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Occurrence of pelagic *Sargassum* in waters of the U.S. Gulf of Mexico in response to weather-related hydrographic regimes associated with decadal and interannual variability in global climate

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Abstract—Pelagic species of *Sargassum*, surface drifting macroalgae, occur in continental shelf and deep basin waters across the Gulf of Mexico (GOM). They often accumulate in mats and “windrows” to form a structured habitat that serves as a source of food and refuge for a diverse assemblage of fish and invertebrates. Long-term temporal data on the distribution and abundance of *Sargassum* species in the GOM are lacking, but there is a time series of occurrence of those species across the U.S. GOM (USGOM) associated with ichthyoplankton surveys conducted by the Southeast Area Monitoring and Assessment Program. The seasonal presence of *Sargassum* species in regions of the USGOM was compared under contrasting weather-related hydrographic regimes using nonparametric tests (Kruskal–Wallis H test, Mann–Whitney U test, Wilcoxon signed rank test). Phases of the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) along with El Niño–Southern Oscillation (ENSO) events influenced seasonal presence of *Sargassum* species across the area of study. Occurrence of *Sargassum* species was highest under the coupled warm AMO and neutral NAO phases and cold ENSO events and was associated with physical and biological processes that transported the macroalgae to the USGOM and maintained them over time.

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Two holopelagic species of *Sargassum*, floating macroalgae (Phaeophyceae), co-occur in continental shelf and deep basin waters across the Gulf of Mexico (GOM): *Sargassum natans* and *S. fluitans*. These 2 species of macroalgae drift in surface waters (Deacon, 1942; Stoner, 1983) through the western Caribbean region into the GOM and exit through the Florida Straits and up the eastern seaboard of the United States in the Gulf Stream, and out into the Atlantic Ocean to the Sargasso Sea (Calder, 1995). The abundance and distribution of the 2 pelagic species of *Sargassum* in the Atlantic Ocean are highly variable over space and time (Gower and King, 2011; Gower et al., 2013). Two historical quantitative studies of the abundance of pelagic *Sargassum* species were conducted in overlapping areas within the Sargasso Sea, the first between 1933 and 1935 (Parr, 1939) and the second between 1977 and 1981 (Stoner, 1983). No differences in overall abundance of these pelagic *Sargassum* species were found with these studies. In a more recent study, Huffard et al. (2014) examined temporal and spatial variability of pelagic *Sargassum* community change over a 40-year period and noted that the distribution, abundance, or circulation patterns (or a combination of these variables) of pelagic *Sargassum* species in the Atlantic Ocean during 2010 and 2011 were highly anomalous compared with the 2003–2010 period. In the spring and summer of 2011, Franks et al. (2011) and Johnson et al. (2013) reported that unprecedented amounts of pelagic *Sargassum* washed ashore along the Caribbean Islands, and satellite observations pointed to waters north of the mouth of the Amazon River as a source region for the event (Gower et al., 2013). Johnson et al. (2013) examined data from satellite- tracked current drifters during 2010 and 2011 but were unable to connect the event to the central North Atlantic Ocean. These authors used an archived numerical circulation model (Hybrid Coordinate Ocean Model) to backtrack pelagic *Sargassum* macroalgae to the North Equatorial Recirculation Region (NERR). They suggested that pelagic *Sargassum* macroalgae bloomed in the NERR, where they may have recirculated over an extended period of time, before being picked up by the North Brazil Current and transported to the eastern Caribbean region. In waters with elevated nutrients (Lapointe et al., 2014), high salinities, high light intensities (low cloud cover), and sea-surface temperatures (SSTs) between 18°C and 30°C (Hanisak and Samuel, 1987), pelagic species of *Sargassum* are capable of rapid growth (Lapointe, 1986; Hanisak and Samuel, 1987).

Climate plays a major role in setting the physical hydrographic processes (Karnauskas et al., 2015) that act to transport, aggregate, or scatter pelagic *Sargassum* species, and it affects algal productivity through its influence on the position of the Intertropical Convergence Zone (ITCZ) (Franks et al., 2011; Schneider et al., 2014; Franks et al., 2016). Climate in the Northern Hemisphere is influenced by oceanic and atmospheric modes of variability from the Atlantic Ocean (Mehta et al., 2000; Sutton and Hodson, 2005) and Pacific Ocean (Wang and Fu, 2000). The Atlantic Multidecadal Oscillation (AMO) represents below (cold AMO [AMOc]) and above (warm AMO [AMOw]) normal SST across the North Atlantic Ocean from 0°N to 70°N latitude (Enfield et al., 2001) and has a characteristic periodicity of around 65–80 years (Kerr, 2000; Gray et al., 2004). The North Atlantic Oscillation (NAO) is associated with an oscillation in the sea-level air-pressure gradient between Iceland and the Azores (Hurrell and Van Loon, 1997). The NAO displays negative (NAOn) and positive (NAOp) phases and responds to the effects of different physical processes on seasonal to multidecadal time scales (Hurrell et al., 2003). The El Niño–Southern Oscillation (ENSO) is the quasiperiodic (2–7 years) warming or cooling of the eastern equatorial Pacific Ocean (Walker, 1924; Bjerknes, 1969; Lighthill, 1969; Godfrey, 1975; McCreary, 1976) with the shift of southeast trade winds over the central and western Pacific Ocean (Krueger and Winston, 1975; Wyrtki, 1975; McPhaden, 1999). The warm phase of the ENSO (ENSOw) is referred to as El Niño and the cool phase (ENSOc) is referred to as La Niña. The phase between ENSOc and ENSOw is referred to as neutral (ENSOn). The ENSO phases are identified by the SST anomaly from the Niño 3.4 region (5°S–5°N and 120°W–170°W) in the equatorial Pacific Ocean.

Phases of the NAO (Seager et al., 2000) and ENSO (Giannini et al., 2001) contribute to the annual variability of SST and winds in the tropical Atlantic Ocean that is measured with an index called the Atlantic Meridional Mode (AMM). These weather-related hydrographic characteristics in the tropical Atlantic Ocean affect the position and strength of the thermal equator and hence the position and strength of the ITCZ with its heated, rising air. The ITCZ is an area where the northeast and southeast trade wind systems meet creating a rain band in the tropical North Atlantic Ocean (Vimont and Kossin, 2007). The position of the ITCZ directly affects hydrographic characteristics in neritic waters of West Africa, northeast Brazil, and Central America and has been associated with variability in rainfall over West Africa (Lamb, 1978; Janicot et al., 1998; Sultan and Janicot, 2000), northeast Brazil (Hastenrath and Heller, 1977; Uvo et al., 1998; Robertson et al., 2004), and Central America (Giannini et al., 2000; Taylor et al., 2002). The ITCZ is important because it affects the cross-equatorial transport of heat and salinity by upper-level ocean currents (Berger and Wefer, 1996; Maslin et al., 1997; Vink et al., 2002) and the strength of the Loop Current (LC), a northward flowing current that enters the Gulf of Mexico (GOM) from the Caribbean Sea (Nürnberg et al., 2008). The LC connects the Yucatan Channel and Straits of Florida (Hurlburt and Thompson, 1980; Oey et al., 2005) and there is a significant link between the intrusion of the LC into the GOM and the estimated transport of the Florida Current (Lin et al., 2010) at low frequencies (time scales longer than 120 days; Lin et al., 2010). The northward intrusion of the LC can extend as far as the Mississippi River Delta and the Florida continental shelf (Huh et al., 1981; Wiseman and Dinnel, 1988). This intrusion deflects Mississippi River discharge westward with hydrographic conditions in surface waters of the northeastern GOM approaching those of the Caribbean Sea (high salinity and SST) (Nürnberg et al., 2008).

Phases of the AMO and NAO affect moist-air–related wind patterns in the GOM. In the summer, under the AMOc phase, the Bermuda High is strengthened and its associated easterly and southeasterly low-level jets can extend well over the warm waters of the Caribbean region. These jets, transport moist air westward along the GOM (Wang et al., 2006; Hu and Feng, 2007). During the NAOp phases, low geopotential heights and high SST levels are set along the GOM, bringing southerly winds in winter over south Florida, and in spring over south Florida and the Florida panhandle (Hurrell and Deser, 2009).

Pelagic species of *Sargassum* often accumulate in mats and windrows (lines of floating *Sargassum* caused by wind, tide or currents) to form a structured habitat and a source of food and refuge for a rich and diverse assemblage of fish and invertebrates (Dooley, 1972; Bortone et al., 1977; Butler et al., 1983; Coston-Clements et al., 1991; Comyns et al., 2002; Wells and Rooker, 2004; Hoffmayer et al., 2005). Habitat of *Sargassum* species was declared essential fish habitat in the U.S. South Atlantic region in 2002 (SAFMC, 2002), and management measures were implemented by the National Marine Fisheries Service (NMFS) in 2003. Seasonal and yearly differences in the abundance and distribution of pelagic *Sargassum* could contribute to the variation observed in recruitment of marine fishes and other marine organisms (Butler et al., 1983). In spite of the importance of *Sargassum* as habitat, few studies have examined the effect of climate regimes on the occurrence of species of pelagic *Sargassum* over decadal and interannual time scales.

The Southeast Area Monitoring and Assessment Program (SEAMAP) is a federal and state cooperative effort to collect, manage, and disseminate fishery-independent data and information in the southeastern United States. The SEAMAP ichthyoplankton database (Hanisko[1]) contains data on observed occurrence of pelagic *Sargassum* species in samples from surveys conducted across the USGOM. Data used for our study were prior to and lead up to the 2011 bloom in the tropical North Atlantic Ocean and are intended to provide linkage to define the relationship between yearly and seasonal *Sargassum* occurrence in the USGOM and weather-related hydrographic regimes imposed by AMO, NAO, and ENSO events. Because the SEAMAP conducts surveys each year, the relationship of recent Caribbean and South American inundation events with *Sargassum* occurrence in the USGOM can be examined in the future. Reference to *Sargassum* occurrence in the following sections is specific to the pelagic species *S. fluitans* and *S. natans*.

Material and methods

Decadal AMO and NAO phases and interannual ENSO events

Characterization of AMO and NAO phases and the individual ENSO events were adopted from Sanchez-Rubio and Perry (2015). Years not included in the latter study (2011–2013) were placed under the coupled AMOw/NAOn (slash denotes coupling of those phases) phase and the 2011 year was identified as ENSOc. The coupling of AMOc and NAOp phases was in place from 1971 through 1994 (first regime, wet); the coupling of AMOw and NAOn phases was in place from 1995 through 2013 (second regime, dry). Although the change from one phase to another is transitional, published studies cite the mid-1990s as the time when the shift occurred (Karnauskas et al., 2015). The years from 1977 to 2010 were identified as ENSOw (1977, 1982, 1986, 1987, 1991–1994, 1997, 2002, 2004, 2006, and 2009), ENSOn (1978–1981, 1985, 1989, 1990, 1995, 1996, 2001, and 2003), and ENSOc (1983, 1984, 1988, 1998-2000, 2005, 2007, 2008, 2010, and 2011) years.

Biological data

Biological data were taken from a series of ichthyoplankton surveys conducted under the state and federal SEAMAP program administered by the NMFS. Data used to determine the occurrence of species of *Sargassum* were, in part, observational and therefore dependent upon the field biologists to record the presence of *Sargassum* species in the sample or sample area. Individuals responsible for field collections were long-term employees of the NMFS thus there was continuity of personnel over the study period (personal observation and NMFS Cruise Reports, Harriet Perry). Although *Sargassum* species were not the primary focus of the surveys, their presence was recorded because they form important nursery habitat for commercially and recreationally sought fishes. Knowledge of the presence of *Sargassum* macroalgae aids in taxonomic resolution of species and provides information on the distribution of the *Sargassum* habitat. Acknowledging problems associated with the use of observational data, the surveys still offer a unique opportunity to examine the relationship between climate variables and algal presence because this data set provides the only long-term, systematic information on the occurrence of these *Sargassum* species in the GOM.

The SEAMAP ichthyoplankton database was obtained from Hanisko.[1] Data from samples in this survey program were available from 1982 to 2012. The SEAMAP sampling area encompasses the USGOM from the 10-m isobath to the U.S. Exclusive Economic Zone. The sampling gear and methods used during SEAMAP surveys have been described by Kramer et al. (1972), Smith and Richardson (1977), and Posgay and Marak (1980). Most SEAMAP survey stations were occupied at approximately 56 km (or 0.5°) intervals in a fixed, systematic grid of transects across the USGOM. Samples were taken upon arrival at each station regardless of time of day or night. Plankton surveys have been consistently conducted over 2 survey time frames (spring–early summer and late summer–early fall) since 1982 (Lyczkowski-Shultz and Hanisko, 2007) and approximately 200 stations have been targeted for sampling. In addition, numerous surveys have been periodically conducted over shorter time frames and with specific targeted species groups. For this study, the complete SEAMAP ichthyoplankton database (Hanisko[1]) was used to increase temporal and spatial resolution of the data. Data on the occurrence of *Sargassum* species were obtained from direct observations recorded in ichthyoplankton data logs during SEAMAP cruises. In addition, the occurrence of species of *Sargassum* was indirectly inferred from the presence of the Sargassumfish (*Histrio histrio*), a species endemic to *Sargassum* (Coston-Clements et al., 1991).

Ichthyoplankton samples associated with *Sargassum* macroalgae were extracted from the main SEAMAP database to form a more manageable data set. The extracted data set contained 1077 samples of which 1051 were collected in neuston net tows and 26 in bongo net tows. All months of the year and most of the years, with the exception of 1982, 1987, and 1988, were represented in the data set of ichthyoplankton samples associated with species of *Sargassum*. Of the 1077 samples associated with *Sargassum* macroalgae, 284 were collected under the coupling of AMOc and NAOp phases and 793 were collected during the coupling of AMOw and NAOn phases. *Sargassum* species occurred in samples from January to November during the coupling of AMOc and NAOp phases and from February to December during the coupling of AMOw and NAOn

[1] Hanisko, D. S. 2015. Unpubl. data. [Historical data set of ichthyoplankton collected in 1982–2012 during Southeast Area Monitoring and Assessment Program surveys.] Miss. Lab., Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 3209 Frederic St., Pascagoula, MS 39568-1207.

phases. The 1077 samples were further characterized as collected after ENSOc (n=394), ENSOn (n=302), and ENSOw (n=381) events. *Sargassum* species occurred in samples from February to November after ENSOc years, from April to December after ENSOn years, and from January to November after ENSOw years.

Samples associated with species of *Sargassum* were subdivided temporally by month of collection and spatially within square degree areas of 1 degree latitude and 1 degree longitude across the USGOM. Monthly samples associated with *Sargassum* species within each square degree area were further subdivided by the weather-related hydrographic regime in place when samples were collected. Monthly samples collected during1982–1994 and 1995–2012 were classified under the influence of the couplings of AMOc and NAOp and AMOw and NAOn phases, respectively. The same monthly samples were also classified by the ENSO event (warm, neutral, or cold) that was present from May of the previous year to February of the year in which samples were collected. The final data set represented the monthly ichthyoplankton samples associated with species of *Sargassum* within square degree areas (1 degree of latitude by 1 degree of longitude) across the USGOM under the influence of the coupling of AMO and NAO phases and ENSO events.

Samples from May to July and from September to November associated with the *Sargassum* species within each square degree area and weather-related hydrographic regime were added to obtain the total number of samples associated with the *Sargassum* species within each square degree area, weather-related hydrographic regime, and summer and fall seasons. Samples associated with species of *Sargassum* within each square degree area, weather-related hydrographic regime, and season were added, multiplied by 100, and then divided by the total number of SEAMAP ichthyoplankton samples collected within each square degree area, weather-related hydrographic regime, and season. If the number of samples collected was fewer than 8 per square degree area, the percentage of seasonal samples associated with *Sargassum* species was not calculated. The calculated values represented the percentage of seasonal SEAMAP samples associated with species of *Sargassum* within each square degree area across the USGOM, weather-related hydrographic regime, and season. Percentages were used because differences in sampling effort (total number of samples and sampling years) existed among hydrographic regimes. The number of samples collected was 7768 (summer) and 5939 (fall) during the coupling of AMOc/NAOp phases, 7910 (summer) and 9196 (fall) samples during the coupling of AMOw/NAOn phases, 6532 (summer) and 5820 (fall) samples after ENSOw events, 4389 (summer) and 4396 (fall) samples after ENSOn events, and 4757 (summer) and 4919 (fall) samples after ENSOc events. The number of samples collected under the AMO and NAO phases and after ENSO events were 15,678 (summer) and 15,135 (fall). After spatially comparing the seasonal occurrences of pelagic species of *Sargassum*, analysis was restricted to data calculated from more than 9 square degree areas per regime. Because the ichthyoplankton surveys did not specifically target areas with *Sargassum* macroalgae, the percentage of samples associated with species of *Sargassum* was considered a measure of occurrence across the USGOM.

Data analysis was limited spatially to survey areas between 81°W to 97°W and 24°N to 29°N and an area that extended from 86°W to 88°W and 30°N. The 90th parallel west divided the general area into western and eastern regions. The study area was also divided into deep basin and continental shelf waters. The deep basin was limited spatially to survey areas between 85°W to 95°W and 24°N to 26°N and an area that extended from 86°W to 88°W and 27°N. To statistically compare the seasonal occurrence of *Sargassum* species within square degree areas in USGOM regions between 2 or more contrasting weather-related hydrographic regimes, 3 nonparametric tests were performed by using SPSS Statistics[2] software, vers. 20.0 (IBM Corp., Armonk, NY). Using the Kruskal–Wallis H test, we compared seasonal occurrences of pelagic species of *Sargassum* in USGOM regions among 3 contrasting weather-related hydrographic regimes associated with ENSO events. With the Mann–Whitney U test, we compared seasonal occurrences of pelagic species of *Sargassum* in USGOM regions between 2 contrasting weather-related hydrographic regimes associated with the coupling of AMO and NAO phases and ENSO events. With the Wilcoxon signed rank test, we compared seasonal occurrences of *Sargassum* species from identical square degree areas in USGOM regions between 2 contrasting weather-related hydrographic regimes associated with the couplings of AMO and NAO phases and ENSO events.

Environmental data

The AMM index was downloaded as monthly values from 1981 through 2009 from the NOAA Earth System Research Laboratory (data available from website, accessed October 2015). This index represents the variations in SST and sea level pressure between the tropical Atlantic Ocean north and south of the ITCZ. The ITCZ is an area where the northeast and southeast trade wind systems meet, creating a rain band in the tropical North Atlantic Ocean (Vimont and Kossin, 2007). Monthly data for Amazon River discharge were downloaded from SO HYBAM (streamflow data available from website, accessed December 2015). The data from 1982 through 2013 were limited to the months (from April to August) of highest river discharge. Wind speed and direction data were downloaded from the NOAA National Data Buoy Center (data available from website, accessed October 2015). These data were recorded hourly at the western (buoy 42002: 1978–2011), central (buoy 42001:1979–2011), and eastern (buoy

[2] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

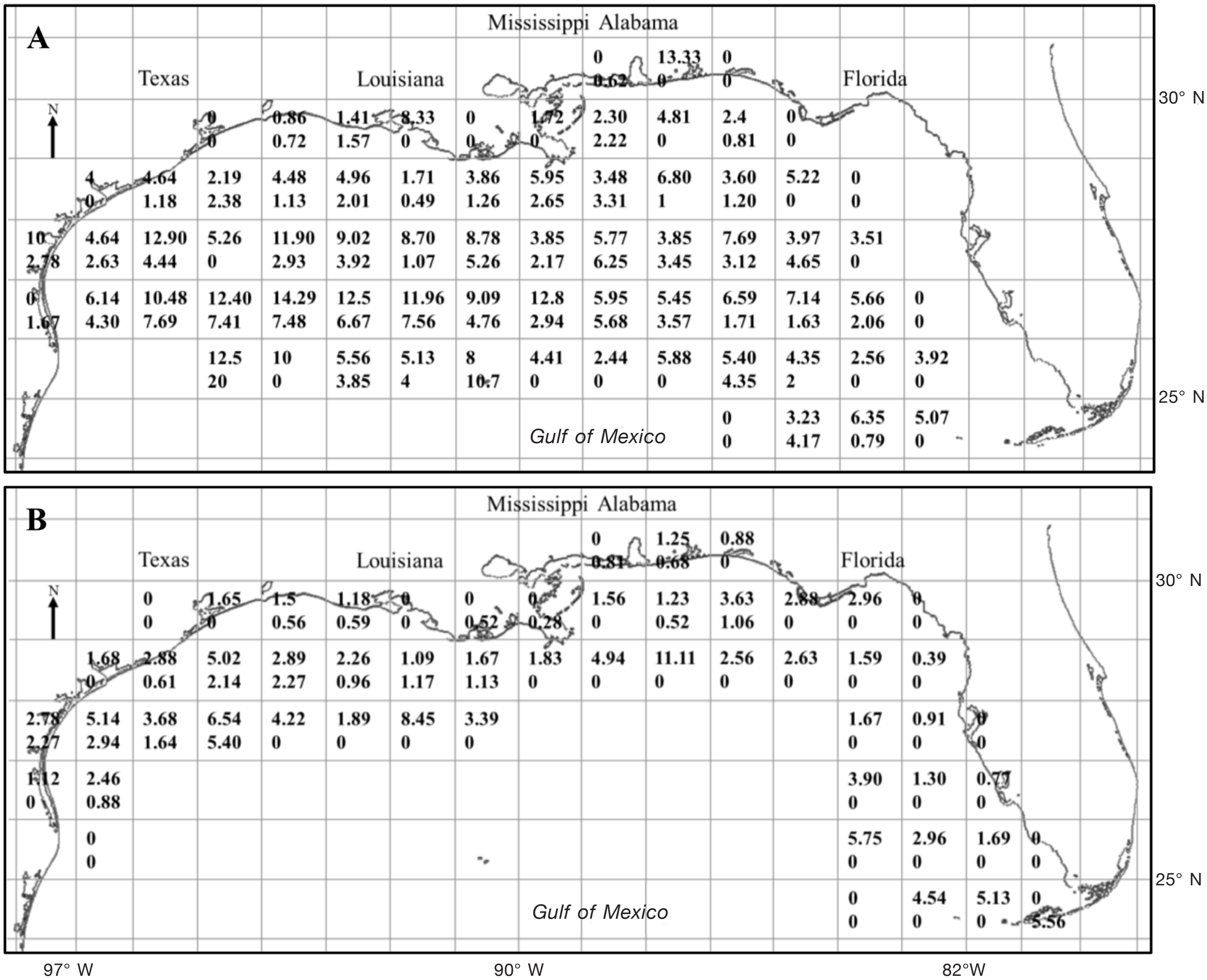

Figure 1

Occurrence of pelagic *Sargassum* macroalgae in (**A**) summer (May–July) and (**B**) fall (September–November) across the U.S. Gulf of Mexico during the coupling of phases of the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) from 1982 through 2012. Values within each square degree area (1 degree of latitude by 1 degree of longitude) represent the percentages of samples associated with species of *Sargassum* during the coupling of AMO warm and NAO negative phases (top values) and AMO cold and NAO positive phases (bottom values).

42003: 1979–2011) GOM regions. The wind data were limited to those months in which more than 400 hours were recorded. The hourly data for each of the buoys were grouped according to the direction of the wind (northern wind: 337.6–22.5°, northeastern wind: 22.6–67.5°, eastern wind: 67.6–112.5°, southeastern wind: 112.6–157.5°, southern wind: 157.6–202.5°, southwestern wind: 202.6–247.5°, western wind: 247.6–292.5°, and northwestern wind: 292.6–337.5°). These data were then divided by season (fall: September–November, winter: December–February, spring: March–May, and summer: June–August). The seasonal average wind speed (meters per second) was calculated for each direction of the wind for each buoy. Using these data, we calculated seasonal wind stress (T) in newtons per square meter:

$$T = \rho \times CD \times U_{10}^2, \tag{1}$$

where ρ = the density of air at 1.225 kg/m^3;
U_{10}, = wind speed in meters per second at 10 m above the water surface; and
CD = the drag coefficient (Hellerman, 1965).

Smith (1980) proposed a formula to calculate CD:

$$1000\ CD = 0.44 + (0.063 \times U_{10}). \tag{2}$$

Seasonal data of wind stress were then transformed to wind momentum (newton-second [Ns] per square meter) by multiplying the wind stress by the average number of seconds per hour that the wind blows for each of the directions. The index of wind momentum represents the direction and flux of water driven by the seasonal winds in the 3 GOM regions. Monthly

Table 1

Mean seasonal occurrence, with 95% confidence intervals, of pelagic species of *Sargassum* across the U.S. Gulf of Mexico and by western and eastern regions during the coupling of phases of the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) from 1982 through 2012. Occurrence represents the percentage of ichthyoplankton samples associated with pelagic *Sargassum*. n= the total number of square degree areas (1 degree latitude by 1 degree longitude) that were compared. Numbers in parentheses are the number of square degree areas (1 degree latitude, 1 degree longitude) with higher percentages of *Sargassum* species occurrence during the coupling of AMO and NAO phases. NS=nonsignificant.

Season	U.S. Gulf of Mexico	n	Cold AMO, positive NAO phases	Warm AMO, negative NAO phases	
Summer (May–Jul)	Whole	71	2.54 ±0.75% (9)	5.51 ±0.90% (55)	P_1= 0
	Western	33	3.63 ±1.39% (5)	6.84 ±1.46% (26)	P_1<0.0001
	Eastern	38	1.59 ±0.58% (4)	4.35 ±0.96% (29)	P_1=0
Fall (Sep–Nov)	Whole	55	0.58 ±0.31% (5)	0.96 ±0.52% (2)	P_1=0
	Western	24	0.96 ±0.52% (2)	2.56 ±0.85% (19)	P_1<0.0001
	Eastern	31	0.29 ±0.36% (3)	2.20 ±0.83% (24)	P_1<0.0001
Summer (May-Jul)	Western	33	3.63 ±1.39%	6.84 ±1.46%	
	Eastern	38	1.59 ±0.58%	4.35 ±0.96%	
			P_2=0.0060	P_2=0.0075	
Fall (Sep-Nov)	Western	24	0.96±0.52%	—	
	Eastern	31	0.29±0.36%	—	
			P_2=0.0036	P_2=NS	

P_1-values given by the Wilcoxon signed rank test for the analysis between AMO and NAO phases.
P_2-values given by the Mann–Whitney U test for the analysis within AMO and NAO phases.

hurricane tracks during the Atlantic Ocean hurricane season (June to November) for each of the 2 AMO-NAO phases were downloaded as maps from 1980 through 2009 (NOAA National Ocean Service, data available from website, accessed October 2015). A hurricane is a tropical cyclone with maximum sustained (1-min) 10-m winds of 33 m/s (65 kt) or greater. The number of hurricanes that occurred from June to November in the NERR and GOM were enumerated for the periods 1980–1994 (AMOc and NAOp phases) and 1995–2009 (AMOw and NAOn phases). Hurricanes were included only when sustained wind speed during at least part of their track in the NERR and GOM was classified as a hurricane. A historical list of monthly shedding of LC's spin-off eddies was obtained from Vukovich (2012). The spin-off eddies were enumerated for the periods 1979–1994 (AMOc and NAOp phases) and 1995–2010 (AMOw and NAOn phases).

To statistically compare monthly and seasonal values of the AMM and wind momentum among weather-related hydrographic regimes imposed by the coupling of AMO and NAO phases and ENSO events, 2 nonparametric rank-sum tests were carried out with SPSS Statistics software. A nonparametric multiple samples test (Kruskal–Wallis H test) was performed to compare the values of the indices among 3 contrasting weather-related hydrographic regimes associated with ENSOw, ENSOn, and ENSOc events. A nonparametric 2-sample test (Mann–Whitney U test) was performed to compare values of the indices between 2 contrasting weather-related hydrographic regimes associated with the couplings of AMOc and NAOp and AMOw and NAOn phases, ENSOw and ENSOn events, ENSOw and ENSOc events, and ENSOn and ENSOc events. To adjust the P-values for multiple comparisons, the α level of each individual test was adjusted downward by using the Bonferroni correction method (Bonferroni, 1935). No statistical test was used to compare the number of years with above or below Amazon River discharge in the NERR, the total number of hurricanes in the NERR and GOM, and LC's spin-off eddies in the GOM waters between the coupling of AMO and NAO phases.

Results

Variability of seasonal occurrence of pelagic Sargassum in USGOM regions in response to the coupling of AMO and NAO phases and ENSO events

Occurrence of species of *Sargassum* differed by season, region, water depth, and climate (Tables 1–4). High-

Table 2

Mean summer (May–July) occurrence, with 95% confidence intervals, of pelagic species of *Sargassum* in waters over the continental shelf and deep basin of the U.S. Gulf of Mexico and the western and eastern regions during phases of the coupling of the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO) from 1982 through 2012. Occurrence represents the percentage of ichthyoplankton samples associated with pelagic *Sargassum*. n=the total number of square degree areas (1 degree latitude by 1 degree longitude) that were compared. Numbers in parentheses represent the number of square degree areas (1 degree latitude, 1 degree longitude) with higher percentages of occurrence of *Sargassum* species during the coupling of AMO and NAO phases.

U.S. Gulf of Mexico	Water depth	n	Cold AMO, positive NAO phases	Warm AMO, negative NAO phases	
Whole	Continental shelf	45	1.36 ±0.44% (5)	4.41 ±1.03% (34)	P_1=0
	Deep basin	26	4.58 ±1.64% (4)	7.42 ±1.43% (21)	P_1=0.0005
Western	Continental shelf	22	1.81 ±0.67% (3)	5.17 ±1.62% (17)	P_1=0.0002
	Deep basin	11	7.28 ±2.99% (2)	10.2 ±1.76% (9)	P_1=0.0375
Eastern	Continental shelf	23	0.93 ±0.53% (2)	3.67 ±1.24% (17)	P_1=0.0002
	Deep basin	15	2.59 ±1.04% (2)	5.40 ±1.43% (12)	P_1=0.0021
Whole	Continental shelf	45	1.36 ±0.44%	4.41 ±1.03%	
	Deep basin	26	4.58 ±1.64%	7.42 ±1.43%	
			P_2<0.0001	P_2=0.0005	
Western	Continental shelf	22	1.81 ±0.67%	5.17 ±1.62%	
	Deep basin	11	7.28 ±2.99%	10.2 ±1.76%	
			P_2=0.0002	P_2=0.0006	
Eastern	Continental shelf	23	0.93 ±0.53%	3.67 ±1.24%	
	Deep basin	15	2.59 ±1.04%	5.40 ±1.43%	
			P_2=0.0099	P_2=0.0183	

P_1-values given by the Wilcoxon signed rank test for the analysis between AMO and NAO phases.
P_2-values given by the Mann–Whitney U test for the analysis within AMO and NAO phases.

est percentages of positive samples (*Sargassum* species present) occurred under the coupling of AMOw and NAOn phases regardless of region and season (Fig. 1, Table 1). Regionally, higher percentages of positive samples occurred in the western GOM, regardless of season and climate regime (Table 1). Comparing the presence of *Sargassum* species over the continental shelf and deep basin during the summer, we found that occurrences were higher under the coupling of AMOw and NAOn phases regardless of region and water depth (Table 2). Occurrences were also higher over the deep basin regardless of region and climate phase (Table 2).

Occurrence of species of *Sargassum* by ENSO event, region, continental shelf or deep basin waters during the summer is shown in Table 3. Presence of *Sargassum* species by region and over the deep basin was not significantly different among ENSO events. Presence of *Sargassum* species was higher in the continental shelf after ENSOc than after ENSOn events. Presence of species of *Sargassum* was higher in the western GOM after ENSOc and ENSOw events and in the deep basin regardless of an ENSO event. Occurrence of *Sargassum* species by ENSO events and regions during the fall is shown in Table 4. Higher values for presence of *Sargassum* species were noted in the western GOM regardless of an ENSO event. Highest, intermediate, and lowest values for the presence of *Sargassum* species were observed after ENSOc, ENSOn, and ENSOw years, respectively, regardless of region.

Variability of weather-related hydrographic characteristics in the NERR and GOM in response to the coupling of AMO and NAO phases and ENSO events

Monthly and seasonal weather-related hydrographic characteristics in the NERR and GOM showed mathematically significant differences between the 2 AMO/NAO phases (Table 5). During the coupled AMOw/NAOn phase, higher values were found for the AMM index, the number of hurricanes, and the above average annual discharge of the Amazon River in the NERR and the number of LC spin-off eddies, num-

Table 3

Mean summer (May–July) occurrence, with 95% confidence intervals, of pelagic species of *Sargassum* across the U.S. Gulf of Mexico and in the western and eastern regions, continental shelf, and deep basin after El Niño–Southern Oscillation (ENSO) events from 1982 through 2012. Occurrence represents the percentages of ichthyoplankton samples associated with pelagic *Sargassum* at the time of their collection. Numbers in parentheses represent the total number of square degree areas (1 degree latitude by 1 degree longitude) that were compared. Numbers in brackets represent the number of square degree areas with higher percentages of *Sargassum* species occurrence after ENSO events. NS=nonsignificant.

U.S. Gulf of Mexico	Cold ENSO	Neutral ENSO	Warm ENSO	
Whole	—	—	—	P_1=NS
Western	—	—	—	P_1=NS
Eastern	—	—	—	P_1=NS
Continental shelf	3.43 ±0.91% (48)	2.02 ±0.77% (48)	2.52 ±0.66% (48)	P_1=0.0424
Deep basin	—	—	—	P_1=NS
Continental shelf	3.31 ±0.92% (48) [24]	2.02 ±0.77% (48) [11]		P_2=0.0022
	—		—	P_2=NS
		—	—	P_2=NS
Western	4.64±1.10% (31)	—	5.28±1.53% (32)	
Eastern	3.62±1.29% (40)	—	2.51±0.74% (40)	
	P_3=0.0455	P_3=NS	P_3=0.0020	
Continental shelf	3.43±0.91% (48)	2.02±0.77% (48)	2.52±0.66% (48)	
Deep basin	5.38±1.83% (23)	7.79±2.38% (24)	6.19±1.85% (24)	
	P_3=0.0188	P_3<0.00001	P_3=0.0002	

P_1-values given by the Kruskal–Wallis H test for the analysis among ENSO events.
P_2-values given by the Wilcoxon signed rank test for the analysis between ENSO events.
P_3-values given by the Mann–Whitney U test for the analysis within ENSO events.

ber of hurricanes and the south and southeast wind momentums in the GOM. A seasonal weather-related hydrographic characteristic in the GOM was also significantly different under ENSO events. Higher values of south wind momentum were detected at the western region in spring during ENSOc events (22.09 ±14.31 Ns/m^2) than during ENSOw events (6.02 ±2.93 Ns/m^2; P=0.007). Higher values of north and northwest wind momentum were found at the central region in spring during ENSOw events (N: 15.88 ±4.41 Ns/m^2; NW: 11.15 ±4.72 Ns/m^2) than during ENSOn events (N: 7.97 ±3.29 Ns/m^2; NW: 2.49 ±1.29 Ns/m^2; P<0.006).

Discussion

Sargassum macroalgae in the western Atlantic Ocean are home to a diverse and unique community of small invertebrates and fish species. Despite the designation of *Sargassum* species as essential fish habitat, long-term data on the distribution and abundance of species of *Sargassum* in the GOM are lacking. The time frame of the SEAMAP ichthyoplankton surveys provided a unique opportunity to examine occurrence of *Sargassum* species under differing decadal and interannual regimes of global climate.

The GOM is part of a broader western Atlantic Ocean region of *Sargassum* occurrence. Historically, the recognized route of floating *Sargassum* macroalgae was through the Caribbean Sea, into the GOM, up the eastern seaboard of the United States within the Gulf Stream, and into the Sargasso Sea (Calder, 1995). A new source area for *Sargassum* species in the tropical North Atlantic Ocean (NERR) was recently discovered (Franks et al., 2011; Gower et al., 2013; Johnson et al., 2013) and provides another route of entry for the macroalgae to the greater Caribbean region and GOM. This newly defined route (NERR) has been cited as the source of the *Sargassum* species currently inundating the Caribbean region, and weather-related hydrographic characteristics (nutrient input, position and strength of the ITCZ) have been identified as contributors to the massive accumulation of the macroalgae (Franks et al., 2011; Franks et al., 2016). Weather-related hydrographic characteristics associated with the NERR (AMM, ITCZ, Amazon River discharge), as well as factors unique to the GOM (LC spin-off eddies) may help to explain differences in abundance of *Sargassum* species across the USGOM in response to shifts in climate regimes.

Table 4

Mean fall (September–November) occurrence, with 95% confidence intervals, of pelagic species of *Sargassum* over the continental shelf across the U.S. Gulf of Mexico and in the western and eastern regions after El Niño–Southern Oscillation (ENSO) events from 1982 through 2012. Occurrence represents the percentage of ichthyoplankton samples associated with pelagic *Sargassum*. The numbers in parentheses represent the total number of square degree areas (1 degree latitude by 1 degree longitude) that were compared. Numbers in brackets represent the number of square degree areas (1 degree latitude, 1 degree longitude) with higher percentages of *Sargassum* species after ENSO events. NS=nonsignificant.

U.S. Gulf of Mexico	Cold ENSO	Neutral ENSO	Warm ENSO	
Whole	2.72 ±0.69% (53)	1.84 ±0.69% (49)	0.87 ±0.38% (53)	P_1=0.0001
Western	2.97 ±1.10% (24)	2.70 ±1.21% (22)	0.96 ±0.53% (24)	P_1=0.0077
Eastern	2.51 ±0.88% (29)	1.13 ±0.69% (27)	0.80 ±0.55% (29)	P_1=0.0022
	P_2=NS	P_2=0.0087	P_2=NS	
Whole	2.63 ±0.67% (49) [29]	1.84 ±0.69% (49) [15]		P_3=0.0075
	2.72 ±0.69% (53) [40]		0.87 ±0.38% (53) [4]	P_3=0
		1.70 ±0.65% (48) [26]	0.92 ±0.41% (48) [10]	P_3=0.0084
Western	—	—		P_3=NS
	2.97 ±1.10% (24) [18]		0.96 ±0.53% (24) [2]	P_3=0.0008
		2.70 ±1.21% (22) [15]	1.05 ±0.57% (22) [4]	P_3=0.0049
Eastern	2.14 ±0.77% (27) [18]	1.13 ±0.69% (27) [6]		P_3=0.0055
	2.51 ±0.88% (29) [22]		0.80 ±0.55% (29) [2]	P_3=0.0001
		—	—	P_3=NS

P_1-values given by the Kruskal–Wallis H test for the analysis among ENSO events.
P_2-values given by the Mann–Whitney U test for the analysis within ENSO events.
P_3-values given by the Wilcoxon signed rank test for the analysis between ENSO events.

Two different decadal regimes of weather-related hydrographic characteristics associated with the coupling of AMO and NAO phases occurred over the time period represented in the SEAMAP samples. Overall percentages of samples with species of *Sargassum* across the USGOM under the coupled AMOc/NAOp and coupled AMOw/NAOn phases were 2.95% and 7.28%, respectively. Factors affecting the occurrence of *Sargassum* species under both regimes are those that influence growth (e.g., temperature, nutrient input), fragmentation (reproduction) and dispersion (e.g., hurricane and eddies), and containment within a region (e.g., wind momentum and eddies).

Productivity in the USGOM is strongly influenced by river flows from the Mississippi and Atchafalaya rivers. Sanchez-Rubio et al. (2011) found the AMO and NAO to be important drivers of climate-related features influencing long-term hydrological conditions across coastal Louisiana and Mississippi. In their study, high river discharge occurred under the coupling of AMOc/NAOp phases and lower volumes were associated with the coupled AMOw/NAOn phase. Low river discharge and a lowered nitrogen:phosphorus ratio (Sanchez-Rubio and Perry, 2015), conditions less favorable for *Sargassum* productivity, characterized the regime with greater *Sargassum* species occurrence; this finding indicates that factors associated with transport and retention may have played a greater role than growth in facilitating the occurrence of *Sargassum* species. Although physical processes associated with the dry regime undoubtedly played a major role in moving and maintaining the occurrence of *Sargassum* species, biological processes may also have contributed to maintenance of the macroalgae in the western GOM. Lapointe et al. (2014) reported that the excretion of ammonium and soluble reactive phosphorus by high abundances of fishes associated with *Sargassum* macroalgae (filefishes and carangids) provides nutrients that help to sustain growth and biomass. They noted that new production of *Sargassum* macroalgae may occur in neritic waters of the western Atlantic Ocean and GOM as a result of this mutualistic association. Thus, both physical and biological processes may facilitate occurrence.

Hurricane activity was higher in the North Atlantic Ocean, Caribbean region (Goldenberg et al., 2001), NERR, and GOM (this study), and the AMM index was higher and positive (this study) for the years after the mid 1990s climate shift. Vimont and Kossin (2007) found that the AMM was strongly related to hurricane activity on both decadal and interannual time frames and noted that the influence of the AMO on hurricane activity was manifested through the AMM. The influ-

Table 5

Monthly mean values, with 95% confidence intervals, of environmental factors from the North Equatorial Recirculation Region (NERR) and Gulf of Mexico (GOM) during the coupling of phases of the Atlantic Multidecadal Oscillation (AMO) and North Atlantic Oscillation (NAO). The numbers in parentheses and *n* represent the total number of values or features that were compared; *P*-values are those given by the Mann–Whitney U test for the analysis of values between AMO and NAO phases. AMM=Atlantic Meridional Mode.

Variables	Region	Month	Wind direction	*P*	Cold AMO, positive NAO phases	Warm AMO, negative NAO phases
AMM	NERR	Aug–Mar		0	–1.56 ±0.81 (13)	1.52 ±0.85 (15)
Wind momentum	Western GOM	Sep–Nov	NW	0.031	4.27 ±2.50 (12)	7.65 ±3.19 (14)
		Dec–Feb	SE	0.005	46.61 ±9.37 (15)	67.64 ±22.89 (10)
		Mar–May	SE	0.030	82.66 ±21.59 (13)	109.80 ±34.02 (12)
	Central GOM	Sep–Nov	S	0.017	6.78 ±1.94 (12)	10.95 ±3.08 (15)
		Jun–Aug	W	0.022	1.03 ±0.48 (7)	1.89 ±0.53 (15)
	Eastern GOM	Sep–Nov	S	0.010	4.18 ±1.74 (9)	9.76 ±3.77 (13)
		Sep–Nov	SW	0.003	1.05 ±0.42 (8)	4.23 ±1.65 (12)
Hurricanes	GOM	Jun–Nov			n=23	n=38
	NERR	Jun–Nov			n=3	n=12
Loop Current eddies	GOM	Jan–Dec			n=17	n=23
Amazon River discharge	NERR	Apr–Aug			Below average (7/13)	Above average (14/19)

ence of hurricanes on abundance of *Sargassum* species is largely undocumented, but biotic characteristics of the macroalgae (such as fragmentation) and its position in the water column (i.e., in surface waters) would cause the species to be responsive to physical processes associated with the passing of tropical storms. Water turbulence associated with hurricanes may positively affect abundances through increased dispersion, transport, upwelling, and fragmentation. Pelagic *Sargassum* species reproduce asexually by fragmentation (Fritsch, 1965; Round, 1981; Awasthi, 2007; Rogers, 2011) when younger parts of the thallus separate from the older parts or when there is physical injury to any part of the plant (Hanisak and Samuel, 1987). Separated parts of the plant have the potential to mature into fully formed organisms (Hanisak and Samuel, 1987). In addition to fragmentation of individual plants, mats of *Sargassum* species could be broken apart and more widely dispersed.

For species of *Sargassum*, the eastern region of the GOM is generally regarded as a zone of transport that serves to move the macroalgae into the GOM via the Yucatan Current and out via the Florida Current. The western zone is considered an area of residence and growth where LC spin-off eddies decay and deposit *Sargassum* macroalgae. Circulation in the eastern GOM is dominated by the LC, a fast-moving current that can reach maximum flow speeds of 1.5 to 1.8 m/s (Gordon, 1967). Degree of northward penetration of the LC into the GOM varies as does the time and number of eddies shed. Eddies are usually mesoscale circulation features but can measure 200-400 km in diameter and extend to a depth of 1000 m (Mooers, 1998). They are shed randomly every 3 to 17 months (Sturges and Leben, 2000) and the majority of them drift to the western GOM where they may persist for weeks (Oey et al., 2005). Species of *Sargassum* can be readily entrained in fronts formed by convergent surface currents associated with large spin-off eddies that appear in satellite images (Gower et al., 2006) as long curving lines. The balance of forces in eddy motions favors entrapment of *Sargassum* around the periphery of anticyclonic (counterclockwise in the Northern Hemisphere) eddies and in the center of cyclonic eddies owing to sea-surface height gradients and frictional processes. More complex patterns, however, are formed by stepwise convergent fronts across the surface of mesoscale eddies and associated lines of *Sargassum* (Zhong et al., 2012) within both cyclonic and anticyclonic eddies.

The higher numbers of eddies shed under the coupled AMOw/NAOn phases and the relatively long period associated with eddy decay may have contributed to the greater incidence of *Sargassum* species observed in the western USGOM in our study. Regional occurrence was 8.46% in the western USGOM and 6.47% in the eastern USGOM under the coupled AMOw/NAOn phases and 3.41% and 2.69% in the western and eastern regions under the coupled AMOc/NAOp phases, respectively. Highest percentages of positive samples (*Sargassum* species present) occurred over the deep basin in the western region irrespective of climate regime: coupled AMOw/NAOn phases (10.2%), coupled AMOc/NAOp phases (7.28%). Gower et al. (2006), using satellite imagery, observed that most *Sargassum* macroalgae were found in the western GOM and noted that in areas where surface waters circulate in slowly rotating gyres, the macroalgae would be expected to accumulate. Wind momentum, a measure of the transport of surface water, also favored retention of species of *Sargassum*. South and southeast wind momentum was higher along the USGOM under the coupled AMOw/NAOn phases. These wind conditions would facilitate retention of *Sargassum* mats within the study region and the transport of new mats of *Sargassum* species from the southern GOM.

Operating within the decadal regimes are weather-related hydrographic characteristics imposed by interannual ENSO events. Higher occurrences of *Sargassum* species in the USGOM were associated with the ENSOc phase. Under ENSOc years, hydrographic characteristics in the NERR, Caribbean Sea, and GOM generally favor production, growth, and dispersion of the macroalgae. During ENSOc years, the ITCZ shifts south of its mean location (Saravanan and Chang, 2000), creating a lower vertical shear over the regions of hurricane genesis and development of the tropical Atlantic Ocean (Gray, 1984; Goldenberg et al., 2001; Vitart and Anderson, 2001). The decrease in vertical shearing enhances the growth of prehurricane disturbances in the Atlantic Ocean and increases the number of hurricane landings on the continental United States (Elsner et al., 2001). The turbulence associated with hurricanes would enhance fragmentation and dispersion of mats of pelagic *Sargassum* species along their paths of circulation. During the ENSOc years, the westward influence of south and southeast winds along the USGOM (Smith et al., 1998) and south wind momentum in spring (March–May) in the western USGOM region (this study) were enhanced and therefore reduced the frequency of cold wind outbreaks, off-shelf water flow (Nowlin and Parker, 1974), and coastal upwelling (Dagg, 1988). These wind conditions would favor retention of *Sargassum* mats in this region. Highest percentages of positive samples (*Sargassum* species present) occurred over the deep basin in the western region after ENSO events. Distributional results were consistent with traditional observations that the eastern region is a zone of transport and the western region is a zone of accumulation for *Sargassum* in the USGOM.

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Literature cited

Awasthi, D. K.
2007. Cryptogams: algae, Bryophyta and Pteridophyta, 448 p. Krishna Prakashan Media, Ltd., Meerut, India.

Berger, W. H., and G. Wefer.
1996. Central themes of South Atlantic circulation. *In* The South Atlantic: present and past circulation (G. Wefer, W. H. Berger, G. Siedler, D. J. Webb, eds.), p. 1–11. Springer-Verlag, Berlin, Germany.

Bjerknes, J.
1969. Atmospheric teleconnections from the equatorial Pacific. Mon. Weather Rev. 97:163–172. Article

Bonferroni, C. E.
1935. Il calcolo delle assicurazioni su gruppi di teste. *In* Studi in onore del professore Salvatore Ortu Carboni, p. 13–60. Bardi, Rome.

Bortone, S. A., P. A. Hastings, and S. B. Collard.
1977. The pelagic *Sargassum* ichthyofauna of the eastern Gulf of Mexico. Northeast Gulf Sci. 1:60–67.

Butler, J. N., B. F. Morris, J. Cadwallader, and A. W. Stoner.
1983. Studies of *Sargassum* and the *Sargassum* community. Bermuda Biol. Stat. Spec. Publ. 22, 307 p.

Calder, D. R.
1995. Hydroid assemblages on holopelagic *Sargassum* from the Sargasso Sea at Bermuda. Bull. Mar. Sci. 56:537–546.

Comyns, B. H., N. M. Crochet, J. S. Franks, J. R. Hendon, and R. S. Waller.
2002. Preliminary assessment of the association of larval fishes with pelagic *Sargassum* habitat and convergence zones in the northcentral Gulf of Mexico. *In* Proceedings of the fifty-third Gulf and Caribbean Fisheries Institute; Biloxi, MS, 6–10 November 2000 (R. L. Creswell, ed.), p. 636–645. Gulf Caribb. Fish. Inst., Fort Pierce, FL.

Coston-Clements, L., L. R. Settle, D. E. Hoss, and F. A. Cross.
1991. Utilization of the *Sargassum* habitat by marine invertebrates and vertebrates: a review. NOAA Tech. Memo. NMFS-SEFSC-296, 32 p.

Dagg, M. J.
1988. Physical and biological responses to the passage of a winter storm in the coastal and inner shelf waters of the northern Gulf of Mexico. Cont. Shelf Res. 8:167–178. Article

Deacon, G. E. R.
1942. The Sargasso Sea. Geogr. J. 99:16–28. Article

Dooley, J. K.
1972. Fishes associated with the pelagic *Sargassum* complex with a discussion of the *Sargassum* community. Contrib. Mar. Sci. 16:1–32.

Elsner, J. B., B. H. Bossak, and X.-F. Niu.
2001. Secular changes to the ENSO-U.S. hurricane relationship. Geophys. Res. Lett. 28:4123–4126. Article

Enfield, D. B., A. M. Mestas-Nuñez, and P. J. Trimble.
2001. The Atlantic Multidecadal Oscillation and its relation to rainfall and river flows in the continental U.S. Geophys. Res. Lett. 28:2077–2080. Article

Franks, J. S., D. R. Johnson, D.-S. Ko, G. Sanchez-Rubio, J. R. Hendon, and M. Lay.
2011. Unprecedented influx of pelagic *Sargassum* along Caribbean island coastlines during summer 2011. *In* Proceedings of the 64th Gulf and Caribbean Fisheries Institute; Puerto Morelos, Mexico, October 31–November 4, p. 6–8. Gulf Carib. Fish. Inst., Marathon, FL.

Franks, J. S., D. R. Johnson and D. S. Ko.
2016. Pelagic *Sargassum* in the tropical North Atlantic. Gulf Carib. Res. 27(1):SC6-SC11. Article

Fritsch, F. E.
1965. The structure and reproduction of algae, vol. II, 939 p. Cambridge Univ. Press, Cambridge, UK.

Giannini, A., Y. Kushnir, and M. A. Cane.
2000. Interannual variability of Caribbean rainfall, ENSO, and the Atlantic Ocean. J. Clim. 13:297–311. Article

Giannini, A., M. A. Cane, and Y. Kushnir.
2001. Interdecadal changes in the ENSO teleconnection to the Caribbean region and the North Atlantic Oscillation. J. Clim. 14:2867–2879. Article

Godfrey, J. S.
1975. On ocean spindown I: a linear experiment. J. Phys. Oceanogr. 5:399–409. Article

Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nuñez, and W. M. Gray.
2001. The recent increase in Atlantic hurricane activity: causes and implications. Science 293:474–479. Article

Gordon, A. L.
1967. Circulation of the Caribbean Sea. J. Geophys. Res. 72:6207–6223. Article

Gower, J. F. R., and S. A. King.
2011. Distribution of floating *Sargassum* in the Gulf of Mexico and the Atlantic Ocean mapped using MERIS. Int. J. Remote Sens. 32:1917–1929. Article

Gower, J., C. Hu, G. Borstad, and S. King.
2006. Ocean color satellites show extensive lines of floating *Sargassum* in the Gulf of Mexico. IEEE Trans. Geosci. Remote Sens. 44:3619–3625.

Gower, J. F. R., E. Young, and S. King.
2013. Satellite images suggest a new *Sargassum* source region in 2011. Remote Sens. Lett. 4:764–773. Article

Gray, W. M.
1984. Atlantic seasonal hurricane frequency. Part I: El Niño and 30 mb quasi-biennial oscillation influences. Mon. Weather Rev. 112:1649–1668. Article

Gray, S. T., L. J. Graumlich, J. L. Betancourt, and G. T. Pederson.
2004. A tree-ring based reconstruction of the Atlantic Multidecadal Oscillation since 1567 A.D. Geophys. Res. Lett. 31:L12205. Article

Hanisak, M. D., and M. A. Samuel.
1987. Growth rates in culture of several species of *Sargassum* from Florida, USA. Hydrobiologia 151–152: 399–404. Article

Hastenrath, S., and L. Heller.
1977. Dynamics of climate hazards in northeast Brazil. Quart. J. Roy. Meteor. Soc. 103:77–92. Article

Hellerman, S.
1965. Computations of wind stress fields over the Atlantic Ocean. Mon. Weather Rev. 93(4):239–244. Article

Hoffmayer, E. R., J. S. Franks, B. H. Comyns, J. R. Hendon, and R. S. Waller.
2005. Larval and juvenile fishes associated with pelagic *Sargassum* in the northcentral Gulf of Mexico. *In* Proceedings of the 56th Gulf and Caribbean Fisheries Institute; Tortola, British Virgin Islands, 10–14 November 2003, p. 259–269. Gulf Caribb. Fish. Inst., Fort Pierce, FL.

Hu, Q., and S. Feng.
2007. Decadal variation of the southwest U.S. summer monsoon circulation and rainfall in a regional model. J. Clim. 20:4702–4716. Article

Huh, O. K., W. J. Wiseman Jr., and L. J. Rouse Jr.
1981. Intrusion of Loop Current waters onto the west Florida continental shelf. J. Geophys. Res. 86:4186–4192. Article

Huffard, C. L., S. von Thun, A. D. Sherman, K. Sealey, and K. L. Smith, Jr.
2014. Pelagic *Sargassum* community change over a 40-year period: temporal and spatial variability. Mar. Biol. 161:2735–2751. Article

Hurlburt, H. E., and J. D. Thompson.
1980. A numerical study of Loop Current intrusions and eddy shedding. J. Phys. Oceanogr. 10:1611–1651. Article

Hurrell, J. W., and H. van Loon.
1997. Decadal variations in climate associated with the North Atlantic Oscillation. Clim. Change 36:301–326. Article

Hurrell, J. W., and C. Deser.
2009. North Atlantic climate variability: the role of the North Atlantic Oscillation. J. Mar. Syst. 78:28–41. Article

Hurrell, J. W., Y. Kushnir, G. Ottersen, and M. Visbeck.
2003. An overview of the North Atlantic Oscillation. *In* The North Atlantic Oscillation: climatic significance and environmental impact. Geophys Monogr. 134 (J. W. Hurrell, Y. Kushnir, G. Ottersen, and M. Visbeck, eds.), p. 1–35. Am. Geophys. Union, Washington, DC.

Janicot, S., A. Harzallah, B. Fontaine, and V. Moron.
1998. West African monsoon dynamics and eastern equatorial Atlantic and Pacific SST anomalies (1970–88). J. Clim. 11:1874–1882.

Johnson, D. R., D. S. Ko, J. S. Franks, P. Moreno, and G. Sanchez-Rubio.
2013. The *Sargassum* invasion of the eastern Caribbean and dynamics of the equatorial North Atlantic. *In* Proceedings of the 65th Gulf and Caribbean Fisheries Institute; Santa Marta, Colombia, 5–9 November 2012, p 102–103. Gulf Caribb. Fish. Inst., Marathon, FL.

Karnauskas, M., M. J. Schirripa, J. K. Craig, G. S. Cook, C. R. Kelble, J. J. Agar, B. A. Black, D. B. Enfield, D. Lindo-Atichati, B. A. Muhling, et al.
2015. Evidence of climate-driven ecosystem reorganization in the Gulf of Mexico. Global Change Biol. 21:2554–2568. Article

Kerr, R. A.
2000. A North Atlantic climate pacemaker for the centuries. Science 288:1984–1985 Article

Kramer D., M. J. Kalin, E. G. Stevens, J. R. Thrailkill, and J. R. Zweifel.
1972. Collecting and processing data on fish eggs and larvae in the California Current region. NOAA Tech. Rep. NMFS Circ. 370, 38 p.

Krueger, A. F., and J. S. Winston.
1975. Large-scale circulation anomalies over the tropics during 1971–72. Mon. Weather Rev. 103:465–473. Article

Lamb, P. J.
1978. Large-scale tropical Atlantic surface circulation patterns associated with Subsaharan weather anomalies. Tellus 30:240–251. Article

Lapointe, B. E.
1986. Phosphorus-limited photosynthesis and growth of *Sargassum natans* and *Sargassum fluitans* (Phaeophyceae) in the western North Atlantic. Deep-Sea Res. Oceanogr., A 33:391–399. Article

Lapointe, B. E., L. E. West, T. T. Sutton, and C. Hu.
2014. Ryther revisited: nutrient excretions by fishes enhance productivity of pelagic *Sargassum* in the western

North Atlantic Ocean. J. Exp. Mar. Biol. Ecol. 458:46–56. Article

Lighthill, M. J.
1969. Dynamic response of the Indian Ocean to onset of the Southwest Monsoon. Philos. Trans. R. Soc. Lond., A, 265:45–92. Article

Lin, Y., R. J. Greatbatch, and J. Sheng.
2010. The influence of Gulf of Mexico Loop Current intrusion on the transport of the Florida Current. Ocean Dyn. 60:1075–1084. Article

Lyczkowski-Shultz, J., and D. S. Hanisko.
2007. A time series of observations on red snapper larvae from SEAMAP surveys, 1982–2003: seasonal occurrence, distribution, abundance, and size. Am. Fish. Soc. Symp. 60:3–23.

Maslin, M., S. Burns, H. Erlenkeuser, and C. Hohnemann.
1997. Stable isotope records from sites 932 and 933. Proc. Ocean Drilling Prog., Sci. Results 155:305–318. Article

McCreary, J.
1976. Eastern tropical ocean response to changing wind systems: with application to El Niño. J. Phys. Oceanogr. 6:632–645. Article

McPhaden, M. J.
1999. Genesis and evolution of the 1997–98 El Niño. Science. 283:950–954. Article

Mehta, V. M., M. J. Suarez, J. V. Manganello, and T. L. Delworth.
2000. Oceanic influence on the North Atlantic Oscillation and associated northern hemisphere climate variations: 1959–1993. Geophys. Res. Lett. 27:121–124. Article

Mooers, C. N. K., and G. A. Maul.
1998. Intra-Americas circulation. *In* The sea, vol. 11. The global coastal ocean: regional studies and syntheses (A. R. Robinson and K. Brink, eds.), p. 183–208. John Wiley & Sons, New York.

Nowlin, W. D., Jr., and C. A. Parker.
1974. Effects of a cold-air outbreak on shelf waters of the Gulf of Mexico. J. Phys. Oceanogr. 4:467–486. Article

Nürnberg, D., M. Ziegler, C. Karas, R. Tiedemann, and M. W. Schmidt.
2008. Interacting Loop Current variability and Mississippi River discharge over the past 400 kyr. Earth Planet. Sci. Lett. 272:278–289. Article

Oey, L.-Y., Jr., T. Ezer, and H.-C. Lee.
2005. Loop Current, rings and related circulation in the Gulf of Mexico: a review of numerical models and future challenges. *In* Circulation in the Gulf of Mexico: observations and models). Geophys. Monogr. 161 (W. Sturges and A. Lugo-Fernandez, eds.), p. 31–56. Am. Geophys. Union, Washington, DC.

Parr, A. E.
1939. Quantitative observations on the pelagic sargassum vegetation of the western North Atlantic. With preliminary discussion of morphology and relationships. Bull. Bingham Oceanogr. Collect. 6:1–94.

Posgay, J. A., and R. R. Marak.
1980. The MARMAP bongo zooplankton samplers. J. Northwest Atl. Fish. Sci. 1:91–99.

Robertson, A. W., S. Kirshner, and P. Smyth.
2004. Downscaling of daily rainfall occurrence over northeast Brazil using a hidden Markov model. J. Climate. 17:4407–4424. Article

Rogers, K. (ed.).
2011. Fungi, algae, and protists, 232 p. Britannica Educational Publishing, New York.

Round, F. E.
1981. The ecology of algae, 653 p. Cambridge Univ. Press, New York.

SAFMC (South Atlantic Fishery Management Council).
2002. Fishery management plan for pelagic *Sargassum* habitat of the South Atlantic region: including a final environmental impact statement, initial regulatory flexibility analysis, regulatory impact review, and social impact assessment/fishery impact statement, 153 p. SAFMC, Charleston, SC. [Available from website.]

Sanchez-Rubio, G., and H. Perry.
2015. Climate-related meteorological and hydrological regimes and their influence on recruitment of Gulf menhaden (*Brevoortia patronus*) in the northern Gulf of Mexico. Fish. Bull. 113:391–406. Article

Sanchez-Rubio, G., H. M. Perry, P. M. Biesiot, D. R. Johnson, R. N. Lipcius.
2011. Oceanic–atmospheric modes of variability and their influence on riverine input to coastal Louisiana and Mississippi. J. Hydrol. 396:72–81. Article

Saravanan, R., and P. Chang.
2000. Interaction between tropical Atlantic variability and El Nino–Southern Oscillation. J. Clim. 13:2177–2194. Article

Schneider, T., T. Bischoff, and G. H. Haug.
2014. Migrations and dynamics of the intertropical convergence zone. Nature 513:45–53. Article

Seager, R., Y. Kushnir, M. Visbeck, N. Naik, J. Miller, G. Krahmann, and H. Cullen.
2000. Causes of Atlantic Ocean climate variability between 1958 and 1998. J. Clim. 13:2845–2862. Article

Smith, S. D.
1980. Wind stress and heat flux over the ocean in gale force winds. J. Phys. Oceanogr. 10:709–726. Article

Smith, P. E., and S. L. Richardson.
1977. Standard techniques for pelagic fish egg and larva surveys. FAO Fish. Tech. Pap. 175, 100 p.

Smith, S. R., P. M. Green, A. P. Leonardi, and J. J. O'Brien.
1998. Role of multiple-level tropospheric circulations in forcing ENSO winter precipitation anomalies. Mon. Weather Rev. 126:3102–3116. Article

Stoner, A. W.
1983. Pelagic *Sargassum*: evidence for a major decrease in biomass. Deep-Sea Res. Oceanogr., A 30:469–474. Article

Sturges, W., and R. Leben
2000. Frequency of ring separations from the Loop Current in the Gulf of Mexico: a revised estimate. J. Phys. Oceanogr. 30:1814–1819. Article

Sultan, B., and S. Janicot.
2000. Abrupt shift of the ITCZ over West Africa and intraseasonal variability. Geophys. Res. Lett. 27:3353–3356. Article

Sutton R. T., and D. L. R. Hodson.
2005. Atlantic Ocean forcing of North American and European summer climate. Science 309:115–118. Article

Taylor, M. A., D. B. Enfield, and A. A. Chen.
2002. Influence of the tropical Atlantic versus the tropical Pacific on Caribbean rainfall. J. Geophys. Res. 107(C9):3127. Article

Uvo, C. B., C. A. Repelli, S. E. Zebiak, and Y. Kushnir.
1998. The relationships between tropical Pacific and Atlantic SST and northeast Brazil monthly precipitation. J. Clim. 11:551–562. Article

Vimont, D. J., and J. P. Kossin.
2007. The Atlantic Meridional Mode and hurricane activity. Geophys. Res. Lett. 34:L07709. Article

Vink, A., A. Brune, C. Höll, K. A. F. Zonneveld, and H. Willems.
2002. On the response of calcareous dinoflagellates to oligotrophy and stratification of the upper water column in the equatorial Atlantic Ocean. Palaeogeogr. Palaeoclim. Palaeoecol. 178:53–66. Article

Vitart, F., and J. L. Anderson.
2001. Sensitivity of Atlantic tropical storm frequency to ENSO and interdecadal variability of SSTs in an ensemble of AGCM integrations. J. Clim. 14:533–545. Article

Vukovich, F. M.
2012. Changes in the Loop Current's eddy shedding in the period 2001–2010. Int. J. Oceanogr. vol. 2012, article ID 439042, 18 p. Article

Walker, G. T.
1924. Correlation in seasonal variations of weather, IX. A further study of world weather. Mem. India Meteorol. Dep. 24:275–332.

Wang, H., and R. Fu.
2000. Influence of ENSO SST anomalies and water storm-tracks on the interannual variability of the upper-tropospheric water vapor over the Northern Hemisphere extratropics. J. Clim. 13:59–73. Article

Wang, C., D. B. Enfield, S. K. Lee, and C. W. Landsea.
2006. Influences of the Atlantic warm pool on Western Hemisphere summer rainfall and Atlantic hurricanes. J. Clim. 19:3011–3028. Article

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

Wiseman, W. J., Jr., and S. P. Dinnel.
1988. Shelf currents near the mouth of the Mississippi River. J. Phys. Oceanogr. 18:1287–1291. Article

Wyrtki, K.
1975. Fluctuations of the dynamic topography in the Pacific Ocean. J. Phys. Oceanogr. 5:450–459. Article

Zhong, Y., A. Bracco, and T. A. Villareal.
2012. Pattern formation at the ocean surface: *Sargassum* distribution and the role of the eddy field. Limnol. Oceanogr. 2:12–27. Article