Characterizing a Sea Turtle Developmental Habitat Using Landsat Observations of Surface-Pelagic Drift Communities in the Eastern Gulf of Mexico

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***Abstract*—Compared with our understanding of most aspects of sea turtle biology, knowledge of the surface-pelagic juvenile life stages remains limited. Young North Atlantic cheloniids (hard-shelled sea turtles) are closely associated with surface-pelagic drift communities (SPDCs), which are dominated by macroalgae of the genus *Sargassum*. We quantified SPDCs in the eastern Gulf of Mexico, a region that hosts four species of cheloniids during their surface-pelagic juvenile stage. Landsat satellite imagery was used to identify and measure the areal coverage of SPDCs in the eastern Gulf during 2003–2011 (1323 images). Although the SPDC coverage varied annually, seasonally, and spatially, SPDCs were present year-round, with an estimated mean area of SPDC in each Landsat image of 4.9 km^2 (SD = 10.1). The area of SPDCs observed was inversely proportional to sea-surface wind velocity (Spearman's $r = -0.33$, $p < 0.001$). The SPDC coverage was greatest during 2005, 2009, and 2011 and least during 2004 and 2010, but the 2010 analysis was affected by the Deepwater Horizon oil spill, which occurred within the study region. In the eastern Gulf, the area of SPDC peaked during June–August of each year. Although the SPDC coverage appeared lower in the eastern Gulf than in other regions of the Gulf and the North Atlantic, surface-pelagic juvenile green, hawksbill, Kemp's ridley, and loggerhead turtles were found to be using this habitat, suggesting that eastern Gulf SPDCs provide developmental habitats that are critical to the recovery of four sea turtle species.**

***Index Terms*—Critical habitat, developmental habitat, Landsat, remote sensing, *Sargassum*, sea turtle.**

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I. Introduction

MARINE ecosystem conservation efforts must often consider dynamic habitats and the varying patterns of occurrence of associated organisms. Many marine species are wide ranging and exhibit complex life-history strategies. As a result, uncertainty regarding their distribution and abundance further challenges conservation efforts [1], [2]. Life histories with juvenile dispersal stages or lengthy migrations are common in marine fauna. Although wide ranging, many highly migratory species spend a majority of the time associated with discrete habitats on which conservation efforts could focus [3]. Sea turtles are no exception; they transition between a variety of marine habitats during different life-history stages [4].

A. Sea Turtle Life History and the "Lost Year"

Sea turtles are long-lived and wide-ranging marine vertebrates. Most sea turtle species have an early developmental phase that takes place within ocean surface waters and in which surface currents may carry early juveniles far from their beach of origin [5]. This early, oceanic developmental stage has proved difficult to access for study and so remains one of the lesser understood aspects of sea turtle biology. Carr *et al.* [4] termed this stage the "lost year", highlighting both the uncertainty and the importance of this part of sea turtle life history. After Carr's [6] surveys of Caribbean *Sargassum* rafts, no direct research on the topic of sea turtles and *Sargassum* was done until Witherington's [7] transect surveys of the habitats of posthatchling loggerheads (*Caretta caretta*) offshore of the eastern Florida loggerhead rookeries. Recently, Witherington *et al.* [8] expanded survey efforts to include eastern Gulf of Mexico waters and discovered juvenile green (*Chelonia mydas*), loggerhead, hawksbill (*Eretmochelys imbricata*), and Kemp's ridley (*Lepidochelys kempii*) turtles in close association with *Sargassum* habitats. Witherington *et al.*'s [8] term "surface-pelagic" is used here to describe the focal habitat of surface-pelagic drift communities (SPDCs) and the early developmental stages of the sea turtles associated with them (surface-pelagic posthatchlings and juveniles).

B. Sargassum-Dominated SPDCs

Sargassum adrift in ocean surface waters forms distinct lines or patches of habitat that constitute unique ecological communities [9]. In SPDCs, *Sargassum* is considered a keystone taxon due to its ecological role [10]. Two holopelagic species of *Sargassum*, *S. natans* and *S. fluitans*, dominate SPDCs in the North Atlantic Ocean; the former is more abundant [11], [12]. Both species reproduce vegetatively through fragmentation and are well adapted for the surface-pelagic environment, having pneumatocysts for buoyancy and dense, rugose foliage [13]. *Sargassum* appears capable of sustained growth even in oligotrophic environments, such as the Sargasso Sea, at the center of the North Atlantic Gyre [14]. Growth and abundance vary seasonally, annually, and spatially [15]–[17]. Lapointe [15] demonstrated that growth of *Sargassum* was limited by nutrient availability, which has implications for its spatial patterns of occurrence (e.g., the northwestern Gulf of Mexico [10]). *Sargassum* growth is greatest in regions of high nutrient availability, and production may also be influenced by nutrient contributions from associated biota, specifically $NH_4{}^+$ from fishes [10], [15].

Physical forces also influence the spatial and temporal distribution and abundance of SPDCs. Major ocean surface currents transport SPDCs throughout the ocean basins [12]. Locally, SPDCs accumulate at the boundary of water masses, along fronts, and within Langmuir circulation cells [18]. Ocean surface winds aid in both the aggregation and disintegration of SPDCs. For example, Marmorino *et al*. [19] found that winds in excess of 5 m s^{-1} (10 knots) resulted in the disintegration of SPDCs. Within the North Atlantic, the distribution of SPDCs is influenced by the North Equatorial Drift, Caribbean Current, Gulf Stream System, and Canaries Current, which surround the Sargasso Sea [18].

A diverse assemblage of epiphytic and motile animals is associated with SPDCs [20]. Butler *et al.* [21] described the food web of SPDCs as unique, ranging from filter feeders and omnivores to carnivores and grazers. Several other authors (e.g., [13], [21], [22]) have presented detailed descriptions of the biota found within North Atlantic *Sargassum*. Several seabird species are known to be associated with *Sargassum* habitats, and patch size may help determine which species. *Sargassum* offers shelter in the marine environment, which attracts a variety of fish species and plays an important role in the life cycle of several species [22]. SPDCs appear to provide both foraging opportunities and shelter for many marine vertebrates.

Although the faunal associates of SPDCs have been well documented, the influence of the amount of SPDC on the number and diversity of associated animals varies. Butler *et al.* [21] found that associated macrofaunal abundance increased with increasing SPDC patch size, though no change in species diversity was observed. Larger seabird species (e.g., Cory's shearwater) have been found to be associated with larger habitat patches, while smaller seabirds (e.g., Phalaropes) are found to be associated with smaller patches [23]. Rooker *et al*. [24] noted that larval sailfish (*Istiophorus platypterus*) abundance increased with *Sargassum* biomass in SPDCs but that abundances of larval white marlin (*Kajikia albida*), blue marlin (*Makaira nigricans*), and swordfish (*Xiphias gladius*) decreased as *Sargassum* biomass increased. The effects of SPDC patch size on sea turtle density and occurrence are not known. Given the complex spatial and temporal dynamics of SPDCs, understanding the influences of habitat patch size on associated species is critical than understanding the effects of habitat loss on population dynamics.

C. Attempts to Quantify Pelagic Sargassum

Obtaining synoptic assessments of *Sargassum* has proved difficult due to the spatial extent of the macroalgae and the temporal variation in its occurrence. Reports on the occurrence of *Sargassum* in the Sargasso Sea exist in ships' logs dating back to Columbus (reviewed by [21]). By the late 1800s and early 1900s, several attempts had been made to quantify *Sargassum* biomass and identify the boundaries of the Sargasso Sea. Parr [11] provided the first quantitative estimates of *Sargassum* biomass based on net tows conducted in the Caribbean Sea, Gulf of Mexico, and northwestern Atlantic. He estimated that approximately 7 million tons of *Sargassum* existed in the North Atlantic; high amounts occurred in the Sargasso Sea and, secondarily, in the Gulf of Mexico. Stoner [25] revisited areas surveyed by Parr [11] and found much less *Sargassum*. Surveys of *Sargassum* that has washed ashore have been conducted in an attempt to measure trends in *Sargassum* in the Sargasso Sea ([21], [26]). The localized nature of ship- and shore-based assessments has led to conflicting conclusions regarding *Sargassum* abundance ([21], [27]).

Recent advancements in satellite remote sensing have provided opportunities for broad assessments of *Sargassum*. Gower *et al*. [16] developed the maximum chlorophyll index (MCI) to identify *Sargassum* using data collected by the medium resolution imaging spectroradiometer (MERIS) and the moderate resolution imaging spectroradiometer (MODIS). Gower and King [28] and Gower *et al*. [17] used the MCI to demonstrate that *Sargassum* was abundant during 2011 in the northwestern Gulf and the eastern Caribbean. Gower and King [28] also observed seasonal shifts in *Sargassum* abundance and developed a seasonal distribution map based on those patterns. They proposed that *Sargassum* from the northwestern Gulf becomes abundant during March and drifts eastward during late spring and early summer. It is then transported by the Loop Current and Gulf Stream into the northwestern Atlantic, arriving in the Sargasso Sea during fall or winter. Gower and King [28] also discussed recent interannual fluctuations in *Sargassum* abundance, though they reported very little *Sargassum* in the eastern Gulf, where surface-pelagic sea turtles and SPDC were observed during the same time period [8]. *Sargassum* lines in the eastern Gulf might not have been large enough to be visible in MERIS or MODIS imagery (approximately 300-m resolution). The higher resolution Landsat Thematic Mapper (TM) sensor (30-m resolution) may be more appropriate for detecting relatively small lines and patches of SPDCs in the eastern Gulf of Mexico.

Hu [29] developed the floating algae index (FAI) to detect and map various species of marine algae floating on the ocean surface. The FAI can be applied to both MODIS and Landsat imagery. The FAI captures the red-edge reflectance [i.e., enhanced reflectance in the near infrared (NIR)] exhibited by all plants by comparing the reflectance in the NIR to a linear baseline interpolated between adjacent red and shortwave-infrared wavelengths. Reflectance values within these three regions of the electromagnetic spectrum should appear low and smooth as most waters without floating vegetation strongly absorb light in all three wavelengths. Thus, spikes in the NIR relative to the baseline (i.e., elevated FAI values) can be used to describe the presence of floating vegetation. The concept has been used to map *Sargassum* in the central West Atlantic [30] and to map Ulva macroalgae in the western Yellow Sea [31] using MODIS

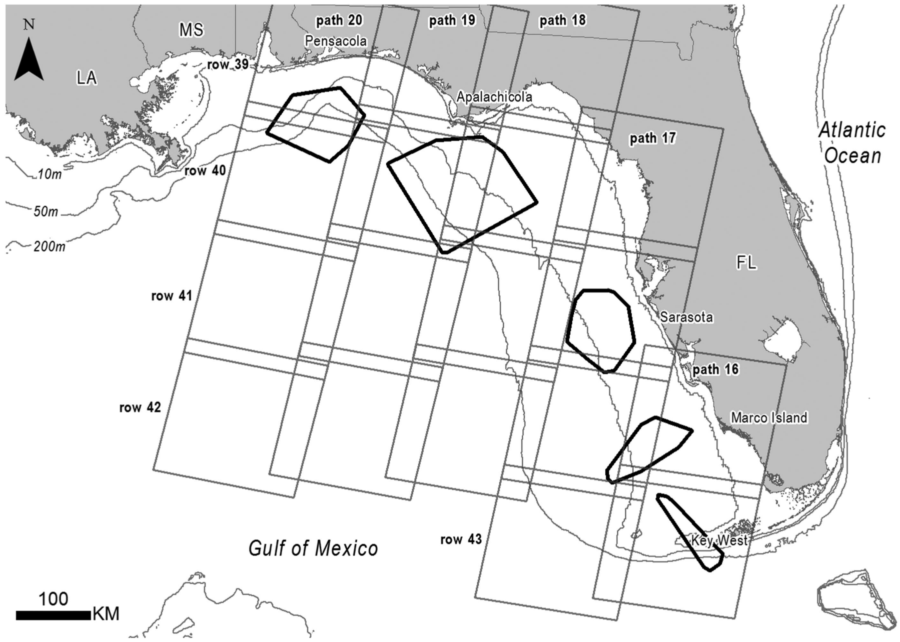

Fig. 1. The extent of Landsat 5 and 7 scenes in the eastern Gulf of Mexico, paths 16–20 and rows 39–42. Paths are labeled at the top; rows are labeled at the left side. The extents of on-water transect surveys conducted by Witherington *et al.* [8] are represented by the polygons (outlined in black).

measurements. Landsat imagery has been used to visualize *Sargassum* slicks for near-real-time warning purposes [32]. Landsat and airborne imagery were combined to examine *Sargassum* coverage in the region of the 2010 oil spill in the northern Gulf of Mexico [33]. However, no previous attempt has been made to map *Sargassum* or other floating algae using Landsat across a broad region and over several years.

D. Objectives

This study had two objectives. We first quantified the spatial extent and areal abundance of SPDC within the eastern Gulf of Mexico using higher resolution imagery (Landsat) to fill this knowledge gap. Second, we estimated the density of surface-pelagic sea turtles based on our SPDC estimates. Because *Sargassum* can be used as a remotely identifiable tracer for SPDCs, and because young sea turtles associate closely with SPDCs, this study can be considered a habitat-mapping effort [8]. The connections among *Sargassum*, SPDCs, and sea turtles are based on the following findings:

1) *Sargassum* is a dominant feature of surface-pelagic drift habitats in the Gulf of Mexico [8], [11], [12], [28].
2) The spectral signature of *Sargassum* renders it readily identifiable in Landsat imagery [29], [34].
3) *Sargassum* accumulates into large lines or mats that persist in surface waters [35].
4) Surface-pelagic life stages of four species of sea turtles are closely associated with SPDCs in the Gulf [8].

II. Methods

A. Study Area

We identified a study area within the eastern Gulf of Mexico based on the overlap of available Landsat satellite imagery and areas in which surface-pelagic juvenile sea turtles were observed by Witherington *et al*. [8] (see Fig. 1). Witherington *et al*. [8] conducted transects from five Florida Gulf ports (listed from north to south): Pensacola, Apalachicola, Sarasota, Marco Island, and Key West.

B. Surface-Pelagic Sea Turtles

Witherington *et al*. [8] provided estimates of density (turtles per km^2 of habitat) for two size classes of turtles that they found in the eastern Gulf: surface-pelagic post-hatchling and surface-pelagic juvenile. Transect studies for surface-pelagic turtles were conducted primarily during May–October. Surface-pelagic posthatchlings were found principally in the eastern Gulf during July–October. Thus, surface-pelagic turtle density estimates are multiplied by habitat areal estimates for each Landsat scene (km^2) for those two life stages. The density estimates used here are based on Witherington *et al*. [8] and have been revised with information from continuing vessel transect surveys (FWC unpublished data).

C. Remote Sensing

We identified SPDCs using two Landsat sensors, the TM and the Enhanced Thematic Mapper Plus (ETM+), which operate onboard Landsat 5 and Landsat 7, respectively. Both TM and ETM+ sensors collect reflectance data at 660, 825, and 1650 nm (bands 3, 4, and 5, respectively; Fig. 2). The spatial resolution of most Landsat spectral bands is 30 m. Landsat images were collected in scenes of fixed dimensions: 180 km (length, N-S) by 185 km (width, W-E). Landsat scenes are arranged into paths (W-E) and rows (N-S). Individual scenes are identified based on their unique path and row position, abbreviated as p##r##. Landsat satellites collect each scene at 16-day intervals; combined Landsat 5 and 7 provided imagery at 8-day temporal resolution. We used imagery from the following Landsat scenes

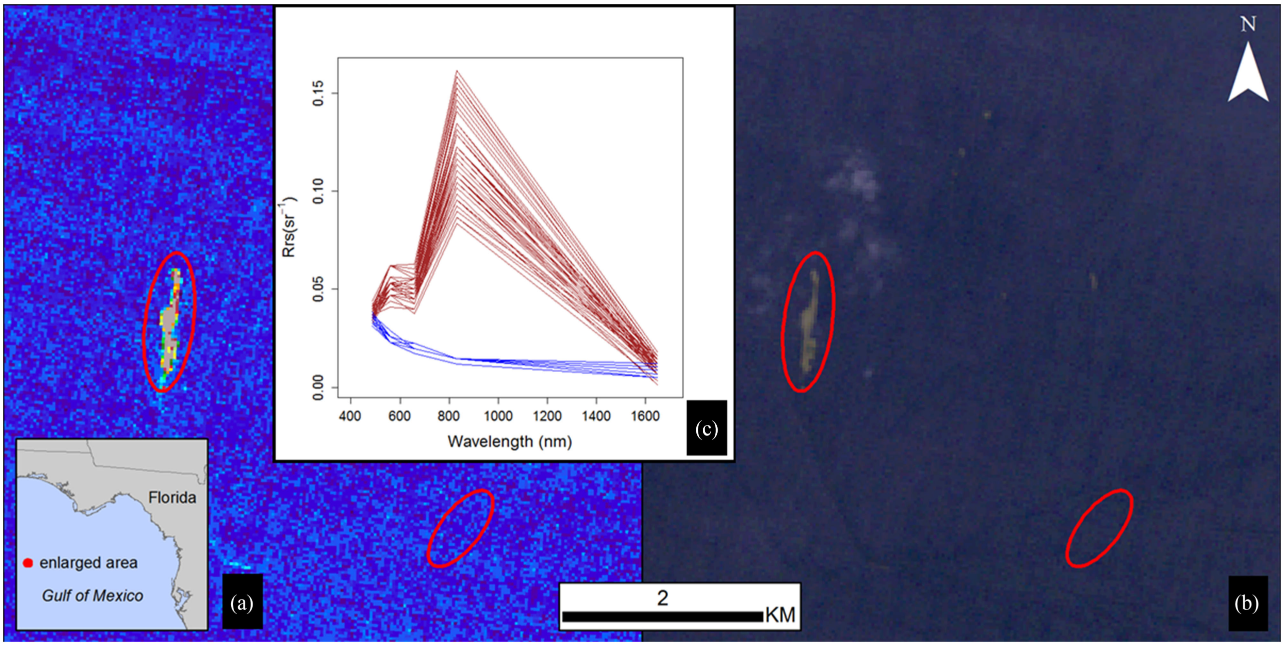

Fig. 2. Landsat 5 image of path 19 row 40 collected on August 1, 2005 over waters southwest of Apalachicola, FL, USA. The floating algae index (FAI, (a)) and true-color (b) images are shown at the same scale and extent. The images highlight a patch of *Sargassum* that was approximately 180 m wide (W-E) and 1400-m long (N-S). The inset plot (c) shows the Rayleigh-corrected remote sensing reflectance values from bands 1–5 for pixels over the *Sargassum* patch ($n = 50$, red lines) and nearby surface water pixels ($n = 50$, blue lines). The red ellipses in frames (a) and (b) identify the regions from which sample pixels representing *Sargassum* and surface water were extracted.

that covered our study area: paths 20–16 and rows 39–43 (see Fig. 1).

Using the U.S. Geological Survey's Global Visualization Viewer (http://glovis.usgs.gov/), we browsed imagery from all Landsat scenes within our study area collected from 2003 through 2011. We selected a minimum of 1 image per month and scene for analysis. Imagery was collected within some offshore Gulf scenes only during the summer of 2010 to assist Deepwater Horizon oil spill response efforts. We did not use a specific percentage of cloud cover as a criterion for excluding images; instead, we browsed all available images and selected those in which large expanses of the sea surface were visible. The FAI technique can detect SPDCs through thin cloud layers. Image processing involved several steps. First, atmospheric correction (removing the effects of ozone absorption and molecular scattering) was applied to calibrated radiance data using a customized set of Interactive Data Language routines ([34]; Exelis Visual Information Solutions, Boulder, CO), resulting in the Rayleigh-corrected reflectance data $(R_{\rm rc})$ for each band. Next, we calculated the FAI using $R_{\rm rc}$ from bands 3, 4, and 5 [29]. The FAI captures the reflectance peak at band 4 (the NIR band) relative to a baseline. The FAI is defined as

$$\mathrm{FAI} = R_{\rm rc,NIR} - R'_{\rm rc,NIR} \quad (1)$$

where $R'_{\rm rc,NIR}$ is the baseline reflectance value calculated for the NIR band using a linear interpolation made from band 3 to band 5.

We simultaneously searched output FAIs and coregistered RGB images for SPDCs in ENVI software (Exelis Visual Information Solutions, Boulder, CO) to reduce the likelihood of false detection of spectrally similar features (e.g., clouds; Fig. 3). We identified SPDCs in FAI images based on physical characteristics of the habitat. SPDCs tend to be present in the open ocean as discrete lines, patches, or linear arrangements of patches. Both *Sargassum* and *Trichodesmium* spp. exhibit high reflectance values within the NIR bands, but *Sargassum* differs from *Trichodesmium* in that it lacks a reflectance peak in the green bands. The technique for distinguishing between *Sargassum* and *Trichodesmium* based on their spectral signatures was detailed by Hu *et al.* [35]. We distinguished SPDCs *Trichodesmium* by examining the spectral shape of the feature of interest using corresponding MODIS reflectance data, because that sensor has greater spectral resolution. This method was applicable when the *Trichodesmium* patch was of sufficient size to be detected in MODIS 250 m resolution imagery. Thus, smaller patches of *Trichodesmium* may have been included in estimates of SPDC. Using ENVI, we digitized SPDCs and recorded the results in a database. We converted the SPDC pixels to vectors (shapefiles) and recorded those as feature classes in an ArcGIS geodatabase (Esri, Redlands, CA). Using the vectorized SPDC observations, we calculated the density of SPDC per kilometer within 500 m cells for each Landsat scene. We then mosaiced the individual scene density images to produce a single mean density raster for the eastern Gulf study area. This raster was used to visualize regional changes in SPDC density.

We scaled the area of SPDC observed within image based on the amount of searchable water within the image as follows:

$$\text{Scaled SPDC area} = \text{observed SPDC area} * (\text{scene water area}/\text{image searchable water area})$$

where scene water area is the area of sea surface water present within the Landsat scene. This was calculated within ArcGIS by removing land from the Landsat scene footprint. Ten of the scenes analyzed in this study contained some land area and eight did not (see Fig. 1). The area of searchable waters was defined as the extent of the image with a clear view of

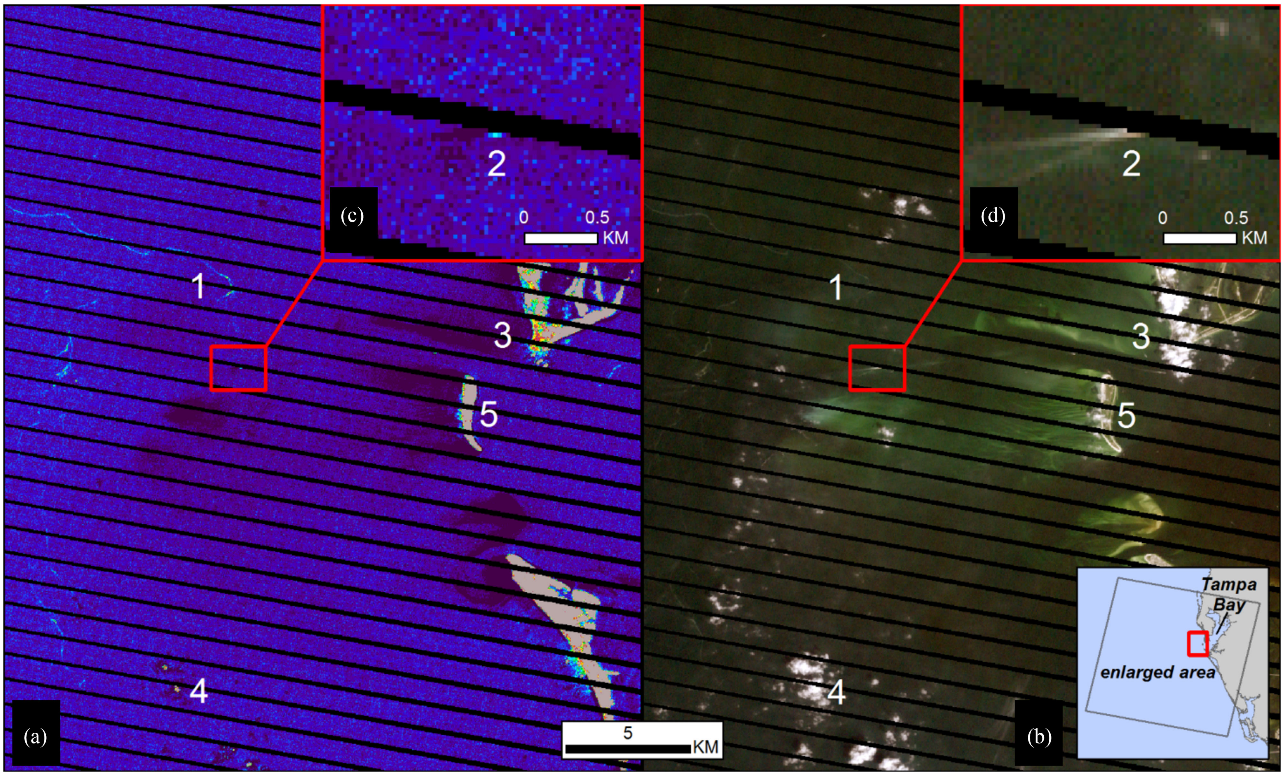

Fig. 3. Landsat 7 image of path 17 row 41 collected on September 15, 2006, showing waters in the Tampa Bay region of west-central Florida. The floating algae index (FAI, (a)) and true-color (b) images are shown at identical scales and extents. The images highlight *Sargassum* features (1) and some anomalies common in Landsat imagery. The horizontal striping has been presented in Landsat 7 imagery since 2003, the result of a failed scan-line corrector. The enlarged regions (frames (c) and (d)) show an under way vessel (2) that exhibited a high FAI response (c) and a V-shaped wake that is apparent only in the true color image (d). Clouds (3 and 4) may exhibit a relatively high ((a), 3) FAI response or appear as saturated pixels in the FAI image (A, 4). These features can easily be identified as clouds using the coregistered true-color image. Land areas appear as no data in the FAI image (5, Egmont Key, at the mouth of Tampa Bay).

surface ocean waters; that is, vessels, thick clouds, and scan line corrector failures (present only in Landsat 7 ETM+ imagery) were excluded (see Fig. 3). We calculated the searchable water area for each Landsat image using custom Python and R routines (R Core Team 2013). The image searchable water estimate was calculated for each image as it accounts for variable detectability across images. The scene water area was calculated once per scene as it removes the area of land from the total scene area.

From April to July 2010, the Deepwater Horizon oil spill, the largest in U.S. history, occurred in the northern Gulf of Mexico. More than 4 million barrels of crude oil were released from a subsurface well during 84 days from 22 April to 15 July [36]. The extensive sea surface oiling prevented full examination of some images collected in 2010. It is difficult to distinguish *Sargassum* from emulsified oil because they both show elevated reflectance values in the NIR [37]. Although only *Sargassum* shows red-edge reflectance, the elevated reflectance in the NIR by oil also results in positive FAI values, making them appear similar in FAI imagery. Therefore, we excluded oiled areas from this analysis. We used the daily MODIS oiling footprint provided by Hu *et al*. [38] to identify oiled areas within Landsat scenes.

Sargassum lines may disintegrate during periods of high sea-surface wind velocity [19]. Thus, wind velocity may influence our ability to detect *Sargassum*. To test this, we extracted wind velocity values for the dates and locations corresponding to each image from the global NCEP/NCAR Reanalysis 2 data set [39] using the RNCEP package for the program R ([40], R Core Team 2013). For each Landsat scene, we extracted zonal and meridional wind velocity values corresponding to image collection dates and the scene's center position. Using ArcGIS, we excluded land from the scene footprint polygons before calculating the geographic center of the scene. We converted zonal and meridional velocity values to wind velocity and direction. We examined this relationship in three ways. We simply counted the number of scenes with and without SPDC detections above and below the 5 m s^{-1} threshold noted by Marmorino *et al*. [19]. Using Spearman's rank correlation test, we examined the correlation between wind velocity and the area of SPDCs observed in each image. We also modeled the effect of wind velocity on the area of SPDC observed using a log-linked quasi-Poisson generalized linear model (GLM), implemented using R.

III. Results

A. *Summary of SPDCs in the Eastern Gulf of Mexico*

We examined 1323 Landsat images collected from 2003 through 2011 in the eastern Gulf of Mexico study area (paths 16–20 and rows 39–42). Each Landsat image covered approximately 33 300 km^2, but the amount of searchable waters varied within scenes due to cloud cover and scan line corrector failures (see Table I). We found SPDCs in 821 (62%) of the eastern Gulf images examined (see Table I). We observed an average of 4.87 km^2 of SPDC per Landsat image (range: 0.01–90.84 km^2,

TABLE I
SUMMARY OF EASTERN GULF OF MEXICO LANDSAT SCENES EXAMINED FOR THE PRESENCE OF SPDCs

Landsat scene index	SPDC observed	Total images	Area searched (x 1000 km^2, mean ± SD)	SPDC area (km^2, mean ± SD)
p16r42	76	154	20.1 ± 3.1	3.96 ± 10.99
p16r43	105	136	27.3 ± 4.4	5.91 ± 10.37
p17r40	68	97	15.3 ± 2.6	7.13 ± 14.04
p17r41	85	143	23.2 ± 2.4	3.75 ± 6.59
p17r42	58	62	33.6 ± 2.9	1.95 ± 3.79
p17r43	60	69	31.6 ± 3.3	5.80 ± 10.92
p18r39	79	96	8.4 ± 3.3	7.54 ± 11.46
p18r40	85	159	27.6 ± 4.8	5.24 ± 12.03
p18r41	4	10	26.9 ± 0.2	0.44 ± 0.19
p18r42	1	9	31.7 ± 4.5	0.29
p19r39	49	77	11.6 ± 2.2	0.93 ± 1.96
p19r40	25	45	33.1 ± 3.0	5.13 ± 6.65
p19r41	5	9	30.5 ± 6.4	0.23 ± 0.18
p19r42	5	7	32.4 ± 4.1	0.23 ± 0.14
p20r39	48	152	15.3 ± 2.7	5.12 ± 7.99
p20r40	59	79	32.6 ± 3.6	7.70 ± 14.98
p20r41	6	9	30.1 ± 4.0	1.01 ± 0.7
p20r42	3	10	28.7 ± 7.6	0.60 ± 0.56
Total (all images)	821	1323	22.6 ± 8.4	4.87 ± 10.08

The scene index is provided as a combination of path and row numbers. The number of images in which SPDCs were detected is noted. The average extent of searchable waters is provided in thousands of km^2 (mean ± SD). The scaled mean area of SPDCs is provided (km^2, mean ± SD).

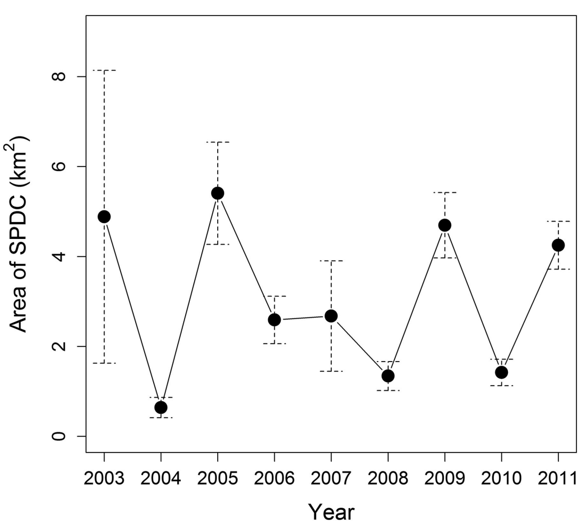

Fig. 4. Annual mean scaled area (km^2) of SPDCs observed in the eastern Gulf of Mexico, 2003–2011. Error bars represent standard errors surrounding the means.

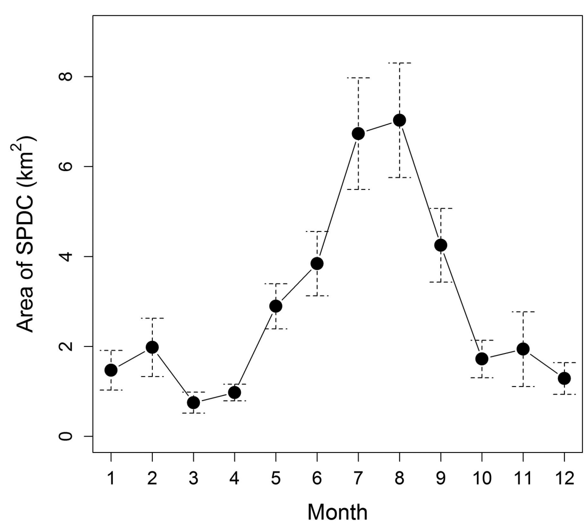

Fig. 5. Monthly mean scaled area (km^2) of SPDCs observed in the eastern Gulf of Mexico between 2003 and 2011. Error bars represent standard errors surrounding the means.

SD: 10.08 km^2). The greatest areal coverage of SPDC (average area per scene) occurred within p20r40, (approximately 150 km south of Pensacola, Florida) and p18r39 (offshore of Florida's Big Bend region). The areal coverage of SPDC was relatively low during 2004, 2008, and 2010 (0.64, 1.34, and 1.42 km^2 per scene, respectively; Fig. 4). The average area of SPDC was greatest during 2005 (5.41 km^2). SPDC estimates also exceeded 4 km^2 during 2003, 2009, and 2011. SPDC monthly areal coverage increased in May, peaked during June–August, and declined during September and October (see Fig. 5).

We examined the monthly areal coverage of SPDC in each Landsat path and observed an eastward shift in the monthly peaks of the SPDC coverage. During May of each year, SPDC abundance typically increased within the study area, During June, SPDC abundance peaked in the westernmost region of the study area (path 20, Fig. 6(a)). During July, SPDC abundance peaked in the two central regions (paths 18 and 19, Fig. 6(b), and (c)). SPDC abundance peaked during August in paths 16 and 17, in the easternmost Gulf (see Fig. 6(d)).

We evaluated SPDC area across all Landsat scenes (see Table I) and within scenes that intersected with specific regions in which transects for sea turtles had been run from 2005–2011 using a research vessel (see Fig. 7). The area of SPDCs was smallest in rows 41 and 42 of paths 19 and 20 (see Table I).

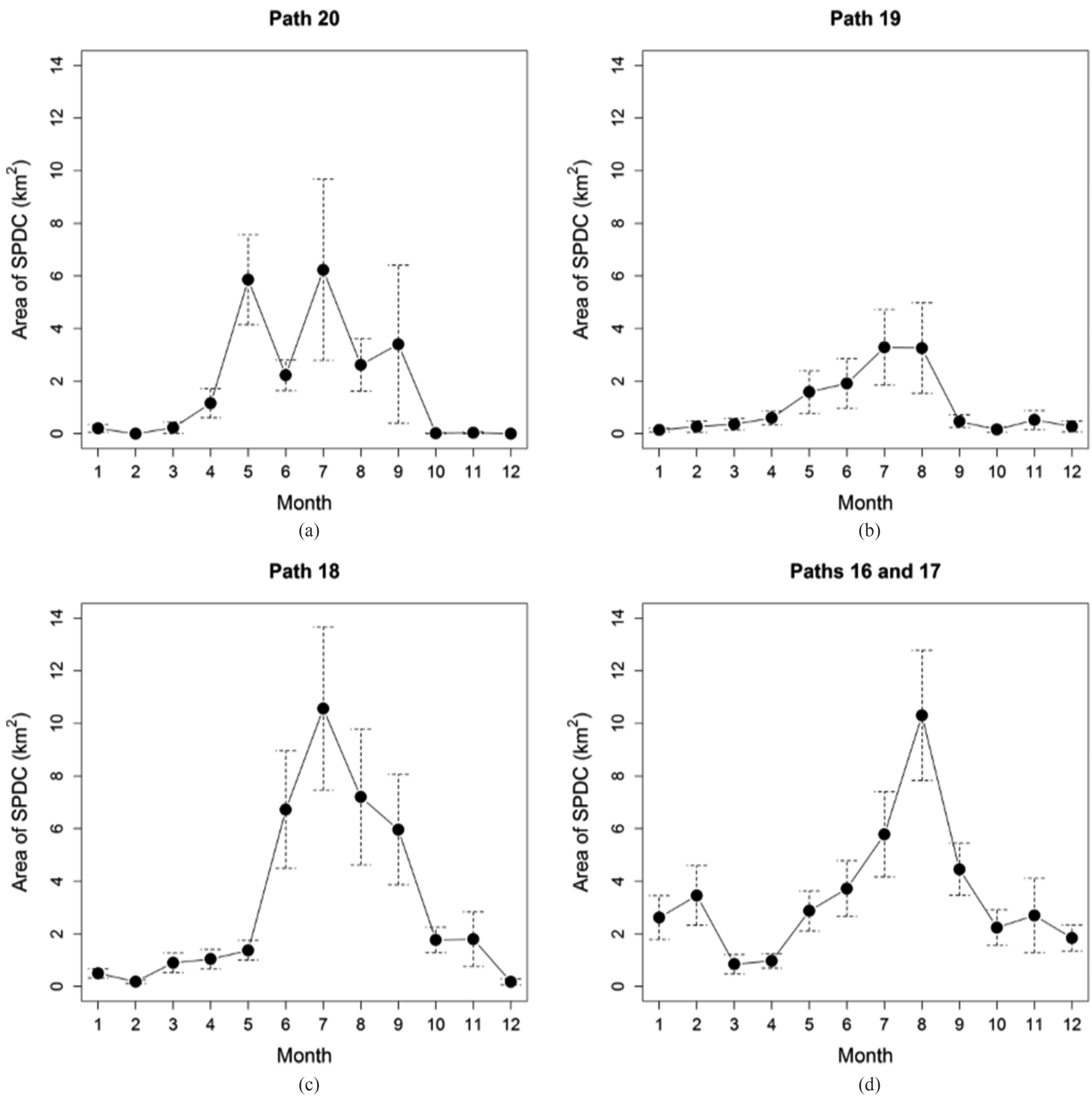

Fig. 6. Monthly mean scaled area (km^2) of SPDCs observed per Landsat path in the eastern Gulf of Mexico. Error bars represent standard errors surrounding the means. Each plot represents the mean area of SPDCs observed in selected Landsat paths. Figures are arranged with paths in decreasing order, from 20 to 16, which corresponds to their geographic order (west–east). Data from paths 16 and 17 were combined (d).

These scenes cover the central Gulf waters that are typically influenced by the Loop Current. SPDCs were distributed throughout the waters near the two northern Gulf sea turtle study areas (see Fig. 7). The Landsat scenes intersecting with the northern Gulf study areas (paths 18–20, rows 39 and 40) contained high densities of SPDC, particularly offshore (see Table I). The area of SPDCs off the central West Florida Shelf (WFS) was less than that for nearshore waters. The area of SPDCs increased on the southern portion of the WFS, north of Key West (see Fig. 7). We observed high SPDC coverage south of Key West, along the edge of the continental shelf and the Florida Current. We also observed the high SPDC coverage near the Florida coast and inshore of the 10-m isobath, within portions of Landsat scenes p17r40 and p18r39 that were outside the areas in which sea turtle transects were conducted.

B. Density of Surface-Pelagic Sea Turtles Within the Eastern Gulf of Mexico

We summarized the area of SPDCs within the two time periods corresponding to those within which densities of surface-pelagic juvenile and posthatchling sea turtles had been estimated in our vessel surveys. We estimated turtle density based on the observed area of SPDCs (see Table II). From May through October, the average area of SPDCs observed per scene ranged from 0.23 to 12.78 km^2. From our vessel-transect surveys, we estimated that the density of surface-pelagic juvenile sea turtles during this time period was 9.73 turtles km^{-2} of SPDC. Thus, the density of surface-pelagic turtles within detectable SPDC across the northern Gulf is estimated as 2.26–124.38 turtles per scene. We also calculated the area of SPDCs per

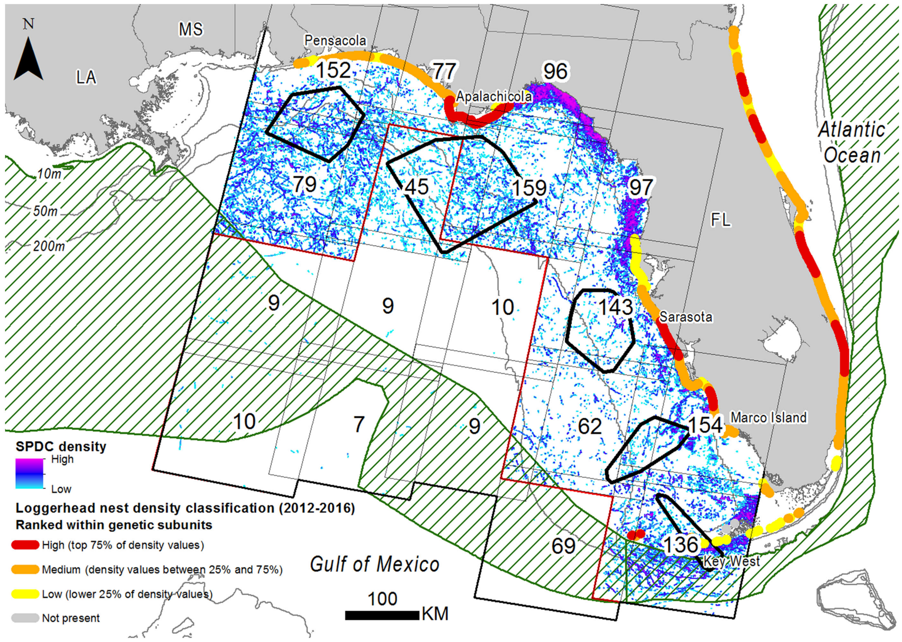

Fig. 7. Density of SPDCs observed in the eastern Gulf of Mexico, 2003–2011. The hatched polygon shows the extent of the recently designated *Sargassum* critical habitat for loggerheads [59]. The density of loggerheads nesting on Florida beaches from 2009 through 2013 is shown (Florida Fish and Wildlife Conservation Commission, Statewide Sea Turtle Nesting Beach Survey Program 2014). The black lines represent the extent of the eastern Gulf of Mexico study area. In the study area, the red line represents the northern extent of the region in which availability of Landsat data was limited. Numbered polygons represent the sample size, the number of Landsat images examined, for each scene.

Landsat scene during the hatching season, July–October, which ranged from 0.19 to 17.12 km^2 per scene. We estimated that surface-pelagic post-hatchling sea turtle density during this period was 1.98 turtles km^{-2} of SPDC. Thus, the average estimated density of surface-pelagic posthatchling sea turtles within detectable SPDCs across the eastern Gulf was 0.39–33.9 turtles per scene.

C. *Wind Velocity and SPDC Abundance*

Wind velocity was significantly greater in Landsat images in which no SPDCs were detected than in images in which SPDCs were detected ($t = 6.7$, $p < 0.01$). Mean wind velocity corresponding to images in which no SPDCs were found was 4.9 m s^{-1} (SD $= 2.5$, $n = 502$ images). Wind velocity corresponding to images in which we observed SPDCs was 3.9 m s^{-1} (SD $= 2.3$, $n = 819$ images). The greatest wind velocity associated with an image in which SPDCs were detected was 11.2 m s^{-1}. Wind velocity ranged from <1 to 13.7 m s^{-1} for scenes in which SPDCs were not detected. For all images, the area of SPDCs was inversely related to wind velocity (Spearman's $r = -0.33$, $p < 0.001$). The relationship between wind velocity and the area of SPDCs observed was nonlinear, so we included a quadratic term for wind in the GLM. We restricted this modeling step to the records in which SPDCs were observed, because the objective was to examine the effect of wind velocity on the area of SPDCs observed. In the GLM, wind velocity had a significant negative effect on the area of SPDCs observed in the Landsat image ($p < 0.001$, Fig. 8). The quadratic term for wind velocity was also significant in the GLM ($p < 0.05$).

IV. Discussion

A. *SPDC in the Eastern Gulf of Mexico*

SPDC was present within the eastern Gulf of Mexico year-round and varied in area seasonally and annually. Both the eastward shift in SPDC peaks and the late summer peaks observed across all years generally agreed with Gower and King's [28] findings, which were based on a remote-sensing examination of *Sargassum* within the Gulf. We detected SPDCs throughout eastern Gulf continental shelf waters. Much of the broad continental shelf within the eastern Gulf is typically isolated from the important deep-water Gulf circulation features (the Loop Current and associated eddies) [41], [42]. SPDCs and surface-pelagic juvenile sea turtles have been regularly encountered within this region [8]. Their presence and physical isolation suggest that SPDCs and associated juvenile sea turtles could be more persistent on the WFS than in continental-slope waters.

Compared to previous studies, the higher spatial resolution of Landsat satellite imagery (30 m) was critical to detecting SPDCs in the eastern Gulf. Gower *et al.* [16] used MERIS imagery and found no *Sargassum* in the eastern Gulf from September 2004 through November 2005 except for the months of July–September 2005. This study, however, found SPDC to be present within the eastern Gulf year-round, with July–September 2005 being a period in which SPDC area was relatively large. The disparity between the findings reported here and those of Gower *et al.* [16] is most likely due to differing spatial resolutions of the satellite imagery. Gower *et al.* [16] used 1-km MODIS and 1.2-km MERIS imagery, whereas this study used Landsat with a spatial resolution of 30 m. Landsat's spatial resolution may be insufficient for more localized studies. For example, Hu *et al.* [33] used higher resolution imagery to cor-

TABLE II
AREA OF SPDCS OBSERVED IN LANDSAT IMAGES FROM THE EASTERN GULF OF MEXICO

Landsat scene	Area of SPDC during May–October (km^2) Mean	SD	Maximum	Surface-pelagic turtles (mean SPDC area × 9.73 turtles km^{-2} SPDC)	Area of SPDC during July–October (km^2) Mean	SD	Maximum	Post-hatchling turtles (mean SPDC area × 1.98 turtles km^{-2} SPDC)
p16r42	4.16	8.25	48.86	41	4.07	9.43	48.86	8
p16r43	7.89	12.45	62.40	77	7.46	13.05	62.40	15
p17r40	12.78	18.64	90.84	124	17.12	21.56	90.84	34
p17r41	4.17	6.22	32.40	41	4.55	6.70	32.40	9
p17r42	2.51	4.75	24.33	24	3.31	5.69	24.33	7
p17r43	10.89	21.07	95.10	106	11.07	16.82	73.50	22
p18r39	10.56	12.99	55.58	103	11.74	13.31	55.58	23
p18r40	6.61	13.85	81.80	64	7.60	15.75	81.80	15
p18r41	0.44	0.19	0.57	4	0.44	0.19	0.57	1
p18r42	0.29	.	0.29	3	0.29	.	0.29	1
p19r39	1.16	2.51	12.94	11	1.25	3.04	12.94	3
p19r40	5.66	6.93	24.09	55	5.90	7.81	24.09	12
p19r41	0.23	0.18	0.45	2	0.19	0.18	0.45	<1
p19r42	0.23	0.14	0.40	2	0.22	0.25	0.40	<1
p20r39	5.91	8.43	39.13	58	6.17	9.76	39.13	12
p20r40	8.80	16.42	76.49	86	11.35	21.97	76.49	23
p20r41	1.11	0.72	2.08	11	0.85	0.67	1.63	2
p20r42	0.33	0.41	0.62	3	0.62	.	0.62	1

Landsat scenes used in this analysis are noted in the far left column. The mean, standard deviation, and maximum area (km^2) of SPDCs are provided for two time periods, May–October and July–October. These periods correspond to the months in which we estimated the density of surface-pelagic juveniles and posthatchlings in SPDC (9.73 and 1.98 turtles km^{-2} of SPDC, respectively). Those values are multiplied by mean SPDC area in the table to provide an estimated number of sea turtles present per scene, based on habitat (Rounded to the nearest whole number).

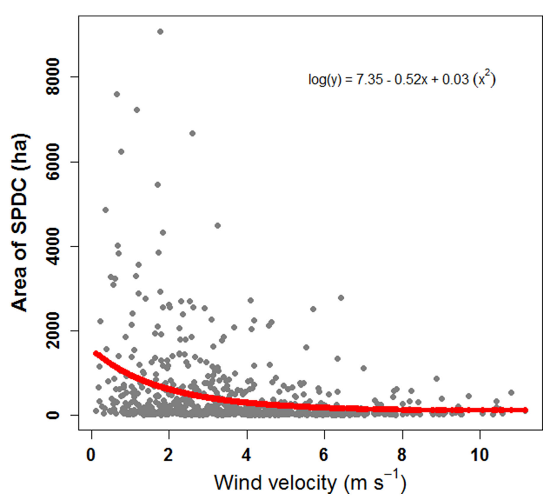

Fig. 8. Area (ha) of SPDCs observed in eastern Gulf of Mexico Landsat images and wind velocity (m s^{-1}) corresponding to the Landsat image date and time. The red line represents a quasi-Poisson GLM fit to the data describing the relationship between the amounts of SPDCs detected and corresponding wind velocity values.

rect Landsat underestimates of *Sargassum* coverage within the region affected by the Deepwater Horizon oil spill. This illustrates an important consideration surrounding spatial resolution, research objectives, and interpretation of results. Using MERIS imagery, Gower and King [28], [43] reconstructed broad-scale patterns of SPDC drift within the Gulf and North Atlantic. Performing a basin-wide analysis across multiple years would not be feasible using the higher resolution Landsat imagery and the methods outlined here. We found Landsat imagery to be appropriate for meeting the principal objective of this study, i.e., to estimate SPDC area within the eastern Gulf at a spatial scale appropriate for comparison to our *in situ* observations.

Wind velocity appears to be an important variable to consider when attempting to forecast the occurrence or predict the persistence of SPDC. Wind velocity values for images in which SPDC was not detected were significantly higher than those for images in which SPDC was detected. When wind speed was <5 m s^{-1} (ca. 10 knots), the SPDC was detected within Landsat scenes more frequently when compared with those scenes with wind velocity >5 m s^{-1}. This value is consistent with the findings of Marmorino *et al.* [19], which indicated lines of SPDC may disintegrate into smaller patches when wind speed exceeds 5 m s^{-1}. The dispersal effect of wind may reduce the likelihood of SPDC detection as patches may become too small and dispersed to be observed using satellite imagery. Wind velocity corresponding to Landsat images explained some, but not all, of the variability in the area of SPDC detected. The area of SPDC also varied spatially, seasonally, and annually.

Large areas of SPDC were detected within the eastern Gulf, inshore of the 10-m isobath, within two regions: along the coastline of Florida's Big Bend region and near the Florida Keys (p16r43, p17r40, and p18r39, Fig. 7). By comparison, most other nearshore waters had relatively low densities of SPDC, especially p19r39 (see Table I, Fig. 7). Carlson and Madley [44] noted that the seagrass beds within these two regions represented the largest contiguous habitats of this type within the continental United States. Seasonal periods of seagrass growth and senescence have been documented within these regions [44], [45]. Benthic seagrass coverage typically declines during fall and winter due to cooler waters and low tides [44]. Perhaps, the high seagrass abundance or the seasonality of seagrass senescence within these regions helps explain the high areal coverage of SPDC near to shore in these areas (see Fig. 7) and the winter peaks in SPDC area within those Landsat paths (see Fig. 6(d)). These areas are inshore of waters in which surface-pelagic sea turtles have been encountered [8]. Seagrass is often present within the surface-pelagic habitats used by sea turtles [8]. Thus, the inclusion of seagrass within our estimates of SPDC does not represent an overestimate. Shallow waters (e.g., <10 m) may not be within the normal range of surface-pelagic juveniles. Additional research is needed to determine the shallow extent of the range of surface-pelagic juvenile sea turtles.

B. Low Area of SPDCs During 2010

The area of SPDCs was relatively low during 2010, and this was likely a result of multiple factors. The Deepwater Horizon oil spill during 2010 affected our ability to identify SPDCs in portions of our study area. Specifically, portions of path 20 contained large amounts of surface oil during May–July; this is a region where we observed high *Sargassum* coverage during other years. Results of this study support previous findings that SPDCs drift eastward across the northern Gulf. Thus, an examination of imagery collected west of the oil spill before and after it occurred (i.e., paths 21–25 during March–May) would aid in interpreting the SPDC areal coverage patterns for the eastern Gulf presented here.

C. Eastern Gulf of Mexico: A Critical Developmental Habitat for Northwestern Atlantic Sea Turtles

The Caribbean Current, Loop Current, and Gulf Stream system influence the distribution of SPDCs and surface-pelagic sea turtles in the eastern Gulf. Possible source regions for SPDCs are the northwestern Gulf, eastern Caribbean, and the central-western Atlantic where large blooms of *Sargassum* have been observed [17], [26], [28], [30], [46]. The ability to detect *Sargassum* blooms at the scale of ocean basins is new, due to recent advances in satellite oceanography. This new information on the distribution of *Sargassum* has benefited studies of sea turtle biology. Based on the observed at-sea behavior of surface-pelagic sea turtles in the northwestern Atlantic (e.g., [7]), it appears that they have evolved dependence on SPDCs as early developmental habitat. Perhaps, this habitat association originates from the geographical arrangement of regions with high amounts of SPDC and sea turtle rookeries. Findings to date suggest that large aggregations of SPDC occur upstream of many important sea turtle nesting beaches. Major western boundary surface currents carry SPDCs near these beaches during hatching seasons, providing habitat to hatchlings departing those beaches.

Witherington *et al*. [8] observed four species of surface-pelagic juvenile sea turtles (green, hawksbill, Kemp's ridley, and loggerhead turtles) in SPDCs in the eastern Gulf. The important green turtle rookeries in the Caribbean upstream of the eastern Gulf are (listed in order of magnitude of nesting activity) Tortuguero, Costa Rica, the Yucatan Peninsula, Mexico, and Aves Island, Venezuela [47]. Hawksbill turtles nest throughout the Caribbean, and many rookeries may contribute surface-pelagic juveniles to the Gulf [48]. The loggerhead nesting beaches that could contribute surface-pelagic juveniles to the Gulf are found in parts of the Caribbean, western Cuba, the Yucatan Peninsula, and the Gulf itself [49], [50]. In the Gulf, loggerhead nesting density is greatest along southwestern Florida, in the Dry Tortugas, and on eastern Florida panhandle beaches [51] (FWC Statewide Nesting Beach Survey Program, unpublished data). On those Florida Gulf beaches, a mean of 7772 loggerhead nests year^{-1} was documented from 2009 through 2013 (FWC Statewide Nesting Beach Survey Program, unpublished data). Brost *et al*. [52] estimated that the mean loggerhead clutch size was 114 eggs and the mean emergence success was 51.6%. Based on these values, 457 180 loggerhead hatchlings could enter the eastern Gulf each year.

The majority of Kemp's ridley nesting occurs along the central-western Gulf shorelines of Mexico and Texas [53]. Turtles emerging from these nesting beaches likely drift eastward across the northern Gulf or encounter westward drifting eddies and remain in the western Gulf [54]. The majority of Kemp's ridley nesting occurs at the beaches near Rancho Nuevo, Mexico. More than 20 000 Kemp's ridley nests were recorded at Rancho Nuevo and adjacent beaches in 2009, a recent year with a high number of nests. NMFS, USFWS, and SEMARNAT [53] presented the following Kemp's ridley reproductive parameters based on observations at a corral (hatchery): mean clutch size $= 97$ eggs nest^{-1}, hatching success $= 67.8\%$, and emergence success $= 100\%$. Based on those 2009 values, more than 1.3 million posthatchling Kemp's ridleys might have entered western Gulf waters (nests $*$ clutch size $*$ hatching success).

Sea turtles originating from Gulf and Caribbean rookeries may be spending all or part of their surface-pelagic phase in SPDC habitat in the eastern Gulf. Research into the genetics of animals captured in the eastern Gulf, coupled with refined models of animal movements, would help identify the source rookeries of sea turtles encountered in the Gulf. Such knowledge is essential for understanding the role of Gulf SPDCs in the life history of North Atlantic sea turtles and how impacts to these habitats might affect their populations.

D. Threats to SPDCs and Conservation Efforts

The greatest threat to SPDC appears to be pollution, both from the constant influx of persistent marine debris and from significant releases of pollution, e.g., the Deepwater Horizon oil spill [7], [55], [56]. Butler *et al*. [21] found that petroleum hydrocarbons were present in *Sargassum* samples and had apparently been ingested by associated invertebrates. Witherington [7] identified plastic pollution and tar in the mouth or gut contents of posthatchling loggerheads collected in the Gulf Stream off the east coast of Florida. Other factors that could affect SPDCs include direct harvest of *Sargassum* for biomedical products, although it appears that no harvesting is under way at present in the southeastern US [57].

During 2009, the government of Bermuda formed the Sargasso Sea Alliance in an effort to improve conservation and management efforts on the high seas surrounding the Bermuda Platform [58]. In support of this effort, Laffoley *et al*. [58] outlined the economic and environmental significance of the region and its namesake, *Sargassum*. As of 2014, four nations (the Azores, Monaco, the U.K., and the U.S.) have joined Bermuda in recognizing the ecological value of *Sargassum* and the Sargasso Sea (Hamilton Declaration, March 2014). The Hamilton Declaration established a Sargasso Sea Commission that is charged with fostering collaborative conservation of the Sargasso Sea. Although the declaration is not legally binding, it is an important acknowledgement of this marine ecosystem and offers an opportunity for collaborative conservation and management.

The National Marine Fisheries Service recently identified five types of marine habitat critical to the survival of loggerheads in the northwestern Atlantic [59]. The *Sargassum* habitat occupied by early juveniles was one of these critical habitats and was defined by the following physical and biological elements:

1) convergence zones, areas of downwelling, margins of major currents, and other locations where concentrated components of the *Sargassum* community exist (including suitable water temperatures);
2) *Sargassum* in concentrations that support prey and provide cover for loggerheads;
3) the presence of *Sargassum*-associated biota; and
4) sufficient depth (10 m) and proximity to currents to ensure that loggerheads are transported out of the surf zone.

The *Sargassum* critical habitat was defined (geographically) as a static region within the U.S. Exclusive Economic Zone including western Gulf waters to the Mississippi Delta, extending southward to the Straits of Florida and north-northwest following the Gulf Stream Current. This designation effectively captures the western Gulf waters where *Sargassum* appears to be most abundant [28]. Most of the eastern Gulf of Mexico, however, is excluded from this boundary, including the areas surveyed by Witherington *et al*. [8] and those examined as part of this study (see Fig. 7). The text associated with this rule acknowledged the difficulty in identifying areas where *Sargassum* was likely to consistently accumulate, particularly within areas that are isolated from major circulation features (e.g., the Loop Current), such as the eastern Gulf [59]. Indeed, SPDC within offshore waters (>10 m) of the eastern Gulf appeared more dispersed and less abundant than that reported from western Gulf surveys. SPDC did, however, persist year-round within the eastern Gulf of Mexico waters examined herein. Considering the findings of Witherington *et al.* [8] and that loggerheads nesting within the eastern Gulf are genetically distinct [60], the proximity to the eastern Gulf loggerhead rookeries appears relevant to the delineation of critical habitat for the species.

Regulatory actions focused on dynamic marine habitats require an understanding of habitat distribution and the spatial ecology of target species. Similar to the loggerhead critical habitat, the designation of sea ice as critical habitat for polar bears (*Ursus maritimus*) established broad and fixed boundaries within which sea ice was known to occur (USFWS 2010). The USFWS was later ordered to vacate this rule, dissolving the established critical habitats, on the grounds that the designation was "too extensive" (Alaska Oil and Gas Association *et al.* versus Salazar *et al.* 2013). Considering this recent case, it was reasonable for NMFS to restrict the loggerhead-*Sargassum* critical habitat designation to waters with high concentrations of *Sargassum*.

Satellite remote sensing has provided opportunities for synoptic assessments of SPDC. Such research has demonstrated that SPDC varies significantly spatially, seasonally, and annually [28], (this study). The abundance of surface-pelagic sea turtles may also vary within the same dimensions. Conservation management processes may benefit from considering the proximity of SPDC to major sea turtle rookeries. Within U.S. Gulf waters, major loggerhead nesting beaches are situated along the northwestern and west-central Florida shorelines (FWC Statewide Nesting Beach Survey, unpublished data; Fig. 7). Witherington *et al*. [8] documented posthatchling loggerheads within eastern Gulf waters near these nesting beaches. This study identified SPDCs in the eastern Gulf year-round. Although SPDC areal coverage may be greater within the western Gulf, the eastern Gulf may serve as critical developmental habitat for loggerheads within the region. Gulf SPDC habitats also support surface-pelagic juvenile green, hawksbill, and Kemp's ridley turtles. If critical habitats are designated for surface-pelagic life stages of these species, the following parameters should be evaluated:

1) spatial distribution of nesting beaches, including nest density and nest productivity;
2) in-water aggregations identified by direct research or anecdotal accounts;
3) duration of the surface-pelagic stages and survivorship;
4) spatial distribution and seasonality of remotely detected SPDCs; and
5) physical oceanographic parameters (e.g., winds and currents) responsible for the distribution of SPDCs and surface-pelagic juvenile turtles.

This study provides a framework for addressing key information deficiencies regarding surface-pelagic juvenile sea turtles. We provide data on the seasonal cycles of SPDCs within the Gulf of Mexico. These habitat data, combined with transect survey findings, provide habitat-based estimates of sea turtle density for the eastern Gulf of Mexico. This approach assumes that surface-pelagic juvenile sea turtle density outside of SPDC is zero. Our previous work indicates that density is not zero but is indeed low, with approximately 80% of turtles being found within 1 m of SPDC [8].

Reviewing this multidisciplinary approach highlights several information deficiencies. The spatial distribution of sea turtle nesting beaches has been characterized for most regions and species, but nest productivity (a measure of the number of turtles emerging from eggs and nests) has not been well-described for many rookeries. In-water research on the surface-pelagic turtles is limited based on the cost and logistical difficulties of accessing SPDCs for direct sampling. Direct sampling is the only means of describing the density and species occurrence of surface-pelagic juveniles in SPDCs. Directed capture studies are also essential for documenting behavior, habitat associations, and genetic compositions of turtles inhabiting SPDCs. Knowledge of the duration of the surface-pelagic juvenile life stage and estimates of survivorship for each species would prove useful for estimating the impacts of known mortality factors (e.g., oil spills) on populations. Since the completion of analyses for this study, we have continued to quantify of SPDC at select regions of the northern Gulf of Mexico using imagery from Landsat 7 and Landsat 8. Remote-sensing efforts for assessing SPDCs should be expanded to other regions where surface-pelagic turtles may aggregate (e.g., the southwestern Gulf and the Sargasso Sea). Although Landsat imagery is collected at a higher resolution than the MODIS or MERIS imagery previously used to map SPDCs, Landsat-derived estimates of SPDC area may still be biased low. Additional ground truthing of remotely sensed SPDCs is necessary for addressing the potential for overestimation or underestimation of SPDC. For example, estimates from this study could be refined with a validation study that combines Landsat imagery with higher resolution imagery and field observations. Such efforts are under way for the northern Gulf but are logistically difficult due to spatial and temporal limitations of imagery and the characteristics of *Sargassum* [33]. Research combining Landsat with higher resolution imagery has proven successful in addressing underestimates [33]. Such research should be expanded to develop scaling factors that can be integrated into any remote sensing assessment of SPDC. Finally, the distribution of surface-pelagic juvenile sea turtles and their habitats cannot be understood without consideration of the physical oceanographic parameters that influence their distribution. Such research, coupled with remote-sensing observations, could be used to develop and test predictive models for the occurrence of SPDC. These methods could be used to conduct near-real-time assessments of SPDC to assist marine conservation management decisions.

V. Conclusion

The satellite remote-sensing methods used in this study proved an effective tool for assessing SPDCs in the eastern Gulf of Mexico. The higher resolution imagery used was appropriate for making comparisons with results from our vessel surveys of SPDCs. Landsat imagery can also be used for near-real-time SPDC detection every 8–16 days to aid in marine conservation management efforts. The temporal resolution of Landsat is a limitation of the method presented herein, but this can be mitigated by combining Landsat and recent Sentinel-2 MSI imagery. Our results provide evidence that high resolution imagery, when available, should be used for SPDC detection as moderate resolution sensors may not detect smaller patches of habitat that are of conservation importance. For example, within the eastern Gulf, our results demonstrate that SPDC is present year-round. The region is downstream of nesting beaches for green, hawksbill, Kemp's ridley, and loggerhead turtles. Witherington *et al.* [8] confirmed the presence of surface-pelagic juveniles of those four species in the eastern Gulf. The year-round persistence of SPDC and the presence of surface-pelagic juvenile sea turtles indicate that the eastern Gulf may serve as critical developmental habitat for surface-pelagic green, hawksbill, Kemp's ridley, and loggerhead turtles.

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