Bioscatter Characteristics Related to Inversion Variability in Atlantic Basin Tropical Cyclones

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(Manuscript received 14 May 2021, in final form 15 October 2021)

ABSTRACT: Tropical cyclones (TCs) routinely transport organisms at their centers of circulation. The TC center of circulation is also often marked by an inversion, and the height of the inversion base may change as the TC intensifies or weakens. In this study, a dataset of 49 dropsonde-measured inversions in 20 separate Atlantic Ocean TCs is compared with spatiotemporally collocated polarimetric radar measurements of bioscatter. Bioscatter signature maximum altitude is found to be a function of temperature lapse rate across the inversion base ($r = 0.473$), and higher inversion bases were generally associated with denser bioscatter signatures, especially when strong hurricanes (minimum pressure < 950 hPa) were considered ($r = 0.601$). Characteristics of the bioscatter signature had some skill in predicting TC inversion characteristics (adjusted r^2 of 16%–40%), although predictability was increased when TC intensity was also included as a predictor (adjusted r^2 of 40%–59%). These results indicate promise for using the bioscatter signature to monitor the TC inversion and represent an example of a situation in which the behavior of organisms in the airspace may be indicative of ongoing atmospheric processes.

SIGNIFICANCE STATEMENT: Tropical cyclone centers of circulation are often associated with an inversion, the base of which changes altitude with system strengthening and weakening. They may also contain a radar-observable bioscatter signature. In this study, we wanted to determine how the bioscatter signature relates to inversion characteristics for the benefit of meteorologists and biologists. Bioscatter signature characteristics were related to strength of the temperature and dewpoint lapse rates across the inversion base, and deeper/denser bioscatter signatures were typically associated with higher inversion bases. The findings suggest that trends in tropical cyclone inversion characteristics could be remotely monitored via the bioscatter signature. They also support prior speculation that some birds may seek the relatively laminar flow above an inversion base.

KEYWORDS: Inversions; Tropical cyclones; Radars/radar observations; Biosphere–atmosphere interaction

1. Introduction

Tropical cyclones (TCs) are common features of the global tropics and serve to bring excess solar energy poleward. They may be violent windstorms with well-defined and repeatable structures, and can have profound impacts on the ecology of impacted locations (e.g., Lin et al. 2020). They have climatological maxima in several ocean basins including the North Atlantic Ocean (e.g., Tippet et al. 2011; Camargo et al. 2020), and their distribution and intensity may be changing as a result of climate variability (e.g., Knutson et al. 2020). TCs may transport birds and insects long distances within their wind fields (e.g., Parry 1930; Herring 1958; Freeman 2003), and these may be evident in radar data (Van Den Broeke 2013). Given hurricane structure including a temperature inversion often apparent in the inner core of well-developed storms (e.g., Willoughby 1998), it has been hypothesized that characteristics of the biological radar signature in TCs may be

used remotely to gain knowledge of TC structure (Van Den Broeke 2013).

The inner core of a well-structured TC consists of a ring of tall thunderstorms (eyewall) surrounding a relatively calm center of circulation (eye). While the eyewall is a region of concentrated ascent, the center of circulation typically contains descent through a deep layer at mid- and upper levels, and a layer of weak ascent just above the surface. The descent is associated with adiabatic compression and warming, and thus the interface between midlevel descent and lower-level ascent is often marked by a temperature inversion. This inversion layer typically occurs between 850 and 500 hPa, and air above the inversion base is often extremely dry, with a typical dewpoint depression of 10–30 K (e.g., Willoughby 1998). Thus, moving up from the surface, the inversion base can be identified by marked drying and warming with height.

Prior studies have noted that the inversion base height changes during TC strengthening and weakening. Willoughby (1998) discusses contributors to inversion base height, including production of moist air below by frictional inflow, turbulent mixing at the ocean surface, and mixing into the eye from the eyewall convection (raising the inversion base) and entrainment of moist air by the eyewall (lowering the inversion base). Given this model, Willoughby (1998) notes that strong eyewall convection and intensification should be associated with a lowering inversion and pronounced sinking

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Earth Interactions is published jointly by the American Meteorological Society, the American Geophysical Union, and the Association of American Geographers.

DOI: 10.1175/EI-D-21-0010.1

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motion above, while weakening eyewall convection should allow net low-level inflow and therefore a rising inversion. Consistently, Franklin et al. (1988) report inversion descent of ~1500 m during a 4.7-h period when the central pressure in Hurricane Gloria (1985) fell by 10 hPa. This indicates that large changes in inversion height may happen quickly when a TC is rapidly strengthening (or, presumably, weakening). Weakening TCs are typically associated with a rising inversion and moistening of the air at low levels and generally weaker descent above the inversion layer (e.g., Kossin and Eastin 2001; Stern and Zhang 2013).

The TC centers of circulation are also associated with transport of birds and insects. Such transport has been reported many times when human observers have been present in a TC eye (e.g., General Weather Service of the United States 1882; Young 1921; Tannehill 1936) and may be observed in radar observations of hurricane centers of circulation (Van Den Broeke 2013). It has been speculated that the inversion base in a TC eye may serve as a natural limit to the maximum altitude reached by many organisms within the eye (Van Den Broeke 2013). Theoretically this may be the case since the inversion is a stable layer and acts as a cap to the upward motion occurring at lower altitudes. Organisms gaining altitude within a TC eye would experience rising motion until they reached the inversion base, at which level they would begin to experience sinking motion, so it would not seem advantageous to gain additional altitude (e.g., Forster 1955). Prior observational studies lend support to this possibility. Strong inversions have been noted as unfavorable for migrant species that prefer to soar on thermals (e.g., Shammoun-Baranes et al. 2003), although migrants in mountainous terrain may prefer to fly above the inversion where conditions are less turbulent (Williams et al. 2001) and some migrants may be relatively unaffected by the presence of an inversion (e.g., Lowery and Newman 1966). Although birds in a TC center of circulation are not there to migrate, they are forced to remain aloft for an extended period. Insects, while likely not analogous to birds, have been observed to favor stable conditions and possibly aggregate near the inversion base at night, with a steep decline in density above (Reynolds et al. 2005). Here, our initial hypothesis is that sinking motion above the inversion base will serve as a natural cap to the altitude reached by most organisms within the TC center of circulation.

This study examines whether bioscatter information derived from polarimetric weather radar observations can be related to the inversion base height within a reasonably large sample of North Atlantic TCs. Specifically, our study questions are the following: 1) How are polarimetric bioscatter signature characteristics related to the inversion base height in real time, and are changes to the bioscatter signature related to periods of TC strengthening and weakening? Answering this question may have benefit for meteorologists. 2) How do organisms behave in the vicinity of the inversion in TC cores? Answering this question may add biological understanding and may have implications for bioscatter behavior in the vicinity of other inversion types, for example, the common nocturnal inversion.

2. Data and methods

Primary datasets include dropsonde data archived by the National Hurricane Center (NHC) and spatiotemporally collocated polarimetric radar datasets from the Weather Surveillance Radar—1988 Doppler (WSR-88D) network of the United States. The NHC aircraft reconnaissance data archive (<https://www.nhc.noaa.gov/recon.php>) was searched for all dropsonde observations taken within the eye/center of circulation of a tropical cyclone at a time when a collocated or nearly collocated polarimetric radar dataset was available from the WSR-88D network. Dropsonde data were required to be taken within 45 min of a time when high-quality polarimetric observations of the bioscatter signature were available (described below); all observations except one were taken within 30 min of quality bioscatter observations. The inversion base was identified in each dropsonde observation (see Fig. 1 for examples), and inversion intensity was quantified. For this study the inversion base was defined as the first level above the surface exhibiting warming with height (Fig. 1a) and/or the first level above the surface exhibiting substantial drying with height (Figs. 1a,b). Rapid drying with height was allowed as a criterion because it indicates downward-mixed dry air rather than the upward-mixed air mass with the ocean surface as a moisture source. Variables estimated from each dropsonde observation include the following:

- 1) Inversion base height (m)—Dropsondes are typically released at a pressure of 700 hPa in TC environments. In the dropsonde data, mandatory-level observations at and below this level (700, 850, and 925 hPa) contained a direct estimate of the height (m), although observations at non-mandatory levels did not. Once pressure (hPa) of the first level above the inversion base was determined (via rising air temperature and/or substantial drying with height), if the height (m) of that level was not directly reported it was estimated using the barometric formula:

$$h = -\frac{RT}{Mg} \ln\left(\frac{p_h}{p_{sfc}}\right), \quad (1)$$

where h = the estimated height of the first level above the inversion base (m), R is the universal gas constant ($8.314 \text{ N m mol}^{-1} \text{ K}^{-1}$), T is the air temperature at the level immediately below the inversion base (K), M is the molar mass of air ($0.029 \text{ kg mol}^{-1}$), g is gravitational acceleration, p_h = pressure at the inversion base (hPa), and p_{sfc} = surface pressure (hPa). Surface pressure was the best-estimate NHC value at the time that the dropsonde was released. It is possible for the inversion base to be higher than 700 hPa, which was clearly the case for some examples in which dropsonde measurements within a well-defined TC eye did not contain an inversion (e.g., Fig. 1c). In these cases, the height of the inversion base was listed as “above 700 hPa.”

- 2) Temperature lapse rate across the inversion base (K hPa^{-1})—defined as air temperature at the first level above the inversion base top minus air temperature at the first level below the inversion base, divided by the depth of that

FIG. 1. Examples of dropsonde observations in tropical cyclone centers of circulation, plotted on skew T diagrams: (a) Hurricane Laura at 0442 UTC 27 Aug 2020, when sustained wind speed was 130 kt and minimum central pressure was 938 hPa, represents a case with an inversion base marked by a large temperature lapse rate, (b) Tropical Storm Cindy at 0513 UTC 22 Jun 2017, when sustained wind was 45 kt and minimum central pressure was 992 hPa, represents a case with a small temperature lapse rate but a large dewpoint lapse rate, and (c) Hurricane Harvey at 2203 UTC 25 Aug 2017, when sustained wind was 105 kt and minimum central pressure was 943 hPa, represents a case for which the inversion base was likely higher than 700 hPa. The red lines are the air temperature, the black lines are the dewpoint, and wind bars follow standard meteorological convention. In (a) and (b), the horizontal blue line marks the inversion base.

layer (hPa). Normalization by layer depth allows comparability between cases in which the layer depth is not the same. Values could be positive (air temperature increased with height across the inversion base) or negative (in this case the air temperature did not increase with height, but substantial and sharp drying with height

indicated a clearly different air mass than was present nearer the surface; Fig. 1b).

3) Dewpoint lapse rate across the inversion base ($K hPa^{-1}$)—defined as dewpoint at the first level above the inversion base minus dewpoint at the first level below the inversion base, divided by the depth of that layer (hPa).

Values of this variable were always negative, indicating drying with height across all observed inversion bases as is theoretically expected and is measured in prior studies (e.g., Willoughby 1998; Kossin and Eastin 2001).

Uncertainty in these variables could be substantial in some cases because of the relatively coarse horizontal sampling. This uncertainty unfortunately cannot be decreased, so the results described here must be taken with the understanding that higher-resolution sampling in the vertical would yield stronger results. In total, 49 dropsonde observations were retained for analysis over 20 unique TCs (Table 1). Three of the dropsonde observations were compared with bioscatter characteristics from two separate radars that were simultaneously sampling that TC. Note that multiple inversion observations from the same storm over several hours is not redundant since the inversion base height can change quickly (e.g., Franklin et al. 1988).

Bioscatter signatures were quantified using polarimetric WSR-88D radar data (Van Den Broeke 2013). Storms considered for analysis had their center of circulation, which was required to be well defined, come within 140 km of a polarimetric WSR-88D in the domain of an Atlantic-basin TC (base-scan beam height in this case is ~ 2.75 km above the surface given standard beam propagation). This threshold was chosen because the bioscatter signature typically becomes less defined beyond this distance, and a clear center of circulation was required to be visible since this is where the inversion is located. Table 1 includes the radar site used to represent each dropsonde observation.

Quantification of the bioscatter signature associated with the TC center of circulation was accomplished with the MATLAB software (version 9.10.0.1602886) following, for example, Van Den Broeke (2013) and Van Den Broeke and Gunkel (2021). Only bioscatter associated with the center of circulation was selected to facilitate comparison with inversion characteristics. To be classified as bioscatter, a voxel had to be associated with reflectivity factor $Z_{HH} > -10$ dBZ and cross-correlation coefficient (CC) < 0.80 . Once these requirements were applied, a manual check was applied to ensure that differential reflectivity Z_{DR} was generally > 2 dB in the same region. This check was manual because of the large Z_{DR} variance inherent to areas with low CC. Once the area of bioscatter had been identified, several characteristics were calculated:

- 1) Area of the bioscatter signature (km^2)—taken from a 500-m constant-altitude plan position indicator (CAPPI). A 500-m CAPPI was used as another means of removing ground clutter, which may have led to an overestimate of the bioscatter signature area. Thus, the lowest-altitude data considered was 500 m above the surface, although base-scan data may be much higher at large distance from the radar.
- 2) Density of the bioscatter signature ($\text{cm}^2 \text{ km}^{-3}$)—also from the 500-m CAPPI, which is total radar cross section within the bioscatter signature (cm^2) divided by total volume of the bioscatter voxels (km^3), as described by Van Den Broeke and Gunkel (2021).

TABLE 1. The 49 dropsonde observations retained for analysis. The corresponding radar used to quantify the bioscatter signature is also indicated for each dropsonde.

Date	Dropsonde time (UTC)	TC	Corresponding radar
29 Oct 2012	2308	Sandy	KDIX
29 Oct 2012	2335	Sandy	KDIX
4 Jul 2014	0008	Arthur	KMHX
4 Jul 2014	0142	Arthur	KMHX
10 May 2015	0257	Ana	KLTX
28 Aug 2015	0137	Erika	TJUA
28 Aug 2015	0308	Erika	TJUA
7 Oct 2016	0626	Matthew	KMLB
8 Oct 2016	0743	Matthew	KCLX
8 Oct 2016	0946	Matthew	KCLX
8 Oct 2016	1825	Matthew	KLTX
22 Jun 2017	0513	Cindy	KLCH
25 Aug 2017	2122	Harvey	KCRP
25 Aug 2017	2203	Harvey	KCRP
25 Aug 2017	2301	Harvey	KCRP
25 Aug 2017	2326	Harvey	KCRP
26 Aug 2017	0307	Harvey	KCRP
6 Sep 2017	2017	Irma	TJUA
7 Sep 2017	0000	Irma	TJUA
10 Sep 2017	0725	Irma	KBYX
10 Sep 2017	1203	Irma	KBYX
20 Sep 2017	0711	Maria	TJUA
8 Oct 2017	0339	Nate	KMOB
8 Oct 2017	0422	Nate	KMOB
8 Oct 2017	0459	Nate	KMOB
28 May 2018	1651	Alberto	KEVX
14 Sep 2018	0553	Florence	KMHX
14 Sep 2018	0700	Florence	KMHX
14 Sep 2018	0803	Florence	KMHX
14 Sep 2018	0859	Florence	KMHX
14 Sep 2018	0934	Florence	KMHX
14 Sep 2018	1034	Florence	KMHX
5 Sep 2018	0219	Gordon	KMOB
6 Sep 2019	0212	Dorian	KLTX
6 Sep 2019	0450	Dorian	KLTX
25 Jul 2020	1910	Hanna	KCRP, KBRO
25 Jul 2020	2002	Hanna	KCRP, KBRO
2 Aug 2020	0822	Isaias	KAMX
2 Aug 2020	1820	Isaias	KMLB
27 Aug 2020	0345	Laura	KLCH
27 Aug 2020	0412	Laura	KLCH
27 Aug 2020	0442	Laura	KLCH
27 Aug 2020	0547	Laura	KLCH
16 Sep 2020	0809	Sally	KMOB
16 Sep 2020	0845	Sally	KMOB
16 Sep 2020	0923	Sally	KMOB
22 Sep 2020	0034	Beta	KCRP
9 Nov 2020	0226	Eta	KAMX
9 Nov 2020	0505	Eta	KAMX, KBYX

- 3) Maximum altitude (km) to which the bioscatter signature is visible in a given volume.

Error in this method is likely small since the Z_{DR} check removes ground clutter (e.g., Park et al. 2009) and light rain that may occur along the edges of the eyewall. Manual

FIG. 2. The TC minimum central pressure (hPa) vs (a) temperature lapse rate across the inversion base (K hPa^{-1}) and (b) dewpoint lapse rate across the inversion base (K hPa^{-1}). In (a), the vertical black line separates features with increasing temperature with height (positive values, to the right of the vertical line) from features in which drying with height was observed but no temperature increase (negative values, to the left of the vertical line).

inspection of each dataset indicated that clutter and rain were not contributing substantially to any of the cases.

To develop representative estimates of these bioscatter characteristics at a time when a dropsonde measured an inversion, all values of a particular bioscatter characteristic (e.g., maximum altitude of the bioscatter signature) were averaged in the 1.5-h window surrounding the dropsonde measurement (45 min on either side of the dropsonde measurement). To have a more precise estimate of bioscatter properties associated with the inversion (though more error-prone because of the smaller number of observations being averaged), this procedure was repeated with a 30-min window (15 min on either side) surrounding the dropsonde measurement. Bioscatter characteristics were then compared with the collocated inversion measurements.

3. Results

Here the inversion characteristics are related to TC intensity and intensity change, and to the characteristics of the bioscatter signature associated with the TC center of circulation.

a. Associations between inversion characteristics and TC intensity

Magnitude of the temperature and dewpoint lapse rates across the inversion base were associated with strength of the corresponding TC (Fig. 2). Stronger warming with height (a steeper temperature lapse rate) was found in more intense TCs, using minimum central pressure as a measure of intensity (Fig. 2a). Pearson's correlation coefficient between the temperature lapse rate across the inversion base and minimum central pressure was -0.337 (significance level $p = 0.048$) when all storms are considered. Storms with no air temperature increase but a marked dewpoint decrease with height (to the left of the vertical line in Fig. 2b) were typically weaker; none of these storms had a minimum central pressure < 945 hPa, and their average minimum pressure was

977 hPa. In contrast, storms with warming with height across the inversion base had an average minimum pressure of 960 hPa. Dewpoint lapse rate also showed a weak association with storm intensity (Pearson's correlation coefficient $r = -0.306$, with $p = 0.074$; Fig. 2b). Most storms exhibiting strong drying with height had relatively high central pressure. The associations described here between inversion characteristics and minimum central pressure are not as strong when maximum sustained wind speed replaces minimum central pressure as a measure of TC intensity (not shown). Inversion base height was not predicted by TC intensity, whether by minimum pressure ($r = -0.004$, with $p = 0.981$) or maximum wind speed ($r = 0.018$, with $p = 0.914$).

TC strengthening is expected to be associated with a lowering inversion base and weakening with a rising inversion base (e.g., Franklin et al. 1988; Willoughby 1998; Stern and Zhang 2013). Few opportunities to test this were present in our dataset since it was limited to storms near enough to the coast to be well sampled by the WSR-88D network. Hurricane Sandy (2012) was sampled during weakening—from 2308 to 2335 UTC 29 October its minimum central pressure increased by 2 hPa and maximum sustained wind speed decreased by 5 kt ($1 \text{ kt} \approx 0.51 \text{ m s}^{-1}$). During this time, its inversion base also rose by 13 m—although this is a small change, the sign of the change was consistent with theory. Hurricane Matthew (2016) underwent substantial weakening from 0743 to 0946 UTC 8 October, with a pressure rise of 4 hPa and no change in sustained wind speed. During this time its inversion base rose by 178 m, consistent with theory. Hurricane Harvey (2017) was sampled across an intensification period on 25–26 August. Four soundings from 2122 to 2326 UTC indicated an inversion base above 700 hPa, and the next sounding at 0307 UTC indicated an inversion base height of 2040 m. This is likely ~ 1000 m lower than prior, consistent with the 6-hPa pressure fall and 10-kt wind speed increase observed during this time. Two storms in 2020 exhibited weak minimum central pressure fluctuations (2 hPa or less) with no

TABLE 2. Pearson's correlation coefficients between TC inversion characteristics and characteristics of the polarimetric bioscatter signature. The TC categories include All (all storms examined) and <980 or <950 (all storms with minimum central pressure of less than 980 or 950 hPa, respectively). The TC variables include inversion base height (Hght; m) and cross-inversion base temperature (Temp; K hPa⁻¹) and dewpoint (Td; K hPa⁻¹) lapse rates. Bioscatter variables include maximum signature altitude (Alt; km), signature area (Area; km²), and signature density (Den; cm² km⁻³), calculated with 90- and 30-min averaging windows (indicated as 90 or 30 at the end of the bioscatter variable name). Italicized values have a magnitude of greater than 0.4, indicating a moderate correlation.

		Alt90	Alt30	Area90	Area30	Den90	Den30
All	Hght	-0.201	-0.256	0.174	0.106	0.281	0.351
	Temp	<i>0.473</i>	<i>0.449</i>	0.131	0.042	-0.188	-0.033
	Td	0.074	0.162	0.204	0.223	-0.205	-0.224
<980	Hght	-0.215	-0.170	0.188	0.143	0.295	0.314
	Temp	<i>0.453</i>	<i>0.430</i>	-0.010	-0.017	-0.138	-0.039
	Td	<i>-0.440</i>	-0.369	0.014	0.051	-0.127	-0.193
<950	Hght	-0.103	-0.106	-0.216	-0.372	<i>0.601</i>	<i>0.575</i>
	Temp	0.359	0.316	<i>0.424</i>	0.277	0.088	0.136
	Td	-0.386	-0.223	-0.349	-0.272	0.063	0.193

corresponding change in maximum wind speed; neither of these storms (Laura in August and Eta in November) exhibited an inversion base height change consistent with the observed minimum pressure change.

b. Associations between inversion characteristics and the polarimetric bioscatter signature

First, height of the bioscatter signature was compared with inversion characteristics (Table 2; Figs. 3a,b). Of all the bioscatter characteristics examined (height, area, and density), maximum height showed the closest associations with inversion characteristics. Bioscatter height was generally not associated with inversion base height, but rather with the temperature lapse rate across the inversion base (Table 2). This association held when all storms were included and when only the stronger storms in the dataset were included (Table 3), although it was marginally strongest for all storms ($r = 0.473$, with $p = 0.004$; Fig. 3a). It was relatively unaffected by the use of a 90-min versus 30-min bioscatter height averaging window. Height of the bioscatter signature was also associated with the dewpoint lapse rate across the inversion base for relatively intense storms (<980 hPa central pressure; Table 2). Among all storms with pressure <980 hPa, larger cross-inversion base dewpoint lapse rates were generally associated with bioscatter signatures extending to greater heights (Fig. 3b; $r = -0.440$, with $p = 0.025$).

Bioscatter signature area was not clearly related to most inversion characteristics (Table 2). The strongest association was between bioscatter area and the cross-inversion temperature (Fig. 3c) and dewpoint lapse rates when the most intense TCs (central pressure < 950 hPa) were considered. A 90-min averaging window for bioscatter area yielded the strongest association with air temperature lapse rate (Fig. 3c; $r = 0.424$,

with $p = 0.194$), though the robustness of this result is unclear because of the small sample size ($n = 11$).

Bioscatter signature density was moderately correlated to inversion base height, especially when a 30-min averaging window was used (Table 2). This association became stronger for intense (central pressure < 950 hPa) TCs (Fig. 3d; $r = 0.601$, with $p = 0.051$). Although the number of points for intense TCs was small, consistency across all storms (Table 2) indicates that inversion base height is likely to be predictive of density of the bioscatter signature in TC centers of circulation. Temperature and dewpoint lapse rates across the inversion base did not appear to be related to bioscatter density for any subset of TCs examined (Table 2).

We also briefly investigated whether the TCs with inversion height base recorded as “likely above 700 hPa” ($n = 14$) were associated with particular bioscatter signature characteristics. Bioscatter signature height averaged 2.21 km in cases with lower inversion bases and 2.81 km in cases with an inversion base likely above 700 hPa (Wilcoxon–Mann–Whitney p value = 0.144). Although not statistically significant, this result was consistent with the hypothesis that a higher inversion base should be associated with bioscatter to higher altitude. Area of the bioscatter signature averaged 482.3 km² for low-inversion TCs and 468.9 km² for high-inversion TCs ($p = 0.829$), indicating that bioscatter signature area is not a function of TC inversion characteristics. Bioscatter signature density was statistically different between low- and high-inversion TCs ($p = 0.003$), with a mean value of 3331.6 cm² km⁻³ for high-inversion TCs and 1400.8 cm² km⁻³ for low-inversion TCs. This indicates that TCs with high-inversion bases may be associated with denser bioscatter signatures.

c. Predictability of inversion characteristics

A goal of the study was to assess whether TC inversion characteristics are predictable using the polarimetric bioscatter signature. Once associations were examined between the bioscatter signature and measured inversion characteristics in TC centers of circulation (prior section), an attempt was made to test the limit of predictability for the dropsonde-measured inversion characteristics (base height, air temperature/dewpoint lapse rates across the inversion base). Note that this is a small dataset and thus high adjusted r -squared values were not generally anticipated; the focus here is on assessing potential value of bioscatter observations to predict inversion characteristics rather than on developing a precise model to accomplish this prediction. Predictability was tested using 1) only radar-derived bioscatter characteristics (e.g., as if only remotely sensed bioscatter data were available) and 2) bioscatter characteristics plus TC minimum pressure and maximum sustained wind speed (e.g., if estimates of TC intensity are available along with remotely sensed bioscatter data). These predictor variables served as input to a stepwise linear regression process that was run with several levels of complexity: 1) linear terms only for each predictor; 2) linear terms plus interaction terms between predictors; 3) linear and squared terms for each predictor; and 4) linear, squared, and interaction terms (MathWorks 2021a). Table 3 reports the

FIG. 3. Bioscatter signature characteristics in comparison with TC inversion characteristics: (a) maximum height of the bioscatter signature (km) vs temperature lapse rate across the inversion base (K hPa^{-1}), (b) maximum height of the bioscatter signature (km) vs dewpoint lapse rate across the inversion base (K hPa^{-1}), (c) area of the bioscatter signature (km^2) vs temperature lapse rate across the inversion base (K hPa^{-1}), and (d) density of the bioscatter signature ($\text{cm}^2 \text{ km}^{-3}$) vs height of the inversion base (km). The r values are Pearson's correlation for each scatterplot. The populations that are plotted are indicated in each panel (all storms or storms with minimum central pressures of less than 980 or 950 hPa).

maximum adjusted r -squared values achieved for predictions of each inversion characteristic.

Given our current understanding of the TC life cycle, inversion base height may be the most important inversion characteristic to predict since changes are related to TC intensity

variability. When all predictors are included, regression models produce adjusted r -squared values of 0.51 for a 90-min averaging period and 0.59 for a 30-min averaging period (Table 3; an example is provided in Fig. 4). These models have explanatory power since a horizontal line does not fit

TABLE 3. Maximum predictability of dropsonde-measured inversion characteristics as a function of bioscatter and TC intensity characteristics. All models were derived using stepwise regression. Italicized values are greater than 0.4, indicating that a moderate percentage of the variance is explained.

Response variable	Predictors	Optimal model	Adjusted r squared
90-min averaging window for bioscatter predictors			
Inversion base height	All	Quadratic	<i>0.513</i>
	Bioscatter only	Linear	0.165
Inversion temperature lapse rate	All	Quadratic	<i>0.530</i>
	Bioscatter only	Quadratic	0.398
Inversion dewpoint temperature lapse rate	All	Linear	0.305
	Bioscatter only	Quadratic	0.216
30-min averaging window for bioscatter predictors			
Inversion base height	All	Quadratic	<i>0.587</i>
	Bioscatter only	Quadratic	0.362
Inversion temperature lapse rate	All	Quadratic	<i>0.574</i>
	Bioscatter only	Linear or quadratic	0.170
Inversion dewpoint temperature lapse rate	All	Quadratic	<i>0.478</i>
	Bioscatter only	Quadratic	0.394

FIG. 4. Added-variable plot (MathWorks 2021b) visualizing the regression model generated when predicting inversion base height as a function of bioscatter characteristics and TC intensity (five predictor variables). Blue points visualize observed vs model-predicted values of inversion base height, the red solid line indicates the model best fit, and dashed red lines indicate the 95% confidence interval. The model has explanatory power because a horizontal line will not fit within the 95% confidence envelope.

within the 95% confidence interval (e.g., Fig. 4). The adjusted r -squared values decline substantially when TC intensity variables are removed from the pool of predictors (to 0.17 for 90-min bioscatter characteristic averaging and 0.36 for 30-min averaging; Table 3), indicating that inversion base height is relatively strongly predicted by TC intensity and that the bioscatter signature does not carry much of the relevant information contained in the TC intensity variables. Values are substantially improved when 30-min averaging is used for the bioscatter variables (Table 3), indicating that inversion base height may change quickly enough that more updated bioscatter characteristics are needed for optimal predictability.

The cross-inversion base temperature and dewpoint lapse rates were also well predicted when all predictor variables were included (adjusted r squared = 0.53 for 90-min averaging and 0.57 for 30-min averaging; Table 3). Substantial declines in predictability of the cross-inversion base temperature lapse rate were noted when only bioscatter characteristics were used as predictors, although moderate predictability was retained with a 90-min averaging window (adjusted r squared = 0.40; Table 3).

Cross-inversion base dewpoint lapse rate may be a measure of the contrast between rising moist air and sinking dry air within the TC center of circulation. It was more poorly predicted in general than the other inversion characteristics (adjusted r squared = 0.31 for 90-min averaging and 0.48 for 30-min averaging; Table 3), though generally better predicted than other inversion characteristics using only bioscatter characteristics. There was generally less decline in predictability

when TC intensity variables were removed from the pool of predictors (adjusted r squared = 0.39 when only bioscatter characteristics are predictors; Table 3). This indicates that the cross-inversion base dewpoint lapse rate may exert a more substantial influence over bioscatter characteristics in TCs (e.g., Fig. 3b).

4. Summary and discussion

In this study, 49 datasets were examined from 20 separate Atlantic TCs for which inversion base height was directly measured by dropsonde and the center of circulation was sampled by a polarimetric WSR-88D. Using these data, associations were examined between measured TC inversion characteristics and several quantified measures of the polarimetric bioscatter signature associated with the TC center of circulation. It was shown that inversion base height can be predicted with some skill given the associated bioscatter characteristics, especially if TC intensity information is added. This study has potential benefit for the meteorological community because it offers a method to monitor inversion height remotely, and inversion height has been related to changes in TC intensity. It has value to biologists because it shows how organisms in the airspace, almost entirely birds in this case, behave in the vicinity of an inversion. This is relevant since inversion layers are common atmospheric features, for instance, occurring commonly at night when birds migrate.

The small sample size and coarse vertical sounding resolution render this study preliminary in nature. Although polarimetry was introduced to the U.S. radar network in 2011 and all radars had polarimetric capability by 2013, relatively few TCs have entered the coastal domain of the network, and even fewer have gotten close enough to a radar site for quality data to be collected at the center of circulation. Collocating these observations with a dropsonde measurement in the center of circulation further reduces the number of available cases. Although a more comprehensive study will be possible when many more datasets have been added in another decade or two, the goal of this study is to assess the potential value of the bioscatter signature to predict changes in TC inversion characteristics, and to examine behavior of the polarimetric bioscatter signature as organisms interact with inversions of known height and strength.

TC inversion characteristics varied with TC intensity. In general, intense TCs were associated with larger air temperature lapse rates (larger temperature increase with height), while weaker TCs were associated with larger dewpoint lapse rates across the inversion (more marked drying with height). Minimum central pressure showed stronger associations with inversion characteristics than maximum sustained wind. This makes sense since sustained wind speed adjusts to changes in the pressure gradient, so pressure should be a more representative measure of current TC intensity. Importantly, inversion base height was not strongly related to TC intensity. If it is hypothesized that maximum altitude of bioscatter is related to inversion base height, then, bioscatter height should be only weakly related to TC intensity (e.g., an intense TC may not be

associated with a deep bioscatter signature). Rather, temporal changes in the height of the bioscatter signature are hypothesized to be more indicative of changes in TC intensity. Observed changes in TC intensity were generally associated with measured inversion base height changes of the appropriate sign (lowering with intensification and rising with weakening; e.g., Franklin et al. 1988; Willoughby 1998).

Maximum altitude of the bioscatter signature was associated with the magnitude of the cross-inversion base temperature lapse rate among all storms and with magnitude of the cross-inversion base dewpoint lapse rate for intense (pressure < 950 hPa) TCs (Figs. 2a,b; Table 2). Stronger warming and stronger drying with height were associated with deeper bioscatter signatures. These inversion characteristics were also typically associated with more intense TCs. Dropsonde-derived inversion base height was much more weakly associated with radar-derived maximum bioscatter signature height. This indicates that sharpness of the change in airmass characteristics across the inversion base may be a stronger control on bird behavior than actual inversion base height. It is unknown why the deepest bioscatter signatures are associated with stronger warming and drying aloft. The author speculates that stronger inversions may be associated with a sharper contrast between laminar flow aloft and relatively turbulent flow closer to the ocean surface, which birds may seek to escape since more energy is required to remain airborne in a turbulent environment. This speculation is contrary to the initial hypothesis that birds will limit their flight altitude to the inversion base height since there is generally sinking motion above. We speculate that the magnitude of sinking motion above the inversion base [$O(1 \text{ cm s}^{-1})$; e.g., Malkus 1958; Gray and Shea 1973; Zhang et al. 2000] may be small enough that it is unimportant relative to the turbulent rising and sinking motion below the inversion. In this case, birds would be willing to expend additional energy to fly to higher altitude in order to save energy in a nonturbulent environment. The distribution of vertical motion within the center of circulation is likely not uniform, and this is not a factor that can be accounted for in the present study. Vertical motion is relatively uniform across many smaller centers of circulation but may vary markedly across larger TC centers of circulation with much stronger subsidence near the edge of the eye than near its center (Schubert et al. 2007). It is beyond the scope and ability of this study to determine whether the bioscatter signature might behave differently in different sectors of the TC eye as a function of local subsidence rate.

Area of the bioscatter signature was not closely associated with inversion characteristics. This was an expected result since bioscatter area should be more closely related to area of the center of circulation, which is not clearly associated with TC intensity or inversion characteristics. Further complicating a potential relationship is the broken nature of eyewall convection in many weaker storms, which may make it difficult to determine what area constitutes the center of circulation. Bioscatter density increased with inversion base height, which cannot be readily explained. It appeared to be a robust outcome, however, and was consistent with the result that bioscatter density was ~138% larger in high-inversion TCs (those

with inversion base at or above 700 hPa) than in low-inversion TCs. It is possible that birds flew at higher altitude in TCs with a high-inversion base and thus were easier to detect via radar.

Bioscatter signature characteristics and inversion base height may both change rapidly over time, introducing uncertainty in the estimates of these variables. There is also error in both the dropsonde-measured inversion base height (due to coarse vertical resolution) and the radar-derived bioscatter characteristics (due to, e.g., rain or clutter being counted as part of the bioscatter signature). Thus, length of the temporal window over which bioscatter characteristics are averaged is a trade-off. Longer averaging windows (90 min in this study) may reduce the effects of errors in the radar-derived estimates of bioscatter properties, while shorter averaging windows (30 min in this study) may be more representative of current conditions. Which averaging window is optimal may be a function of how fast the inversion characteristics are changing, which varies between storms and could not be controlled for in this study. Given the results (Table 2), neither averaging window was clearly superior, though the 90-min window often produced marginally better results.

Inversions are often more sharply defined in the cores of intense TCs, giving motivation to examine whether associations were stronger between TC inversion characteristics and the polarimetric bioscatter signature for stronger TCs (Table 2). Although there were some indications that these associations were stronger for the most intense TCs in the dataset (pressure < 950 hPa), manifest as larger values of Pearson's correlation, overall, there were few consistently stronger associations when stronger subsets of storms were examined. This may be partially due to the small sample sizes of datasets representing intense storms ($n = 37$ for pressure of less than 980 hPa; $n = 17$ for pressure of less than 950 hPa). When sufficient data have been accumulated, it would be valuable to examine these associations again, especially for the subset of more intense TCs.

This study provides an example of an application where characteristics of the bioscatter signature from radar data could be useful to meteorologists in real time, especially if no dropsonde or other remotely sensed data are available. According to the assessment of predictability of inversion characteristics described here, it is reasonable to expect to be able to predict about one-half of the variability of inversion base height and cross-inversion base temperature lapse rate if both bioscatter and TC intensity characteristics are used as predictors (e.g., Fig. 4). This is encouraging given that a relatively small training dataset was used to generate these models, and further improvement is likely given the addition of new datasets. If only bioscatter characteristics are used to inform a model, predictability typically decreases to 16%–40% (Table 3). These sometimes-sharp predictability decreases indicate that TC intensity is a key contributor to inversion characteristics. Temporal changes in predicted inversion characteristics may be more valuable as they may indicate TC intensification or weakening. Nevertheless, enough storms were examined in this study to impart confidence that the bioscatter signature has value for inversion

monitoring, especially if TC intensity data are also available. Changes in the bioscatter signature with distance from the observing radar should also be accounted for, though a process for doing this is not yet well understood.

Atmospheric inversions are very common, especially during the night and in the early morning hours after the surface has cooled overnight (e.g., Munn et al. 1970; Bradley et al. 1992; Bish et al. 2019). Most birds that fly at high altitude, especially overnight, will frequently encounter an inversion. If midlatitude bioscatter interactions with inversions are analogous to the interactions observed between bioscatter and TC inversions, it appears that the presence of an inversion may not be important. In fact, there is some evidence in the present study that birds may fly just above the inversion base, and there may be some advantage of being there because of reduced turbulence. Subsidence above a typical midlatitude radiation inversion is likely to be less than above the inversion base in a TC, so this may indicate even less reason for birds to be deterred by the presence of an inversion. When migrating, birds may gravitate to the vertical level in the atmosphere where flow assistance is maximized (e.g., Kemp et al. 2012). The low-level jet is often vertically collocated with the warmest air temperature in the inversion (Blackadar 1957), so this may be a preferred level for birds to fly at in order to minimize their energy expenditure while migrating. This situation is different from a TC center of circulation, in which birds are attempting to keep airborne and to keep out of the intense eyewall convection (or thunderstorms near the center of circulation, in the absence of an eyewall).

In this study results have been reported that may be of interest to the biological and meteorological communities. This is an example of a situation where knowledge of the behavior of airborne organisms may meaningfully inform weather applications. Since organisms are of necessity responsive to their environment including surrounding weather conditions, future research is encouraged in which the characteristics and behavior of biological scatter observed in radar data are used to develop meteorological methods.

Acknowledgments. The lead author is supported by National Science Foundation Grant 1545261 and an academic appointment at the University of Nebraska–Lincoln.

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