lifespan regardless of variety. Laboratory experiments assessing influences of salinity and/or temperature on benthic *Sargassum* growth and health have utilized species from a range of locations, however few comparable studies have focused on holopelagic *Sargassum* (Hanisak & Samuel, 1987; Changeaux et al., 2023; Magana-Gallegos et al., 2023; Schell et al., 2023). Only Hanisak & Samuel (1987) and Schell et al. (2023) directly considered the impacts of salinity on *Sargassum* growth, no other investigations have documented changes in overall health, and all known varieties are dramatically under-examined with respect to their responses to shifting ocean conditions. These gaps were targeted in Schell et al.'s (2024) three-week environmental tolerance greenhouse experiments (methods described in Section 2.4).

Seven temperature/salinity treatments (20–32°C, 28–40 psu) were applied while photoperiod, irradiance, and nutrient (open ocean ambient, non-enriched) concentrations were controlled. Growth rate, blade and float loss, and coloration were examined daily as metrics of overall health for specimens of all common holopelagic *Sargassum* varieties. Overall, *Sf* was most robust in terms of growth and structural integrity while *Sn_w* had the lowest growth rate in six of seven treatments. Blades and floats discolored and were lost from *Sargassum* specimens under all treatments and across all varieties albeit to different degrees, with direct impacts to the algae's buoyancy. In marine macroalgae, blades, stems, and floats all participate in photosynthesis and nutrient uptake, therefore their surface area loss also reduces capacity for these processes (not directly measured in the described experiments).

Extreme temperatures negatively impacted growth rate and health, with *Sn_n* most sensitive to conditions above 27°C and *Sf* above 29°C, while at the cold end of the

Temperature Treatments (°C)	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
<i>Sf</i>	U	T	F	F	F	F	F	F	F	F	F	F	T	T	U
<i>Sn_n</i>	F	F	F	F	F	F	F	F	F	F	T	T	U	U	U
<i>Sn_w</i>	U	U	T	F	F	F	F	F	F	F	F	F	F	F	T

Salinity Treatments (psu)	28	29	30	31	32	33	34	35	36	37	38	39	40	Growth/Health Response Key
<i>Sf</i>	U	T	T	F	F	F	F	F	F	F	F	F	T	Favorable
<i>Sn_n</i>	U	T	T	F	F	F	F	F	F	F	F	F	T	Tolerant
<i>Sn_w</i>	T	F	F	F	F	F	F	F	F	F	F	F	F	Unfavorable

FIGURE 6.5. Temperature and salinity ranges within which the growth rate and health metric of each holopelagic *Sargassum* variety was favorable (“F”/green), merely tolerated with no positive growth (“T”/yellow), and unfavorable with significantly reduced health (“U”/red). *Sf* = *Sargassum fluitans* var. *fluitans*; *Sn_n* = *Sargassum natans* var. *natans*; *Sn_w* = *Sargassum natans* var. *wingei*. Table synthesizes experimental results of Hanisak & Samuel (1987), Schell et al. (2023), and Schell et al. (2024).

tested range *Sn_w* was negatively impacted below 21°C and *Sf* below 20°C (Figure 6.5). Across all varieties, blade and float loss was <15% at low temperatures and >80% at high temperatures; enhanced decay area followed the same pattern, except *Sn_w* additionally had marked increases in decay under cold conditions. Holistically, *Sn_n* was cold tolerant and *Sf* preferred temperate conditions. *Sn_w* was most capable in hot waters, with a clear, warmer lower temperature threshold compared to that of *Sf* or *Sn_n*. All varieties experienced reduced growth rates at the lowest tested salinity (28 psu) and optimal growth at highest salinity, with mixed responses to intermediate conditions (Figure 6.5). More variability in blade and float loss among varieties was noted in response to salinity than temperature.

To predict spatial and temporal dynamics of *Sargassum* blooms, understanding the temperature/salinity/nutrient tolerances and growth of different varieties under the full range of natural environmental conditions is essential. When *Sargassum* drifts into suboptimal waters, it may decline, fragment, and eventually sink. Hence, interannual variability in both magnitude of the GASB (Wang et al., 2019) and algal variety composition of coastal inundations (García-Sánchez et al., 2020; Alleyne et al., 2023) is driven by a confluence of factors related to *Sargassum* growth and decay. Proportional composition of the stock biomass in the origin region plus whether or not environmental characteristics there are ideal for the dominant variety at the start of its annual growth cycle underpin annual GASB development timing and magnitude. Physiological benefits of nutrient enrichment may be countered by low salinity effects if supplied by

riverine inputs versus offshore upwelling or wind-driven water column mixing. As illustration, *Sf* appears favored in recent years, but the original GASB was *Sn_w*-dominated (Schell et al., 2015).

Critically, experimental observations of *Sargassum* growth will vary depending upon specimen collection site and season, each with different ambient environmental conditions impacting the initial health of the algae (Schell et al., 2024). Moreover, each collection location represents a different point along a particular clump’s transport pathway; as *Sargassum* ages, its overall health declines and the areal proportion of senescence to active growth increases (Stoner & Greening, 1984). As older algae are unlikely to grow at the same rate as young, just as specimens collected from cooler waters may respond less to a cold treatment or more dramatically in a hot treatment, it is therefore important to document starting health and environmental conditions when conducting such *Sargassum* research and integrate these factors into data interpretations.

Environmental tolerance experimental results (Figure 6.5; Schell et al., 2023; Schell et al., 2024) may explain the unprecedented May 2023 GASB biomass decline (Barnes et al., 2023) that followed several months of equally unusual, persistently high (>29°C) sea surface temperatures in the tropical Atlantic. Such conditions were at and above temperatures where Hanisak & Samuel (1987), Corbin & Oxenford (2023), and Magana-Gallegos et al. (2023) also documented markedly reduced *Sargassum* growth rates.

6.3 Future Implications for the Sargasso Sea

Interannual variability in holopelagic *Sargassum* abundance

has always been part of the ecological story in the Sargasso Sea. In nearly 50 years of field observations, decadal cycles with intervals of lower and higher algal density are prominent (Figure 4.4) and not tied to the existence or behavior of the GASB because they pre-date the onset of this feature. Generally lower biomass since 2016 in the Sargasso Sea is on par with that seen during prior low intervals in the 1970s and late 1990s/early 2000s; while *Sargassum* concentrations in the North Sargasso Sea specifically have decreased in the recent period (Figure 6.3), it continues to be present in SEA's neuston tows and hourly visual survey data during all sampled seasons, albeit at lower levels and in fewer aggregated windrows than previously (Figures 5.4 and 5.5). South Sargasso Sea *Sargassum* biomass has increased in the last decade due to a combination of GASB-sourced contributions via the highly-dynamic Antilles Current zone and locally-seeded blooms. Both S_{n_n} and S_f are expected to remain the prevailing holopelagic varieties in the Sargasso Sea into the future; their relative proportions will vary from year to year. With its Sargasso Sea source region, local environmental conditions drive S_{n_n} seasonality, abundance, and resilience of the locally-seeded population. S_f quantity and timing of arrival to the Sargasso Sea are believed more strongly linked to conditions in the Gulf of Mexico, Florida Straits, and Gulf Stream. Episodic easing (and strengthening) of subtropical gyre boundary currents have allowed more (or less) *Sargassum* to drift out of the Sargasso Sea into the Antilles Current and Caribbean Sea, particularly via eddy activity near the Bahamas eddies.

Since the 2011 onset of the GASB and surge of S_{n_w} to the North Atlantic, the likelihood of this previously-rare variety becoming established in the Sargasso Sea has been a lingering question. To date, S_{n_w} was documented mostly in the tropical Atlantic and eastern Caribbean, with lower quantities directly downstream in the Antilles Current, western Caribbean, and Florida Straits (Figure 6.3). No field observations suggest that it thrives, or even survives, in the Sargasso Sea (Figures 6.2 and 6.3), nor that it has established a new source region or seed population outside the tropics. Thus far S_{n_w} blooms continue to occur in and are linked to the North Equatorial region as part of the GASB (Franks et al., 2016; Wang et al., 2019). Given S_{n_w} co-occurs with S_{n_n} and S_f in much of its geographic range, that it has not become established in the Sargasso Sea in over a decade is surprising but probably reflects future distribution as well. A suite of factors likely contribute - environmental conditions (temperature, salinity, nutrients), biomass growth

stage upon arrival to the region, seasonal timing, and potential competition between varieties - none of which have been examined *in situ*. Anecdotally, SEA researchers have noted decaying small fragments of S_{n_w} in the Florida Straits and Gulf Stream, not healthy clumps or sizable aggregations. S_{n_w} that reaches the North Sargasso Sea by this transport pathway encounters conditions presently too cold for its survival (Figure 6.5).

The ecological value of holopelagic *Sargassum* for species from zooplankton to seabirds is directly related to its overall quantity, aggregation state, and seasonal presence (Section 5.2). During extended intervals of lower total algal density, fewer windrows or mats exist and less forage or shelter space is available. S_{n_w} provides less robust habitat for motile epifauna, thus its distribution and abundance have implications throughout the region (Section 5.4; Martin et al., 2021). Epifaunal assemblages will likely continue to shift with changes in *Sargassum* variety balance and biomass, as they have over several decades (Table 5.2). *Sargassum* variety-level differences in nekton, larval eel, or megafauna associates have not been studied, and minimal research (Rooker et al., 2006; Turner & Rooker, 2006; Mazoudier et al., 2023) exists on consumption of motile epifauna by larger taxa to illustrate the potential trophic ripple effects of increasing S_{n_w} across the Caribbean Sea and/or into the Sargasso Sea.

Ongoing ocean warming across the full North Atlantic range of holopelagic *Sargassum* will, without a doubt, be physiologically influential for all varieties. At present, S_{n_n} , S_{n_w} , and S_f coexist in the tropical Atlantic and Caribbean Sea. Notably, few field studies track algal health status or growth stage and neither characteristic can be determined by remote sensing, so it is unknown if the three varieties are blooming concurrently or merely drifting together at different ages/conditions. If sea surface temperatures continue to increase, individual varieties are expected to drop out (senesce then sink upon entry to unfavorable environments) based on their respective temperature tolerances (Hanisak & Samuel, 1987; Corbin & Oxenford, 2023; Magana-Gallegos et al., 2023; Schell et al., 2024). Aging algae is less resilient to environmental changes, thus when during *Sargassum*'s suspected approximately 1-year lifespan challenging temperatures are encountered influences its physical and ecological responses (Gower & King, 2011; Stoner & Greening, 1984; Schell et al., 2024). Frequent and intense marine heatwave events in the Gulf of Mexico (Feng et al., 2023) directly impact *Sargassum* biomass and health in the Sargasso Sea, given its source region role for S_f . If the

Gulf becomes too warm for *Sargassum* to bloom and/or survive there, the quantity transported by the Gulf Stream to the North Sargasso Sea each year may decrease. Finally, it is possible that *Sn_w*'s present hypothesized cold temperature barrier to the Sargasso Sea will disappear in the future, with warmer conditions allowing it to infiltrate the subtropical gyre and impact the marine food web. The magnitude and timeline for warming climate effects on North Atlantic *Sargassum* growth, survival, and geographic range have not been investigated or modeled at basin or regional scale.

Current and future climate threats, coupled with the ongoing negative perception of *Sargassum* in the Caribbean Sea, Mexico, Florida, and other areas subject to annual GASB inundations, suggest that conserving this unique high seas ecosystem within the Sargasso Sea is essential. There is an urgent need to continue highlighting holopelagic *Sargassum*'s ecological value and role when most public messaging presently describes macroalgae as a nuisance with economic and public health consequences while industry/community action works to remove it from the marine environment by collection and forced sinking. Although North and South Sargasso Sea subregions do not always behave alike and may be subject to different ecological pressures and environmental changes, it is critical to conserve the Sargasso Sea as a whole. Nonetheless, ocean circulation links the South Sargasso more directly to the tropics and GASB while the North Sargasso is influenced by the Gulf of Mexico - regional connectivity demands this more nuanced consideration when anticipating future *Sargassum* ecosystem dynamics in the Sargasso Sea.

Beyond the above implications for *Sargassum* and associated fauna within the Sargasso Sea, two other datasets included in this report offer long-term records that inform their respective future trajectories. Floating tar is expected to remain at very low levels (Figure 3.5) within the subtropical gyre given existing international

maritime policies and the commercial shipping industry's dedication to pollution reduction. An oil spill within or upstream of the Sargasso Sea along any of the major oceanographic currents flowing into the region (Figure 6.1) would yield surface hydrocarbon slicks and tar balls with environmental and ecological consequences. Such events are extremely rare but not impossible; *Sargassum* as well as pelagic or migratory fauna exposed to oiling effects would experience severe negative impacts.

SEA's multidecadal microplastics data show inter-annual variability in sampled concentrations, increasing in recent decades (Figure 3.3). Advanced analyses leveraging the same observations found a significant positive trend that paralleled global plastics production (Wilcox et al., 2019), results reinforced by future predictions based on plastic waste emissions and modern management strategies (Borrelle et al., 2020; Tekman et al., 2022). As such, both large marine debris and microplastics will persist, at enhanced concentrations, in the Sargasso Sea from the ocean surface to the seafloor; nanoplastics (<0.1µm) are also ubiquitous, although outside the scope of SEA's current sampling methods due to net mesh size (ten Hietbrink et al., 2025). Plastics of all dimensions pose physical and chemical threats to marine organisms from plankton to whales, with impacts to individuals, populations, and ecosystems (Tekman et al., 2022). These adverse health effects will continue, likely amplified by greater quantities of plastics, while large floating objects hosting rafting species are a vector for dispersal of non-native taxa that risk the Sargasso Sea's unique biodiversity (Tekman et al., 2022). Although under discussion, no cohesive international policy yet exists to reduce influx of debris to the marine environment, reduce losses of fishing gear, or implement large-scale mitigation efforts (Borrelle et al., 2020). Found in all the world's oceans, from beaches and coastal zones to the remotest and deepest waters, plastic pollution is truly an increasingly complex transboundary problem.

CHAPTER 7

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CHAPTER 8

References

- Abé H, Komatsu T, Kokubu Y, Natheer A, Rothäusler E, Shishido H, Yoshizawa S, and Ajisaka T. 2013.** Invertebrate fauna associated with floating *Sargassum horneri* (Fucales: Sargassaceae) in the East China Sea. *Species Diversity* 18:75-85. doi: 10.12782/sd.18.1
- Alleyné K, Johnson D, Neat F, Oxenford H, and Vallès H. 2023.** Seasonal variation in morphotype composition of pelagic *Sargassum* influx events is linked to oceanic origin. *Scientific Reports* 13:3753. doi: 10.1038/s41598-023-30969-2
- Amaral-Zettler L, Dragone N, Schell J, Slikas B, Murphy L, Morrall C, and Zettler E. 2017.** Comparative mitochondrial and chloroplast genomics of a genetically distinct form of *Sargassum* contributing to recent "Golden Tides" in the western Atlantic. *Ecology and Evolution* 7:516-525. doi: 10.1002/ece3.2630
- Angel M, and Pugh P. 2000.** Quantification of diel vertical migration by micronektonic taxa in the northeast Atlantic. *Hydrobiologia* 440:161-179.
- Barnes B, Xie Y, and Hu C. 2023.** Outlook of 2023 *Sargassum* blooms in the Caribbean Sea and Gulf of Mexico: May 31, 2023. University of South Florida Optical Oceanography Lab. https://optics.marine.usf.edu/projects/SaWS/pdf/Sargassum_outlook_2023_bulletin5_USF.pdf
- Beardsley G. 1967.** Age, growth, and reproduction of the dolphin, *Coryphaena hippurus*, in the Straits of Florida. *Copeia* 1967:441-451. doi: 10.2307/1442132
- Berline L, Ody A, Jouanno J, Chevalier C, Andre J-M, Thibaut T, and Menard F. 2020.** Hindcasting the 2017 dispersal of *Sargassum* algae in the tropical North Atlantic. *Marine Pollution Bulletin* 158:111431. doi: 10.1016/j.marpolbul.2020.111431
- Bonhommeau S, Castonguay M, Rivot E, Sabatié R, and Le Pape O. 2010.** The duration of migration of Atlantic *Anguilla* larvae. *Fish and Fisheries* 11:289-306. doi: 10.1111/j.1467-2979.2010.00362.x
- Borrelle S, Ringma J, Law K, Monnahan C, Lebreton L, McGivern A, Murphy E, Jambeck J, Leonard G, Hilleary M, Eriksen M, Possingham H, De Frond H, Gerber L, Polidoro B, Tahir A, Bernard M, Mallos N, Barnes M, and Rochman C. 2020.** Predicted growth in plastic waste exceeds efforts to mitigate plastic pollution. *Science* 369:1515-1518. doi: 10.1126/science.aba3656
- Bortone S, Hastings P, and Collard S. 1977.** The pelagic *Sargassum* ichthyofauna of the eastern Gulf of Mexico. *Northeast Gulf Science* 1:60-67. doi: 10.18785/negs.0102.02
- Butler J, Morris B, Cadwallader J, and Stoner A. 1983.** Studies of *Sargassum* and the *Sargassum* community. Bermuda Biological Station, Special Publication No. 22. ISBN: 0917642228 9780917642227
- Butler J, and Stoner A. 1984.** Pelagic *Sargassum*: Has its biomass changed in the last 50 years? *Deep Sea Research* 31:1259-1264.
- Cacabelos E, Olabarria C, Incera M, and Troncoso J. 2010.** Effects of habitat structure and tidal height on epifauna assemblages associated with macroalgae. *Estuarine, Coastal and Shelf Science* 89:43-52. doi: 10.1016/j.ecss.2010.05.012
- Calder D. 1995.** Hydroid assemblages on holopelagic *Sargassum* from the Sargasso Sea at Bermuda. *Bulletin of Marine Science* 56:537-546. ISSN:0007-4977
- Carpenter E. 2022.** A very short informal history of marine plastic pollution. *Limnology and Oceanography Bulletin* 31:107-109. doi: 10.1002/lob.10518
- Carr A, and Meylan A. 1980.** Evidence of passive migration of green turtle hatchlings in *Sargassum*. *Copeia* 1980:366-368. doi: 10.2307/1444022
- Casazza T, and Ross S. 2008.** Fishes associated with pelagic *Sargassum* and open water lacking *Sargassum* in the Gulf Stream off North Carolina. *Fishery Bulletin* 106:348-363.
- Changeux T, Berline L, Podlejski W, Guillot T, Stiger-Pouvreau V, Connan S, and Thibaut T. 2023.** Variability in growth and tissue composition (CNP, natural isotopes) of the three morphotypes of holopelagic *Sargassum*. *Aquatic Botany* 187:103644. doi: 10.1016/j.aquabot.2023.103644
- Chemello R, and Milazzo M. 2002.** Effect of algal architecture on associated fauna: Some evidence from phytoplankton. *Marine Biology* 140:981-990. doi: 10.1007/s00227-002-0777-x
- Chong F, Spencer M, Maximenko N, Hafner J, McWhirter A, and Helm R. 2023.** High concentrations of floating neustonic life in the plastic-rich North Pacific Garbage Patch. *PLoS Biology* 21:e3001646. doi: 10.1371/journal.pbio.3001646
- Corbin M, and Oxenford H. 2023.** Assessing growth of pelagic *Sargassum* in the tropical Atlantic. *Aquatic Botany* 187:103654. doi: 10.1016/j.aquabot.2023.103654
- Coston-Clements L, Settle L, Hoss D, and Cross F. 1991.** Utilization of the *Sargassum* habitat by marine invertebrates and vertebrates: A review. NOAA Technical Memorandum NMFS-SEFSC-296.
- de Boer M, and Saulino J. 2020.** Marine megafauna (cetaceans, turtles, seabirds, and elasmobranchs) associate with pelagic *Sargassum* off Suriname. *Academic Journal of Suriname* 11:41-66. <https://adekus-journal.uvs.edu/index.php/acjournu/article/view/23>
- Dias J, and Lopes C. 2009.** Occurrence, distribution and abundance of *Halobates micans* Eschscholtz, 1822 (Heteroptera, Gerridae) along the southeastern Brazilian coast. *Brazilian Journal of Biology* 69:67-73. doi: 10.1590/S1519-69842009000100008
- DiBenedetto M, Donohue J, Tremblay K, Edson E, and Law K. 2023.** Microplastics segregation by rise velocity at the ocean surface. *Environmental Research Letters* 18:024036. doi: 10.1088/1748-9326/acb505

- Dibner S, Martin L, Thibaut T, Aurelle D, Blanfuné A, Whittaker K, Cooney L, Schell J, Goodwin D, and Siuda A. 2021.** Consistent genetic divergence observed among pelagic *Sargassum* morphotypes in the western North Atlantic. *Marine Ecology* 00:e12691. doi: 10.1111/maec.12691
- Djakoure S, Araujo M, Hounsou-Gbo A, Noriega C, and Bourles B. 2017.** On the potential causes of the recent pelagic *Sargassum* blooms events in the tropical North Atlantic Ocean. *Biogeosciences Discussions*. doi: 10.5194/bg-2017-346
- Dooley J. 1972.** Fishes associated with the pelagic *Sargassum* complex, with a discussion of the *Sargassum* community. *Contributions in Marine Science* 16:1-32.
- Egger M, Quiros L, Leone G, Ferrari F, Bergen C, and Tishler M. 2021.** Relative abundance of floating plastic debris and neuston in the eastern North Pacific Ocean. *Frontiers in Marine Science* 8:626026. doi: 10.3389/fmars.2021.626026
- Faller A, and Woodcock A. 1964.** The spacing of windrows of *Sargassum* in the ocean. *Journal of Marine Research* 22:22-29.
- Feng, Y-T, Bethel B, Tian Y, Dong C-H, Liang J, Yao Y-L, Yuan J, Chen Y, Chen S-J, and Yu Y. 2023.** Marine heatwaves in the Gulf of Mexico 1983-2021: Statistics, recent intensifications, and threats on coral reefs. *Advances in Climate Change Research* 14:560-572. doi: 10.1016/j.accre.2023.08/006
- Fine M. 1970.** Faunal variation on pelagic *Sargassum*. *Marine Biology* 7:112-122. doi: 10.1007/bf00354914
- Franks J, Johnson D, and Ko D. 2016.** Pelagic *Sargassum* in the tropical North Atlantic. *Gulf and Caribbean Research* 27:SC6-11. doi: 10.18785/gcr.2701.08
- Garcia-Sanchez M, Graham C, Vera E, Escalante-Mancera E, Alvarez-Filip L, and van Tussenbroek B. 2020.** Temporal changes in the composition and biomass of beached pelagic *Sargassum* species in the Mexican Caribbean. *Aquatic Botany* 167:103275. doi: 10.1016/j.aquabot.2020.103275
- Goldstein M, Rosenberg M, and Chang L. 2012.** Increased oceanic microplastic debris enhances oviposition in an endemic pelagic insect. *Biology Letters* 12:817-820. doi: 10.1098/rsbl.2012.0298
- Goodwin D, Siuda A, and Schell J. 2020.** 25-year record of *in situ* pelagic *Sargassum* observations in the western North Atlantic and Caribbean reveals a shift in distribution and range expansion of three common morphotypes. *Ocean Sciences Meeting, San Diego, CA*. <https://agu.confex.com/agu/osm20/meetingapp.cgi/Paper/651375>
- Goodwin D, Siuda A, and Schell J. 2022.** *In situ* observation of holopelagic *Sargassum* distribution and aggregation state across the entire North Atlantic from 2011 to 2020. *PeerJ* 10:e14079. doi: 10.7717/peerj.14079
- Govindarajan A, Cooney L, Whittaker K, Bloch D, Burdorf R, Canning S, Carter C, Cellan S, Eriksson F, Freyer H, Huston G, Hutchinson S, McKeegan K, Malpani M, Merkle-Raymond A, Ouellette K, Petersen-Rockney R, Schultz M, and Siuda A. 2019.** The distribution and mitochondrial genotype of the hydroid *Aglaophenia latecarinata* is correlated with its pelagic *Sargassum* substrate type in the tropical and subtropical western Atlantic Ocean. *PeerJ* 7:e7814. doi: 10.7717/peerj.7814
- Gower J, and King S. 2011.** Distribution of floating *Sargassum* in the Gulf of Mexico and North Atlantic mapped using MERIS. *International Journal of Remote Sensing* 32:1917-1929. doi: 10.1080/01431161003639660
- Guiry M, and Guiry G. 2025.** *AlgaeBase*. World-wide electronic publication, National University of Ireland, Galway. <https://www.algaebase.org>
- Gutow L, Beermann J, Buschbaum C, Rivadeneira M, and Thiel M. 2015.** Castaways can't be choosers - Homogenization of rafting assemblages on floating seaweeds. *Journal of Sea Research* 95:161-171. doi: 10.1016/j.seares.2014.07.005
- Haney J. 1986.** Seabird patchiness in tropical oceanic waters: The influence of *Sargassum* "reefs." *The Auk* 104:141-151. doi: 10.1093/auk/103.1.141
- Hanisak M, and Samuel M. 1987.** Growth rates in culture of several species of *Sargassum* from Florida, USA. *Hydrobiologia* 151:399-404. doi: 10.1007/BF00046159
- Helm R. 2021.** The mysterious ecosystem at the ocean's surface. *PLoS Biology* 19:e3001046. doi: 10.1371/journal.pbio.3001046
- Hemphill A. 2005.** Conservation on the High Seas - Drift algae habitat as an open ocean cornerstone. *Parks* 15:48-56.
- Hobday A. 2000.** Persistence and transport of fauna on drifting kelp (*Macrocystis pyrifera* (L.) C. Agardh) rafts in the Southern California Bight. *Journal of Experimental Marine Biology and Ecology* 253:75-96. doi: 10.1016/s0022-0981(00)00250-1
- Hu C, Murch B, Barnes B, Wang M, Maréchal J-P, Franks J, Johnson D, Lapointe B, Goodwin D, Schell J, and Siuda A. 2016.** *Sargassum* Watch warns of incoming seaweed. *Eos* 97. doi: 10.1029/2016EO058355
- Huffard C, von Thun S, Sherman A, Sealey K, and Smith K. 2014.** Pelagic *Sargassum* community change over a 40-year period: Temporal and spatial variability. *Marine Biology* 161:2735-2751. doi: 10.1007/s00227-014-2539-y
- Johns E, Lumpkin R, Putman N, Smith R, Muller-Karger F, Rueda-Roa D, Hu C, Wang M, Brooks M, Grammar L, and Werner F. 2020.** The establishment of a pelagic *Sargassum* population in the tropical Atlantic: Biological consequences of a basin-scale long distance dispersal event. *Progress in Oceanography* 182:102269. doi: 10.1016/j.poccean.2020.102269
- Jouanno J, Berthet S, Muller-Karger F, Aumont O, and Sheinbaum J. 2025.** An extreme North Atlantic Oscillation event drove the pelagic *Sargassum* tipping point. *Communications Earth & Environment* 6:95. doi: 10.1038/s43247-025-02074-x
- Joyce P. 1998.** Floating tar in the western North Atlantic and Caribbean Sea, 1982-1996. *Marine Pollution Bulletin* 36:167-171. doi: 10.1016/S0025-326X(97)87422-X
- Kergosien N, Helias M, Le Grand F, Cérantola S, Simon G, Nirma C, Thibaut T, Berline L, Changeux T, Blanfuné A, Connan S, and Stiger-Pouvreau V. 2024.** Morpho- and chemotyping of holopelagic *Sargassum* species causing massive strandings in the Caribbean Region. *Phycology* 4:340-362. doi: 10.3390/phycology4030018
- Klecka J, and Boukal D. 2014.** The effect

of habitat structure on prey mortality depends on predator and prey microhabitat use. *Oecologia* 176:183-191. doi: 10.1007/s00442-014-3007-6

Kracht R, and Tesch F. 1981. Progress report on the eel expedition of R.V. 'Anton Dohrn' and R.V. 'Friedrich Heincke' to the Sargasso Sea 1979. *Environmental Biology of Fishes* 6:371-375. doi: 10.1007/BF00005768

Kukulka T, Proskurowski G, Moret-Ferguson S, Meyer D, and Law K. 2012. The effect of wind mixing on the vertical distribution of buoyant plastic debris. *Geophysical Research Letters* 39:GL051116. doi: 10.1029/2012GL051116

Laffoley D, Roe H, Angel M, Ardron J, Bates N, Boyd I, Brooke S, Buck K, Carlson C, Causey B, Conte M, Christiansen S, Cleary J, Donnelly J, Earle S, Edwards R, Gjerde K, Giovannoni S, Gulick S, Gollock M, Hallett J, Halpin P, Hanel R, Hemphill A, Johnson R, Knap A, Lomas M, McKenna S, Miller M, Miller P, Ming F, Moffitt R, Nelson N, Parson L, Peters A, Pitt J, Rouja P, Roberts J, Roberts J, Seigel D, Siuda A, Steinberg D, Stevenson A, Sumaila V, Swartz W, Thorrold S, Trott T, and Vats V. 2011. The protection and management of the Sargasso Sea: The golden floating rainforest of the Atlantic Ocean. Sargasso Sea Alliance Report. http://www.sargassoseacommission.org/storage/documents/Sargasso_Report.9.12.pdf

Langmuir I. 1938. Surface motion of water induced by wind. *Science* 87:119-123.

Law K, Moret-Ferguson S, Maximenko N, Proskurowski G, Peacock E, Hafner J, and Reddy C. 2010. Plastic accumulation in the North Atlantic Subtropical Gyre. *Science* 329:1185-1188. doi: 10.1126/science.1192321

Law K, Donohue J, and Miller R. 2024. Plastic marine pollution in the Gulf of Maine. *Maine Policy Review* 32:175-183. doi: 10.53558/AKIM4009

Leibovich S. 1983. The form and dynamics of Langmuir circulations. *Annual Reviews in Fluid Mechanics* 15:391-427.

Leite F, Tanaka M, and Gebara R. 2007. Structural variation in the brown alga *Sargassum cymosum* and its effects

on associated amphipod assemblages. *Brazilian Journal of Biology* 67:215-221. doi: 10.1590/s1519-69842007000200006

Magana-Gallegos E, Villegas-Munoz E, Salas-Acosta E, Barba-Santos M, Silva R, and van Tussenbroek B. 2023. The effect of temperature on the growth of holopelagic *Sargassum* species. *Phycology* 3:138-146. doi: 10.3390/phycolgy3010009

Mahadik G, Agusti S, and Duarte C. 2019. Distribution and characteristics of *Halobates germanus* population in the Red Sea. *Frontiers in Marine Science* 6:408. doi: 10.3389/fmars.2019.00408

Marechal J-P, Hellio C, and Hu C. 2017. A simple, fast, and reliable method to predict *Sargassum* washing ashore in the Lesser Antilles. *Remote Sensing Applications: Society and Environment* 5:54-63. doi: 10.1016/j.rsase.2017.01.001

Marmorino G, Miller W, Smith G, and Bowles J. 2011. Airborne imagery of a disintegrating *Sargassum* drift line. *Deep-Sea Research I* 58:316-321. doi: 10.1016/j.dsr.2011.01.001

Martin L, Taylor M, Huston G, Goodwin D, Schell J, and Siuda A. 2021. Pelagic *Sargassum* morphotypes support different rafting motile epifauna communities. *Marine Biology* 168:115. doi: 10.1007/s00227-021-03910-2

Mazoudier S, Kingsford M, Strickland J, and Pitt K. 2023. Stable isotopes reveal *Sargassum* rafts provide a trophic subsidy to juvenile pelagic fishes. *Estuarine, Coastal and Shelf Science* 295:108548. doi: 10.1016/j.ecss.2023.108548

McGillicuddy D, Morton P, Brewton R, Hu C, Kelly T, Solow A, and Lapointe B. 2023. Nutrient and arsenic biogeochemistry of *Sargassum* in the western Atlantic. *Nature Communications* 14:6205. doi: 10.1038/s41467-023-41904-4

Miller M. 2002. The distribution and ecology of *Ariosoma balearicum* (Congridae) leptocephali in the western North Atlantic. *Environmental Biology of Fishes* 63:235-252. doi: 10.1023/A:1014311429809

Miller M, and McCleave J. 2007. Species assemblages of leptocephali in the southwestern Sargasso Sea. *Marine Ecology Progress Series* 344:197-212. doi: 10.3354/meps06923

Monroy-Velázquez L, Rodríguez-Martínez R, van Tussenbroek B, Aguiar T, Solís-Weiss V, and Briones-Fourzán P. 2019. Motile macrofauna associated with pelagic *Sargassum* in a Mexican reef lagoon. *Journal of Environmental Management* 252:109650. doi: 10.1016/j.jenvman.2019.109650

Moret-Ferguson S, Law K, Proskurowski G, Murphy E, Peacock E, and Reddy C. 2010. The size, mass, and composition of plastic debris in the western North Atlantic Ocean. *Marine Pollution Bulletin* 60:1873-1878. doi: 10.1016/j.marpolbul.2010.07.020

Morris B, and Mogelberg D. 1973. Identification manual to the pelagic *Sargassum* fauna. Bermuda Biological Station, Special Publication No. 11.

Moser M, Auster P, and Bichy J. 1998. Effects of mat morphology on large *Sargassum*-associated fishes: Observations from a remotely operated vehicle (ROV) and free-floating video camcorders. *Environmental Biology of Fishes* 51:391-398.

Moser M, and Lee D. 2012. Foraging over *Sargassum* by western North Atlantic seabirds. *Wilson Journal of Ornithology* 124:66-72. doi: 10.1676/11-0671

National Marine Fisheries Service (NMFS). 2003. Fisheries of the Caribbean, Gulf of Mexico and South Atlantic: Pelagic *Sargassum* habitat of the South Atlantic region (Final rule). *Federal Register* 68:57375.

Ody A, Thibaut T, Berline L, Changeaux T, André J-M, Chevalier C, Blanfuné A, Blanchot J, Ruitton S, Stiger-Pouvreau V, Connan S, Crelet J, Aurelle D, Guéné M, Bataille H, Bachelier C, Guillemain D, Schmidt N, Fauvelle V, Guasco S, and Ménard F. 2019. From *in situ* to satellite observations of pelagic *Sargassum* distribution and aggregation in the tropical North Atlantic Ocean. *PLoS One* 14:e0222584. doi: 10.1371/journal.pone.0222584

Parr A. 1939. Quantitative observations on the pelagic *Sargassum* vegetation of the western North Atlantic with preliminary discussion of morphology and relationships. *Bulletin of the Bingham Oceanographic Collection* 6:7.

Peters A, and Siuda A. 2015. A review of observations of floating tar in the Sargasso

Sea. *Oceanography* 27:217–221. doi: 10.5670/oceanog.2014.25

Putman N, Goni G, Gramer L, Hu C, Johns E, Trinanes J, and Wang M. 2018. Simulating transport pathways of pelagic *Sargassum* from the Equatorial Atlantic to the Caribbean Sea. *Progress in Oceanography* 165:205–214. doi: 10.1016/j.pocean.2018.06.009

Rooker J, Turner J, and Holt S. 2006. Trophic ecology of *Sargassum*-associated fishes in the Gulf of Mexico determined from stable isotopes and fatty acids. *Marine Ecology Progress Series* 313:249–259. doi: 10.3354/meps313249

Schell J, Goodwin D, and Siuda A. 2015. Recent *Sargassum* inundation events in the Caribbean: Shipboard observations reveal dominance of a previously rare form. *Oceanography* 28:8–10. doi: 10.5670/oceanog.2015.70

Schell J, Goodwin D, Volk R, and Siuda A. 2023. Preliminary explorations of environmental tolerances and growth rates of holopelagic *Sargassum* morphotypes. *Aquatic Botany* 190:103723. doi: 10.1016/j.aquabot.2023.103723

Schell J, Siuda A, Goodwin D, and Martin L. 2024. Holopelagic *Sargassum* morphotype growth and decay responses to temperature and salinity during a multi-week *ex situ* experiment. *Ocean Sciences Meeting*, New Orleans, LA.

Scofield A, and Siuda A. 2013. Biogeography of eel larvae in surface and sub-surface waters of the Sargasso Sea. 26th International Congress for Conservation Biology, Baltimore, MD.

Siuda A. 2011. Long-term Sea Education Association Sargasso Sea surface net data. Sargasso Sea Alliance Science Report Series, No. 10. http://www.sargassosea-commission.org/storage/documents/No10_Surface.Net_HI.pdf

Siuda A, Blanfuné A, Dibner S, Verlaque M, Boudouresque C-F, Connan S, Goodwin D, Stiger-Pouvreau V, Viard F, Rousseau F, Michotey V, Schell J, Changeaux T, Aurelle D, and Thibaut T. 2024. Morphological and molecular characters differentiate common morphotypes of Atlantic holopelagic *Sargassum*. *Phycology* 4:256–275. doi: 10.3390/phycolgy4020014

Stelling-Wood T, Gribben P, and Poore A. 2020. Habitat variability in an underwater forest: Using a trait-based approach to predict associated communities. *Functional Ecology* 34:888–898. doi: 10.1111/1365-2435.13523

Stoner A. 1983. Pelagic *Sargassum*: Evidence for a major decrease in biomass. *Deep Sea Research* 30:469–474.

Stoner A, and Greening H. 1984. Geographic variation in the macrofaunal associates of pelagic *Sargassum* and some biogeographic implications. *Marine Ecology Progress Series* 20:185–192. doi: 10.3354/meps020185

Taylor W. 1960. Marine algae of the eastern Tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor. ISBN:0472088416

Tekman M, Walther B, Peter C, Gutow L, and Bergmann M. 2022. Impacts of plastic pollution in the oceans on marine species, biodiversity and ecosystems. WWF Germany, Berlin. doi: 10.5281/zenodo.5898684

ten Hietbrink, S, Materic D, Holzinger R, Groeskamp S, and Niemann H. 2025. Nanoplastic concentrations across the North Atlantic. *Nature* 643:412–415. doi: 10.1038/s41586-025-09218-1

Torres-Conde E, van Tussenbroek B, Rodríguez-Martínez R, and Martínez-Daranas B. 2023. Temporal changes in the composition of beached holopelagic *Sargassum* spp. along the northwestern coast of Cuba. *Phycology* 3:405–412. doi: 10.3390/phycolgy3040027

Trinanes J, Putman N, Goni G, Hu C, and Wang M. 2021. Monitoring pelagic *Sargassum* inundation potential for coastal communities. *Journal of Operational Oceanography* 16:48–59. doi: 10.1080/1755876X.2021.1902682

Turner J, and Rooker J. 2006. Fatty acid composition of flora and fauna associated with *Sargassum* mats in the Gulf of Mexico. *Marine Biology* 149:1025–1036. doi: 10.1007/s00227-006-0269-5

Ullman D, Cornillon P, and Shan Z. 2007. On the characteristics of subtropical fronts in the North Atlantic. *Journal of Geophysical Research* 112:C01010. doi: 10.1029/2006JC003601

Vandendriessche S, Vincx M, and Degraer S. 2007. Floating seaweed and the influences of temperature, grazing and clump size on raft longevity - A microcosm study. *Journal of Experimental Marine Biology and Ecology* 343:64–73. doi: 10.1016/j.jembe.2006.11.010

Wang M, and Hu C. 2016. Mapping and quantifying *Sargassum* distribution and coverage in the central west Atlantic using MODIS observations. *Remote Sensing of the Environment* 183:350–367. doi: 10.1016/j.rse.2016.04.019

Wang M, and Hu C. 2017. Predicting *Sargassum* blooms in the Caribbean Sea from MODIS observations. *Geophysical Research Letters* 44:3265–3273. doi: 10.1002/2017GL072932

Wang M, and Hu C. 2021. Satellite remote sensing of pelagic *Sargassum* macroalgae: The power of high resolution and deep learning. *Remote Sensing of the Environment* 264:112631. doi: 10.1016/j.rse.2021.112631

Wang M, Hu C, Barnes B, Mitchum G, Lapointe B, and Montoya J. 2019. The great Atlantic *Sargassum* belt. *Science* 365:83–87. doi: 10.1126/science.aaw7912

Ware C, Dijkstra J, Mello K, Stevens A, O'Brien B, and Ikedo W. 2019. A novel three-dimensional analysis of functional architecture that describes the properties of macroalgae as a refuge. *Marine Ecology Progress Series* 608:93–103. doi: 10.3354/meps12800

Wells D, and Rooker J. 2004. Spatial and temporal patterns of habitat use by fishes associated with *Sargassum* mats in the northwestern Gulf of Mexico. *Bulletin of Marine Science* 74:81–99.

Wernberg T, Thomsen M, Staehr P, and Pedersen M. 2004. Epibiota communities of the introduced and indigenous macroalgal relatives *Sargassum muticum* and *Halidrys siliquosa* in Limfjorden (Denmark). *Helgoland Marine Research* 58:154–161. doi: 10.1007/s10152-004-0180-8

Wilbur J. 1987. Plastic in the North Atlantic. *Oceanus* 30:61–68.

Wilcox C, Hardest B, and Law K. 2019. Abundance of floating plastic particles is increasing in the western North Atlantic Ocean. *Environmental Science and Technology* 54:790–796. doi: 10.1021/acs.est.9b04812

Winge O. 1923. The Sargasso Sea, its boundaries and vegetation. Report on the Danish oceanographical expeditions (1908-1910). 3:1-34.

Witherington B, Hiram S, and Hardy R. 2012. Young sea turtles of the pelagic *Sargassum*-dominated drift community:

Habitat use, population density, and threats. Marine Ecology Progress Series 463:1-22. doi: 10.3354/meps09970

Woodcock A. 1950. Subsurface pelagic *Sargassum*. Journal of Marine Research 9:77-92.

Woodcock A. 1993. Winds subsurface pelagic *Sargassum* and Langmuir circulation. Journal of Experimental Marine Biology and Ecology 170:117-125. doi: 10.1016/0022-0981(93)90132-8



Floating microplastics and holopelagic *Sargassum*
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