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A little bit of *Sargassum* goes a long way: seafloor observations of *Sargassum fluitans* and *Sargassum natans* in the Western Atlantic Ocean

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The North Atlantic Ocean features high seasonal productivity of the brown seaweed Sargassum, which floats on the ocean surface and accumulates in large numbers in the Sargasso Sea. Sargassum blooms can stretch from the west coast of Africa to the Gulf of Mexico, and have created the largest seaweed blooms ever observed. Sargassum blooms have increased in intensity in recent years, and can negatively impact coastal communities when they wash up onshore in large quantities and decay. While seaweed sinking from surface waters to the seafloor may be an important carbon sink by removing carbon from the atmosphere, the magnitude of carbon sequestration by Sargassum and other macroalgae remains poorly understood. Given the magnitude of Sargassum blooms in the North Atlantic, they may pose a significant mechanism for carbon sequestration in the deep sea, though direct observations are rare. In this study, we documented the presence and distribution of Sargassum seaweed on the seafloor using video from ten remotely operated vehicle dives conducted on NOAA Ship Okeanos Explorer. Locations included sites in the Gulf of Mexico, in the Caribbean Sea, and off the Southeastern United States. Sargassum was observed in numbers ranging from 0 to over 112 per dive, and a frequency of between 0-11.23 observations for every 100 meters of horizontal distance. These observations suggest that Sargassum does make its way to the deep sea in potentially significant amounts. Natural systems like Sargassum sinking could serve as natural laboratories for understanding and managing seaweed burial as a climate mitigation strategy. Long-term monitoring of the fate of sunken Sargassum on the seabed is needed in order to determine how much is ultimately sequestered rather than recycled back into the system. Such observations would inform the feasibility of Sargassum farming and/or facilitated sinking as potential carbon dioxide removal strategies.

KEYWORDS

Sargassum, macroalgae, ocean exploration, carbon sequestration, algae blooms, Okeanos Explorer, deep seafloor

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1 Introduction

Macroalgae (commonly referred to as seaweed) provide many important ecological, environmental, and economic services. Seaweed is important food and habitat to a range of animals, including commercially-important fisheries species. Seaweed has market value for direct human consumption, and compounds derived from seaweed are commonly used in a range of commercial products like cosmetics, supplements, and fertilizers (Sugumaran et al., 2022). Through photosynthesis, algae fix carbon dioxide and can ultimately sequester organic carbon in coastal sediments and in the deep ocean for hundreds to thousands of years (Raven, 2017). Protection and restoration of macroalgae habitats can help preserve these blue carbon ecosystems. Seaweed cultivation and sinking is being proposed as a possible strategy to reduce atmospheric carbon dioxide (Duarte et al., 2017; National Academies of Sciences, Engineering, and Medicine, 2022). Seaweeds are also being studied for potential use as a biofuel (Godvin et al., 2021). However, when they occur in excess, seaweeds can outcompete, smother, or block sunlight from reaching other photosynthetic organisms and can wash ashore, accumulating in noxious heaps (Rodríguez-Martínez et al., 2019).

Sargassum is a genus of brown seaweed that is widespread in temperate, subtropical, and tropical waters. Sargassum morphology includes a holdfast, a cylindrical main axis, small leaflike blades, and gas-filled bladders, or pneumatocysts (Graham et al., 2009). A flexible body helps it withstand strong currents. There are two species of Sargassum that occur in the Atlantic Ocean off the coast of the United States and in the Gulf of Mexico: Sargassum fluitans and Sargassum natans. These forms are unique in that they are freefloating and do not have a holdfast or attach to a substrate at any stage in their life cycle. They are the only species of Sargassum that are holopelagic, meaning that they remain pelagic drifters throughout their entire life cycle, and free-floating Sargassum is only found in the Atlantic Ocean (Doyle and Franks, 2015; Stiger-Pouvreau et al., 2023). These pelagic species of Sargassum can double in size every 9-13 days (Hanisak and Samuel, 1987).

The two free-floating *Sargassum* species can occur in extensive, highly productive rafts on the ocean's surface that harbor distinctive communities of organisms adapted to the buoyant *Sargassum* habitat, including juvenile fish species such as amberjack and triggerfish (Wells and Rooker, 2004). *Sargassum natans* and *Sargassum fluitans* only reproduce asexually through fragmentation, a type of vegetative asexual reproduction where an individual *Sargassum* breaks into two or more parts, each of which continues to live and grow (Lee, 2008). *Sargassum's* fast growth rate contributes to its rapid spread. Hereafter in this paper both *Sargassum fluitans* and *Sargassum natans* will be referred to as "*Sargassum*".

1.1 Sargassum blooms

The North Atlantic Gyre is a circular system of ocean currents in the Atlantic Ocean that, through the rotating pattern of currents and effects of wind and weather, amasses *Sargassum* in an area known as the Sargasso Sea. The Sargasso Sea is the only sea bounded by currents rather than by land (NOAA, 2019). The Gulf Stream acts as a conduit that transports *Sargassum* through the Caribbean, into the Gulf of Mexico, and off the coast of the southeastern United States, and evidence suggests that much of the *Sargassum* transported through the Gulf of Mexico originates from the North Equatorial Recirculation Region, a complex system of currents around western Africa and South America, in addition to the Sargasso Sea (Franks et al., 2016).

Since 2011, giant floating Sargassum mats in the Atlantic have increased in density and range to form an 8,850 kilometer-long belt, called the Great Atlantic Sargassum Belt, that can extend from West Africa to the Gulf of Mexico (Wang et al., 2019). High quantities of Sargassum have washed up on beaches and inundated coastlines in the Southeast U.S., Gulf of Mexico, and the Caribbean in recent years, presenting a logistical challenge for coastal communities to manage the tons of seaweed piling up on their shores (Lamb, 2018; Conley and Oliver, 2019). Satellite measurements suggest that Sargassum blooms start to develop in the Central Western Atlantic in February-March and are transported by winds and currents to the Caribbean as massive blooms from May-August (Wang and Hu, 2017). A changing climate may have unexpected impacts on Sargassum productivity and sinking as well as its tendency to be transported, aggregated, and scattered due to climate influences on algal productivity, weather patterns, and ocean currents (Sanchez-Rubio et al., 2018).

There have been recent efforts to quantify the amount of *Sargassum* on the sea surface through methods such as satellite imagery analysis (Wang and Hu, 2016), numerical models (Schamberger et al., 2022), and field measurements (Ody et al., 2019). A 2019 study that analyzed satellite remote sensing data from 2000 to 2018 found a significant increase in estimated *Sargassum* biomass in the Great Atlantic *Sargassum* Belt beginning in 2011, with the highest biomass estimated at more than 20 million metric tons in June 2018, the last year of the study (Wang et al., 2019). Given the economic impacts of these *Sargassum* blooms, new monitoring systems (Duffy et al., 2019; Valentini and Balouin, 2020) have been developed to better plan for and respond to *Sargassum* accumulation on coasts.

1.2 Sargassum ecology

Sargassum is abundant in the Atlantic Ocean and forms an essential surface habitat that supports a diversity of marine organisms, including fish, invertebrates, sea turtles, marine birds, and marine mammals. Floating *Sargassum* mats serve as a primary nursery area for many fish species, some of which are commercially important (dolphinfishes, jacks, and amberjacks), and they provide a source of energy in an otherwise nutrient-poor area of the Atlantic (Casazza and Ross, 2010). These *Sargassum* mats provide essential habitat for approximately 120 species of fish and more than 120 species of invertebrates (Doyle and Franks, 2015).

Carbon sequestration is the process of storing carbon dioxide and other forms of carbon out of the atmosphere for long periods of time. It has been suggested that marine primary producers such as

phytoplankton, macroalgae, mangroves, and seagrasses are more efficient at sequestering carbon than their terrestrial counterparts due to their high productivity and efficiency in trapping sediments and associated organic carbon (Mcleod et al., 2011; Arenas and Vaz-Pinto, 2015). Through photosynthesis, Sargassum converts sunlight, carbon dioxide, and ocean nutrients into sugars and other carbon compounds. This organic material, and the carbon it contains, can then end on a number of different pathways, such as washing up on beaches, being eaten by herbivores, or sinking to the bottom of the ocean. Once it ends up in deep ocean currents or seafloor sediments hundreds of meters below the surface, the carbon is prevented from being exchanged with the atmosphere over several hundred to several thousand years (Volk and Hoffert, 2013). Traditionally, seagrasses and mangroves have been considered the dominant form of oceanic carbon sequestration (Duarte and Cebrián, 1996); however, in recent years researchers have been looking at seaweeds like Sargassum's role as important carbon sinks (N'Yeurt et al., 2012; Raven, 2017; Kokubu et al., 2019).

The gravitational sinking of Sargassum from the surface to the seafloor, and degradation of Sargassum within the water column and at the seafloor, are poorly understood processes. The mechanisms that deliver drifting seaweed to marine sediments include wind-induced Langmuir circulation that can transport floating seaweed fragments to a depth where pressure collapses its air bladders, rendering the seaweed negatively buoyant and removing it from the surface (Krause-Jensen and Duarte, 2016). Additionally, Sargassum living in the shaded understory of floating Sargassum may be prevented from photosynthesizing and lose buoyancy and die and start to degrade. It will also lose buoyancy with age and from encrustation of epizoans (Stoner, 1983). Once it achieves negative buoyancy, the Sargassum sinks at an estimated rate of 3.5 cm per second (Johnson and Richardson, 1977). At this rate, Sargassum would reach the seafloor at 1000 meters in just 8 hours. This is relatively fast for sinking particles and does not allow much time for remineralization, consumption, or degradation (Giering et al., 2020; Omand et al., 2020).

Sargassum sinking has been studied before using Autonomous Underwater Vehicle (AUV)-collected seafloor photographs in the southern part of the North Atlantic ocean (three stations between ~10-12° N and ~36-50° W), within the North Atlantic Subtropical Gyre where the Sargasso Sea is located. The biomass density of Sargassum deposited on the seafloor was estimated at 0.07 to 3.75 g/ m², which is greater than the surface biomass as estimated through literature review at 0.024-0.84 g/m² (Baker et al., 2017). Krause-Jensen and Duarte (2016) estimated that 11 percent of macroalgal particulate organic carbon (POC) export, or 35 TgC/yr, reaches the deep sea globally, serving as an important carbon sink. Start-up companies and financial investors have noted the potential for macroalgae aquaculture for commercial products like bioplastics and food or to sink and bury on the deep seafloor to sequester carbon from the atmosphere (López Miranda et al., 2021; Oxenford et al., 2021). Sargassum in particular has been identified as a target species for such efforts because of its naturally high abundance and reproductive rate.

The factors that contribute to organic carbon export in the open ocean and its subsequent carbon sequestration are driven by a complex combination of ecological, biogeochemical, and physical oceanographic processes. Developing a predictive understanding of carbon export pathways for seaweeds including *Sargassum* is critical for understanding present and future rates of ocean carbon sequestration and informing the emerging marine carbon dioxide removal industry. This study provides an initial characterization of *Sargassum* on the seafloor by describing the number of *Sargassum* observed, its relationship to benthic composition, any interactions with benthic organisms, and geological features of the dive sites explored. We revisited a series of archived deep ocean exploration visual surveys that took place on seabed areas underlying known and likely *Sargassum* surface blooms as one step toward understanding the fate of sinking *Sargassum* in the marine system.

2 Methods

2.1 NOAA Ship Okeanos Explorer

The National Oceanic and Atmospheric Administration (NOAA)'s Office of Ocean Exploration and Research is a U.S. federal program dedicated to exploring the unknown ocean for public benefit, filling in knowledge gaps about the marine environment through scientific discovery, technological advancements, and access to data. It conducts interdisciplinary ocean exploration expeditions on NOAA Ship Okeanos Explorer and other research vessels. Okeanos Explorer is a 68-meter research ship outfitted with an array of mapping sonars and a dual body Remotely Operated Vehicle (ROV) system: ROV Deep Discoverer (D2) and ROV Seirios. A unique and advantageous aspect of Okeanos Explorer operations is its ability to facilitate real-time communication and collaboration with shore-based scientists (Peters et al., 2019). Scientists on the ship and on land collaborate through a live video feed, text chatroom, shared conference phone line, and video annotation system, allowing participants not only to follow along live but to provide feedback and scientific expertise in real-time during the ROV dives (Kennedy et al., 2016; Selig et al., 2019).

2.2 Deep Discoverer and Seirios ROVs

Kennedy et al. (2019) describe the technical details on the Okeanos Explorer's seafloor mapping and ROV systems and operations. All ROV dives examined in this study were conducted with NOAA's dual body ROV system Deep Discover (D2) and Seirios, although only video from D2 was reviewed. The main capability of D2 is the ability to capture high-definition video, with its primary camera able to zoom in and provide close-up video of relatively small organisms (Kennedy et al., 2019). Seirios is directly tethered to the Okeanos Explorer via a fiber-optic cable and is also tethered to D2, a configuration that allows Seirios to absorb the sway of the ship while keeping D2 stable. The cable

provides the ROVs with power and allows for data transfer between the ROVs and the ship. Both *Seirios* and *D2* are equipped with a suite of sensors to measure environmental parameters like temperature, dissolved oxygen, salinity, and depth. Surveys conducted with this two-body system are exploratory in nature, providing baseline information on the broader biological, geological, and physical context of poorly explored regions of the ocean (Selig et al., 2019; Cantwell et al., 2020). Because the ROV time is maximized for a variety of objectives, true quantitative analyses of the imagery are not always possible, yet important insights may still be gleaned.

2.3 ASPIRE campaign

From 2018-2022, *Okeanos Explorer* conducted a series of expeditions as part of the Atlantic Seafloor Partnership for Integrated Research and Exploration (ASPIRE), a multi-national collaborative ocean exploration campaign to raise the collective knowledge and understanding of the North Atlantic Ocean. Three of the four expeditions reviewed – Océano Profundo 2018: Exploring Deep-sea Habitats off Puerto Rico and the U.S. Virgin Islands (EX1811), Windows to the Deep 2019: Southeast and Mid-Atlantic U.S Continental Margin, Port Canaveral, FL to Norfolk, VA (EX1903L2), and 2019 Southeastern U.S. Deep-sea Exploration (EX1907) – were part of this ASPIRE campaign.

2.4 Site selection

A subset of expeditions and ROV dive sites were selected for this study based on the following considerations:

- Expedition took place in region with known seasonal occurrences of *Sargassum* (Wang and Hu, 2017).
- "Sargassum" or "seaweed" was noted in SeaTube annotations at some point during the dive.
- High algal density on the sea surface was observed through the University of South Florida's Satellite-based *Sargassum* Watch System (SaWS) (Trinanes et al., 2023) - this informed selection of EX1811 Dives 7 and 8 and EX1907 Dives 11 and 12.
- Dives were selected to represent different types of bathymetric and ecological features (for instance a canyon versus coral mounds) and depths to sample a variety of site characterizations.

Details on bathymetric and ecological features are available in Supplementary Information Table 1.

2.5 ROV video footage review, *Sargassum* annotation, and site characterization

Okeanos Explorer ROV video footage is streamed live through SeaTube V3, a platform developed by Ocean Networks Canada (ONC) for scientists to view and annotate ROV footage both in real time and afterwards (Selig et al., 2019). SeaTube V3 provides open access and archives of dive videos, dive imagery, dive logs, navigational data, and metadata for deep ocean exploration (Jenkyns et al., 2013). An informal science chatroom developed by the Global Foundation for Ocean Exploration is also used for sidebar conversations between scientists and captures some of the annotations as well; the messages of the chat are then archived for future access^{1,2}.

Annotations of *Sargassum* were done manually, by reviewing the selected footage from the *Deep Discoverer* ROV. Each of the dives selected for review was viewed in SeaTube V3 from the start of the ROV's descent from the surface to the end of its ascent back to the surface to account for the possibility of *Sargassum* being observed in the water column. An object was identified as *Sargassum* based on its shape, color, texture, and movement. Figure 1 shows screen grabs of the ROV video to show the variability of what the *Sargassum* looks like when it reaches the seafloor.

When there was an object that was potentially *Sargassum* but identification was questionable, higher-resolution footage of that part of the dive was accessed and viewed in NOAA's Ocean Exploration Video Portal³. If after reviewing the high-resolution footage the object could not with absolute certainty be identified as *Sargassum*, the annotation included the note "likely *Sargassum*" to indicate a degree of uncertainty. Annotations with "likely *Sargassum*" designation were counted as *Sargassum* in this report. All other observations were identified to the *Sargassum* genus referencing the World Register of Marine Species (WoRMS) system of classification and annotated in SeaTube V3.

For dives with abundant Sargassum, a new Sargassum annotation was made for every new frame of view that contained Sargassum. For instance, even if there were five clumps of Sargassum in the frame, this was counted as one Sargassum annotation. As soon as the ROV had Sargassum in its frame of view that was not clearly visible in the previous annotation, this was entered as a new annotation. Each Sargassum annotation was classified as "low," "medium," or "high" biomass based on visual estimation of the approximate amount of Sargassum within the frame of view on a scale from 1-8 (Supplementary Information Table 2). Additionally, when mobile animals were observed on or in the near vicinity of the Sargassum detritus, this was noted, as well as whether the animal appeared to be grazing on the Sargassum. Bathymetric features (rocks, sediment, etc.) and other observations (high marine snow, presence of anthropogenic debris) were also noted in Supplementary Information Table 2.

In addition to reviewing the ROV footage and accompanying audio commentary, the archived chatroom logs that include expert perspectives, and post-dive summaries, accessed through NOAA's

¹ https://exdata.tgfoe.org/OkeanosCruises/.

² https://oceanexplorer.noaa.gov/okeanos/collaboration-tools/imeventlog/participating-eventlog.html.

³ https://www.nodc.noaa.gov/oer/video/.



Institutional Repository⁴, were reviewed to help characterize each dive site.

Distance transited along the seafloor was calculated by importing spatial coordinates from the ROV recorded while at depth and plotting them in ESRI's ArcGIS Pro 2.9 software. A line was then generalized based on the points and the length in meters was calculated for each dive. Distance transited varied from approximately 250 meters to over 1,000 meters per dive.

3 Results

Video from a total of 10 NOAA Ship Okeanos Explorer ROV dive sites across four expeditions was reviewed for this study, totaling 55 hours, 54 minutes of time on bottom (Table 1). A total of approximately 7,350 linear meters were traveled horizontally. Sargassum was observed at 9 of the 10 dive sites, with a total of 237 instances of Sargassum annotated and between 0 to over 112 Sargassum observed per dive. Although we reviewed video from descent to ascent, no Sargassum was observed in the water column. Figure 2 shows location and Sargassum observations for all ROV dives included in the study.

3.1 Dive site characterizations

3.1.1 Gulf of Mexico 2018 (EX1803), April 11 - May 3, 2018 Pascagoula, Mississipi to Key West, Florida

Gulf of Mexico 2018 was a 23-day expedition in the Gulf of Mexico Basin to identify, map, and explore the diversity and distribution of deep-sea habitats in the region. The 15 ROV dives of this expedition, which ranged from 305 to 3,010 meters in bottom depth, focused on benthic habitats, including fish habitats, deep-sea coral and sponge communities, chemosynthetic communities (brine pools, gas seeps, mud volcanoes), and biological communities around shipwrecks (Maxon et al., 2018).

3.1.1.1 Hidalgo Basin (Dive 6)

This dive targeted Hidalgo Basin (Figure 3A), an area that was being considered for expansion of the Flower Garden Banks National Marine Sanctuary but was not ultimately included in the expansion⁵. Specifically, this dive explored a mound feature for hard-bottom communities, particularly deep-sea corals, sponges, and associated fauna. Approximately 250 kilometers south of central Louisiana, this is a relatively unexplored area that was first observed in 2014 by Okeanos Explorer. A high abundance of bivalve shells and carbonate rocks were seen on this dive. Anthropogenic debris from the surface - fishing line, canvas, metal container - was observed at this site. Parts of this site had signs of past seepage, including bacterial mats and a high abundance of bivalves, mostly empty shells but some living. A gastropod appeared to be grazing on Sargassum. The seafloor was heavily sedimented, with large depressions and pockmarks. There was a slight current on the bottom with high turbidity in the water column. This dive transited 932 linear meters along the seafloor. Thirty Sargassum observations were made over this distance, for an average 3.22 Sargassum observations per 100 meters (Table 1). The average depth for Sargassum observations was 1,077 meters.

3.1.1.2 DeSoto Canyon (Dive 8)

This dive targeted the northern end of the West Florida Escarpment in the DeSoto Canyon region (Figure 3B). At the time

⁴ https://repository.library.noaa.gov/.

⁵ https://flowergarden.noaa.gov/management/sanctuaryexpansion.html.

Expedition Name	Dive Site Name (Dive Number)	Date	Depth Range (m)	Bottom Time (hh:min)	# Sargassum Observations	# Sargassum Observations per 100m
Gulf of Mexico 2018 (EX1803)	Hidalgo Basin, Gulf of Mexico (Dive 6)	4/19/2018	1050 - 1104	5:59	30	3.22
Gulf of Mexico 2018 (EX1803)	DeSoto Canyon, Gulf of Mexico (Dive 8)	4/25/2018	2315 - 2635	5:25	7	1.49
Océano Profundo 2018 (EX1811)	Punta Yeguas, Puerto Rico (Dive 6)	11/6/2018	636 - 877	7:10	16	4.11
Océano Profundo 2018 (EX1811)	Caja de Muertos Island, Puerto Rico (Dive 7)	11/7/2018	401 - 535	4:35	>19*	3.32
Océano Profundo 2018 (EX1811)	South of La Parguera, Puerto Rico (Dive 8)	11/8/2018	804 - 1101	6:57	>112*	11.23
Océano Profundo 2018 (EX1811)	Mona Canyon, Puerto Rico (Dive 10)	11/10/2018	2536 - 2766	3:36	>25*	3.79
Windows to the Deep 2019 (EX1903L2)	Stetson Mesa South Mounds, Eastern Florida (Dive 2)	6/22/2019	728 -784	5:44	16	1.54
Windows to the Deep 2019 (EX1903L2)	"Dodge" Canyon, North Carolina (Dive 11)	7/3/2019	1209 - 1348	3:29	6	2.39
2019 Southeastern U.S. Deep-sea Exploration (EX1907)	Key West Deep (Dive 11)	11/18/2019	1168 - 1208	6:08	6	0.65
2019 Southeastern U.S. Deep-sea Exploration (EX1907)	"Berg Bits", Southwestern Florida (Dive 12)	11/19/2019	927 - 973	6:51	0	0.00

TABLE 1 Summary of Sargassum observations during the selected ROV dives.

Full dive names are: Gulf of Mexico 2018 (EX1803), Océano Profundo 2018: Exploring Deep-sea Habitats off Puerto Rico and the U.S. Virgin Islands (EX1811), Windows to the Deep 2019: Southeast and Mid-Atlantic U.S Continental Margin, Port Canaveral, FL to Norfolk, VA (EX1903L2), 2019 Southeastern U.S. Deep-sea Exploration (EX1907). *For dives with abundant *Sargassum*, a new *Sargassum* annotation was made for every new frame of view that contained any *Sargassum*. For instance, even if there were 5 clumps of *Sargassum* in frame, this was counted as one *Sargassum* annotation.



FIGURE 2

Location of ROV dive sites that were included in this study. The size of the circles indicates the range of the number of *Sargassum* observations. The number of *Sargassum* observations are shown in parentheses. (Gulf of Mexico 2018 (EX1803) - Dive 6: Hidalgo Basin and Dive 8: DeSoto Canyon, Océano Profundo 2018: Exploring Deep-sea Habitats off Puerto Rico and the U.S. Virgin Islands (EX1811) - Dive 6: Punta Yeguas, Puerto Rico, Dive 7: Caja de Muertos Island, Puerto Rico, Dive 8: South of La Parguera, Puerto Rico, and Dive 10: Mona Canyon, Puerto Rico, Windows to the Deep 2019: Southeast and Mid-Atlantic U.S Continental Margin, Port Canaveral, FL to Norfolk, VA (EX1903L2) - Dive 2: Stetson Mesa South Mounds, Eastern Florida and Dive 11: "Dodge" Canyon, North Carolina, 2019 Southeastern U.S. Deep-sea Exploration (EX1907) - Dive 11: Key West Deep and Dive 12: "Berg Bits", Southwestern Florida).

of the expedition this area was being considered for expansion of the Flower Garden Banks National Marine Sanctuary but was not ultimately included in the expansion. Dive 8 explored the escarpment feature at depths between 2,200-2,600 meters for hardbottom communities, particularly deep-sea corals, sponges, and associated fauna. There have been five previous scientific ROV dives in this general area, all of which documented extensive and diverse deep-sea coral communities, which are the deepest high-density communities known in the Gulf of Mexico (McLetchie et al., 2018). Approximately 220 kilometers off Alabama, this site was characterized by a hard substrate. It also featured a steep carbonate rock wall with highly fractured detached boulders at the base of the wall. Terrace features with relatively gentle slopes had a blanket of sediment cover. This dive transited 469 linear meters along the seafloor. Seven Sargassum observations were made over this distance, for an average 1.49 Sargassum observations per 100 meters (Table 1). The average depth for Sargassum observations was 2,534 meters.

3.1.2 Océano Profundo 2018: Exploring deep-sea habitats off Puerto Rico and the U.S. Virgin Islands (EX1811), October 30 - November 20, 2018 San Juan, Puerto Rico to San Juan, Puerto Rico

Océano Profundo 2018 was a 22-day expedition to explore the unknown and poorly understood deep-water areas surrounding Puerto Rico and the U.S. Virgin Islands. The 19 ROV dives of this expedition, which ranged from 250 to 5,000 meters in depth, surveyed a diversity of habitats and geological features, including midwater habitats, deep-sea coral and sponge communities, deepsea fish habitats, submarine canyons, and submarine landslides. In combination with deep-sea mapping operations, information and data were collected to increase understanding of deep-sea ecosystems of this poorly studied area, as well as to provide publicly-accessible data to spur further research, exploration, and management (Wagner et al., 2018).



FIGURE 3

Dive sites reviewed from Gulf of Mexico 2018 (EX1803). (A) Hidalgo Basin (Dive6) (B) DeSoto Canyon (Dive 8).



FIGURE 4

Dive sites reviewed from EX1811 Océano Profundo 2018: Exploring Deep-sea Habitats off Puerto Rico and the U.S. Virgin Islands. (A) Dive 6: Punta Yeguas, Puerto Rico, (B) Dive 7: Caja de Muertos Island, Puerto Rico, (C) Dive 8: South of La Parguera, Puerto Rico, (D) Dive 10: Mona Canyon, Puerto Rico.

3.1.2.1 Punta Yeguas, Puerto Rico (Dive 6)

The site was located within the Inés María Mendoza Nature Reserve, also known as Punta Yeguas (Figure 4A). This dive targeted the potential habitats of deep-water fish species, including snappers and groupers. Approximately 8 kilometers off the southeastern coast of Puerto Rico, this dive took place at approximately 860 meters depth up a steep mound, which has a prominent ridge on the crest of the mound. Flat areas were fairly heavily sedimented, and there was a slight current on the bottom. High turbidity was observed in the water column, and there was an abundance of benthic organisms swimming in the water column. This dive transited 389 linear meters along the seafloor. Sixteen *Sargassum* observations were made over this distance, for an average 4.11 *Sargassum* observations per 100 meters (Table 1). The average depth for *Sargassum* observations was 757 meters.

3.1.2.2 Caja de Muertos Island, Puerto Rico (Dive 7)

This site was located to the south of the Caja de Muertos Island, south of Ponce, Puerto Rico (Figure 4B). The dive started on a steep slope (40 degrees), traversed northeast along a gentle slope area, and then moved up a mound. The habitat at the start of the dive was dominated by soft sediment with a few scattered boulders, with transitions between larger boulders to smaller boulders to soft sediment. At the beginning of the dive, small clumps of Sargassum were observed slowly tumbling along a steep, sedimented slope. This tumbling movement was not seen at any other sites included in this study. An urchin appeared to be grazing on a piece of Sargassum towards the beginning of the dive. The second half of the dive along the ridge was dominated by carbonate boulders with intermittent soft-bottom expanses. In addition to Sargassum, turtlegrass and anthropogenic debris were often observed on this dive. The ROV pilots mentioned that there had been high amounts of Sargassum observed on the surface in the area. Since Sargassum was so abundant on this dive, it is worth noting that a new Sargassum annotation was made for every new frame of view that contained Sargassum, not for every piece of Sargassum observed. Thus, while 19 Sargassum observations were recorded on this dive, the number of individual Sargassum was higher. This dive transited 572 linear meters along the seafloor. Nineteen Sargassum observations were made over this distance, for an average 3.32 Sargassum observations per 100 meters (Table 1). The average depth for Sargassum observations was 470 meters.

3.1.2.3 South of La Parguera, Puerto Rico (Dive 8)

This dive explored an unexplored ridge feature (Figure 4C) off La Parguera in southwest Puerto Rico. Beginning near the bottom of a steep slope (average 30 degree incline), this dive continued eastward toward a more moderate ridge. With a gentle slope dominated by soft sediment, the seafloor was largely homogeneous in composition, and no hard substrate was observed. Scours and burrows were common in this area, and *Sargassum* was often seen gathered in pits and burrows in the sediment. There were quite a few pieces of wood and other organic debris, like seagrass blades and *Sargassum*. *Sargassum* was observed in abundance at the beginning of the dive where the seafloor was relatively flat. *Sargassum* continued to be present on the slope, but in lesser quantities than on the flat surfaces. Many really small pieces of *Sargassum* were observed throughout the dive that were able to be positively identified in zoomed-in shots. During this dive, the science watch lead noted that the *Sargassum* on the surface had been a bit of a hazard for the ship for the past few days. Since *Sargassum* was so abundant on this dive, it is worth noting that a new *Sargassum* annotation was made for every new frame of view that contained *Sargassum*, not for every piece of Sargassum observed. Thus, while 112 *Sargassum* observations were recorded on this dive, the number of individual *Sargassum* was higher. This dive transited 997 linear meters along the seafloor. 112 *Sargassum* observations were made over this distance, for an average 11.23 *Sargassum* observations per 100 meters (Table 1). The average depth for *Sargassum* observations was 936 meters.

3.1.2.4 Mona Canyon, Puerto Rico (Dive 10)

This dive took place along the north side of the Mona Passage in the Mona Canyon (Figure 4D). Approximately 50 kilometers off the northwest side of Puerto Rico, this site is more exposed to the greater North Atlantic Ocean than the other sites from this expedition that we included in this study. This dive traversed up the western wall of a giant landslide scarp. Seafloor bathymetry and imagery in this area may provide evidence of historical landslide activity that could pose a potential geohazard to this region of the Atlantic Ocean. The dive started with high quantities of Sargassum detritus in large clumps, much larger than were observed on the other dives. At steeper features, such as large rocks on a steep canyon wall face, or on a rock avalanche geologic feature, there were many fewer Sargassum observations. Several instances of anthropogenic debris (metal cans, etc.) were also observed. Few other organisms were encountered throughout the dive. Since Sargassum was so abundant on this dive, it is worth noting that a new Sargassum annotation was made for every new frame of view that contained Sargassum, not for every piece of Sargassum observed. Thus, while 25 Sargassum observations were recorded on this dive, the number of individual Sargassum was higher. This dive transited 659 linear meters along the seafloor. Twenty-five Sargassum observations were made over this distance, for an average 3.79 Sargassum observations per 100 meters (Table 1). The average depth for Sargassum observations was 2,725 meters.

3.1.3 Windows to the Deep 2019: Southeast and Midatlantic U.S continental margin (EX1903L2), June 20 - July 12, 2019 Port Canaveral, Florida to Norfolk, Virginia

The second leg of Windows to the Deep 2019 was a 23-day expedition to explore the deepwater areas offshore Florida, Georgia, South Carolina, and North Carolina. This expedition mapped and characterized these areas, which are some of the least-explored off the U.S. East Coast, with the goal of providing baseline information to support science needs and management of sensitive habitats, maritime heritage sites, and potential resources. The 19 ROV dives of this expedition, which ranged from 298 to 3,490 meters in depth, focused on improving the knowledge of unexplored areas within the U.S.



FIGURE 5

Dive sites reviewed from EX1903L2, Windows to the Deep 2019: Southeast and Mid-Atlantic U.S Continental Margin, Port Canaveral, FL to Norfolk, VA. (A) Dive 2: Stetson Mesa South Mounds, Eastern Florida, (B) Dive 11: "Dodge" Canyon, North Carolina.

Exclusive Economic Zone (EEZ), particularly the deep-sea habitats of the U.S. continental margin and the connections between marine communities throughout the Atlantic Basin (Cantwell et al., 2019).

3.1.3.1 Stetson Mesa South Mounds, Eastern Florida (Dive 2)

This dive explored several deep-water coral mounds (Figure 5A) in the Stetson Miami Terrace Deep Water Coral Habitat Area of Particular Concern (HAPC), approximately 150 kilometers off the east coast of Florida. This dive also included several hours of water column exploration. The area explored was just inside the Gulf Stream, and it started out with a high quantity of marine snow at 500-700 meters. The general trend observed throughout the dive was a large abundance of coral rubble at the bottom of each mound with increasing abundance of live coral coverage on the east to southeastern side of each mound. A pancake urchin appeared to be grazing on a piece of *Sargassum*. This dive transited 1,041 linear meters along the seafloor. Sixteen *Sargassum* observations were made over this distance, for an average 1.54 *Sargassum* observations per 100 meters.

3.1.3.2 "Dodge" Canyon, North Carolina (Dive 11)

This dive explored the Deep "Dodge" Canyon, specifically the mouth of an inner canyon/minor canyon area (Figure 5B) approximately 65 kilometers offshore of the Outer Banks, North Carolina. This site was characterized by a soft, heavily sedimented silty bottom, a lot of marine snow, and poor visibility. This is likely a result of organic material produced at the surface and in the midwater sinking and washing down the slope to accumulate on

the bottom. The seafloor continued to be heavily sedimented, even while traversing up a relatively steep slope (>30 degrees), and almost no organisms were actually attached and growing on the benthos. This was a canyon dive and closer to shore than most of the other dives in this expedition, which had more elevated mounds with clearer water and exposed rocky substrate. Six *Sargassum* were observed on this dive, with two of the *Sargassum* under a light layer of silt. This dive transited 251 linear meters along the seafloor. Six *Sargassum* observations were made over this distance, for an average 2.39 *Sargassum* observations per 100 meters (Table 1). The average depth for *Sargassum* observations was 1,288 meters.

3.1.4 2019 Southeastern U.S. Deep-sea Exploration (EX1907), October 31-November 20, 2019

Miami, Florida to Key West, Florida

2019 Southeastern U.S. Deep-sea Exploration was a 21-day expedition to explore a diversity of poorly known deep seafloor and midwater habitats, as well as unique geological features, in areas off the U.S. Southeast. The 12 ROV dives of this expedition, which ranged from 404 to 1,218 meters in maximum depth, explored a diversity of poorly explored deepwater habitats and geological features, such as biogenic mounds, deep-sea coral and sponge habitats, and fish habitats, that are of interest to resource managers and scientists (White et al., 2019). In combination with deep-sea mapping operations, critical information and data were collected to characterize unknown and poorly known areas of the southern U.S. continental margin, with the goal of increasing our understanding of deep-sea ecosystems and supporting ecosystembased management of marine resources (White et al., 2019).



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3.1.4.1 Dive 11: Key West Deep

The primary objective of this dive was to explore and characterize a small canyon (Figure 6A) that has the potential to be suitable habitat for deep-water coral, sponges, and associated fauna. This dive explored two small mounds that rise about 5 meters from the surrounding seafloor as well as an escarpment feature and a potential seep site with authigenic carbonate and bacterial mats. The current was swift on the bottom. The soft, silty seafloor continued to be sedimented even when traversing up a relatively steep slope (>30 degrees), and there were many little mounds from bioturbation. There were large terraces on the escarpment with unconsolidated sediment cover. The vast majority of this dive was exploring near vertical inclines on the boulders and escarpment feature. Sargassum was observed on the little horizontal sandy surface that was explored. Six Sargassum were observed on this dive, including one patch of Sargassum at 19:25 that was more degraded than the other Sargassum observed in this study. This dive transited 927 linear meters along the seafloor. Six Sargassum observations were made over this distance, for an average 0.65 Sargassum observations per 100 meters (Table 1). The average depth for Sargassum observations was 1,208 meters.

3.1.4.2 Dive 12: "Berg Bits", Southwestern Florida

Fifty nautical miles southwest of the Dry Tortugas, this dive explored two mounds and an escarpment at the base of the "Antarctica mound" (Figure 6B) - a plateau shaped like Antarctica with "bergie bits," or iceberg-like carved out features, surrounding the plateau. The plateau at the top of the escarpment and the seafloor in between mounds were sedimented. While approaching both mounds, small blocks from the escarpment decorated the sediment. Live coral was observed on the mounds, while standing dead coral and coral rubble was also prevalent on the mounds, along with seagrass. Most of the horizontal movement was done in transit from one feature to the next, so the ROV was moving fairly quickly and did not stop and zoom on features to allow a positive identification of Sargassum. No Sargassum were positively identified on this dive. Given the speed and distance from the ROV, it was not possible to distinguish between Sargassum and coral rubble and it is possible that there was Sargassum present. This dive transited 932 linear meters along the seafloor. The maximum depth reached was 973 meters.

4 Discussion

Because the deep sea is so under-studied, any new observations can lend valuable insight into the dynamics of deep-sea communities and how the deep sea is connected to the surface and to global environmental processes. *Sargassum* has been directly observed at local scales on the sea surface for centuries. The use of satellite-technologies has scaled up the spatial and temporal resolutions at which *Sargassum* can be observed, helping to better understand the species trajectory at the surface. However, once *Sargassum* dies and loses buoyancy, its fate is poorly understood after it sinks below the sea surface.

Through the use of deep submersible technologies and archived video, this study documented significant quantities of intact Sargassum on the seafloor in areas with known surface blooms. Sargassum was observed on 9 of the 10 dives reviewed for this project, in numbers ranging from 0 to more than 112 observations per dive. Given the limited spatial scale of our observations, we can surmise that Sargassum makes its way to the deep sea in likely significant amounts. Though we reviewed the descents and ascents for all the ROV dives, no Sargassum was observed within the water column, indicating that Sargassum might sink quickly once it loses its buoyancy, consistent with the relatively fast sinking rate estimated by Johnson and Richardson (1977). The relatively low volume of water imaged by the ROV may limit the ability to observe Sargassum sinking through the water column. It is also possible that some portion of the sinking Sargassum is consumed by pelagic herbivores.

Though we do not have quantitative estimates of *Sargassum* at the sea surface for each of the dives in this study, we do note two instances where expedition participants noted the heavy presence of *Sargassum* at the surface (e.g., Caja de Muertos Island and South of La Parguera). These dives correspond with some of the highest *Sargassum* observation numbers (more than 112 and more than 19), supporting the expectation that where *Sargassum* blooms are thick at the surface, large numbers sink below. *Sargassum* blooms have continued since this study time period, with March 2023 setting records for the most *Sargassum* observed in the month of March (University of South Florida (USF) and Optical Oceanography Lab, 2023). *Sargassum* has continued to wreak havoc in the Southeastern U.S. and Caribbean coastal communities, even interfering with ocean exploration operations⁶.

For this study, we considered the general environmental and ecological context of a dive site to explore whether there are areas that may be aggregators of Sargassum. There were no obvious patterns, though a few things to consider. "Dodge" Canyon off North Carolina was characterized by thick sediment and poor visibility, likely as a result of the high amount of marine snow that was observed both in the water column and on the seafloor. This marine snow indicates that there is likely high productivity on the surface to produce so much organic material. However, this large amount of marine snow may have quickly buried any Sargassum on the bottom, as two of the Sargassum that were observed there were partially covered in a fine layer of silt. Although only 6 specimens of Sargassum were observed on this dive, the second lowest out of the 10 dives surveyed, there may have been more there just buried from view. If the Sargassum is in fact being buried under silt at high surface productivity sites, this could remove the availability of the Sargassum to feeding by abyssal omnivores and scavengers such as sea urchins and gastropods, thus increasing the likelihood of sequestration. The high number of anthropogenic debris observed relatively far offshore (approximately 250 kilometers) at the Hidalgo Basin dive site indicates there might be some factor leading to accumulation here, such as currents or seafloor depressions also aggregating Sargassum. The bathymetry of the Mona Canyon dive

⁶ https://oceanexplorer.noaa.gov/okeanos/explorations/22voyage-to-the-ridge/features/sargassum/sargassum.html.

site may have resulted in the larger piles of *Sargassum* observed at this dive, with the steep walls of the underwater canyon helping to funnel the *Sargassum* into large aggregations. The shallowest of the dives studied (Caja de Muertos, 470 meters) also included the only observation of *Sargassum* slowly tumbling down a slope. It is possible that, being closer to the surface, the *Sargassum* was more intact and thus more likely to be transported in this way.

There were three instances of invertebrates (two sea urchins and one gastropod) appearing to graze on *Sargassum*, observed on separate dives. This provides evidence that *Sargassum* is a source of food for benthic animals, with the further implication that some carbon is not being sequestered but instead is cycled back into the marine system. Bacterial degradation of the *Sargassum* would additionally diminish the carbon removal potential.

Part of the inherent value of exploration-driven study of the ocean is that some of the most interesting and impactful insights that may be gleaned from the research are typically unknown at the outset and unplanned for (e.g., Selig et al., 2019; Ford et al., 2020; Simon-Lledo et al., 2023). Although the Okeanos Explorer expeditions did not explicitly seek to study Sargassum on the seabed, through review of these 10 exploratory video surveys, we were able to significantly increase the number of confirmed direct observations of Sargassum on the deep seabed and contribute to broader understanding of the fate of sinking Sargassum. While observations of the Southeast U.S. and Gulf of Mexico remain sparse, they are comparatively well explored areas, with a decades-long history of submersible surveys (e.g., Harbor Branch Oceanographic Institute's Johnson Sea-Link submersible). Further investigation could delve into available archived video footage to investigate trends in the quantity of Sargassum on the seafloor over time as blooms have increased in quantity. Additionally, we acknowledge that our study has inherent bias in that sites were intentionally selected where Sargassum were known to be observed. Further studies could use a random sampling design to provide an unbiased and quantitative assessment of Sargassum sinking at the seafloor.

Macroalgal ecosystems like those harboring *Sargassum* may sequester and store significant amounts of carbon from the atmosphere and ocean and hence are now recognized for their role in mitigating climate change. Developing a predictive understanding of carbon export pathways such as gravitational sinking is thus critical to diagnosing present and future rates of ocean carbon sequestration. Using ROV dive surveys to study the fate of *Sargassum* confirmed that relatively large amounts of *Sargassum* complete the first step in the process toward potential carbon sequestration on the seabed – sinking to the seafloor. Longterm monitoring of the fate of sunken *Sargassum* on the seabed is needed in order to determine how much is ultimately sequestered rather than returned back into the system. Such observations would inform the feasibility of *Sargassum* farming and/or facilitated sinking as potential carbon dioxide removal strategies.

Further observations throughout the global ocean are required to fill in the gaps in the distribution of *Sargassum* in the deep sea. Further observation of the fate of *Sargassum* blooms on the deep seabed could serve as a natural model to inform research and development for emerging seaweed sequestration programs for climate mitigation.

Data availability statement

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

Author contributions

AP conceived of this project, conducted the video analysis, created the plots and figures, and led the drafting of the manuscript. AN advised on deep-sea video analysis and NOAA Ship *Okeanos Explorer* operations and wrote sections of the manuscript. HB provided guidance on plotting the dive and *Sargassum* observations and CTD data analysis and conducted analysis of distance traveled. VH advised on potential machine learning applications. AN, HB, and VH all provided feedback and guidance on the project design. All authors contributed to the article and approved the submitted version.

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Conflict of interest

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

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necessarily reflect the views of NOAA or the Department of Commerce.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1250150/full#supplementary-material

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