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Gulf Stream intrusion and deep current upwelling drive dynamic patterns of temperature and food supply within cold-water coral reefs

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Abstract

One of the most significant features of the Northwest Atlantic, the Gulf Stream influences high magnitude environmental fluctuations in deep habitats across the South Atlantic Bight. Amid this variability, the Blake Plateau harbors extensive reefs formed by cold-water corals that were previously assumed to rely on narrow ranges of temperature, currents, and particulate supply. A benthic lander collected near-bed conditions at the Richardson Reef Complex, a cold-water reef dominated by the scleractinian *Desmophyllum pertusum* at 830 m within the path of the Gulf Stream. Specific behavior of the Gulf Stream resulted in recurring environmental patterns at depth. During offshore meanders, deep stream components intruded onto the reef and caused rapid (3.74°C per hour) temperature increases up to 10.8°C (> 5°C above the site mean) and increased chlorophyll. Within 2 d of peak temperatures, intrusions were replaced by strong, turbid upwelling currents that rapidly cooled the site to temperature minima (4.13°C). While considerable environmental variability from the Gulf Stream may otherwise implicate a thermally stressful setting for corals, high-temperature events were likely mitigated by their short duration (< 37.4 h) and physical coupling with enhanced organic material. This hypothesis was supported by high-density clustering of *D. pertusum* occurrences within 50 km around the Gulf Stream's position along the South Atlantic Bight. This suggests that cold-water corals experiencing environmental variability can be sustained by relationships between food supply, temperature, and currents that vary in strength along stochastic time scales, shedding further light on the niche of cold-water corals.

Abutting the shallower, upper continental shelf at its west, the Blake Plateau comprises a broad (> 300 km wide; Fig. 1a), gently sloping shelf of intermediate depth (approximately 500–1000 m) that drops off steeply at around 76°W toward the Atlantic basin at the Blake Escarpment. High environmental variability has been recorded within benthic habitats in this region (Mienis et al. 2014), which is attributed to the activity of the Gulf Stream, a western boundary current of the Atlantic Meridional Overturning Circulation that flows poleward along the shelf. As one of the most prominent regional currents on earth, the Gulf Stream represents significant large-scale wind-driven circulation and transport, biochemical cycling, and climate function in the North Atlantic (Heiderich and Todd 2020). The Gulf Stream is a unique driver of habitat for benthic marine species due to its wave-like meanders and frontal eddies, which simultaneously induce short-term environmental fluctuations and stimulate regional primary productivity (Lee and Waddell 1983; Lee et al. 1991; Gaube and McGillicuddy 2017). At the seafloor, intrusions of deep Gulf Stream components bring swift currents and warm temperatures to benthic environments as the stream oscillates onshore and offshore (Lee and Waddell 1983; Mienis et al. 2014). Both vertical and cross-stream exchange is enhanced during meandering, resulting in significant production of fresh organic material as nutrients are supplied to phytoplankton at the surface (Gula et al. 2016; Wenegrat et al. 2020). These processes are further enhanced by upwelling within frontal eddies and eddy filaments (Atkinson 1977; Lee et al. 1991), helping to sustain the biological pump as surface-derived material is exported to depth (Lee and Nurser 2012; Pascual et al. 2015; Wenegrat et al. 2020).

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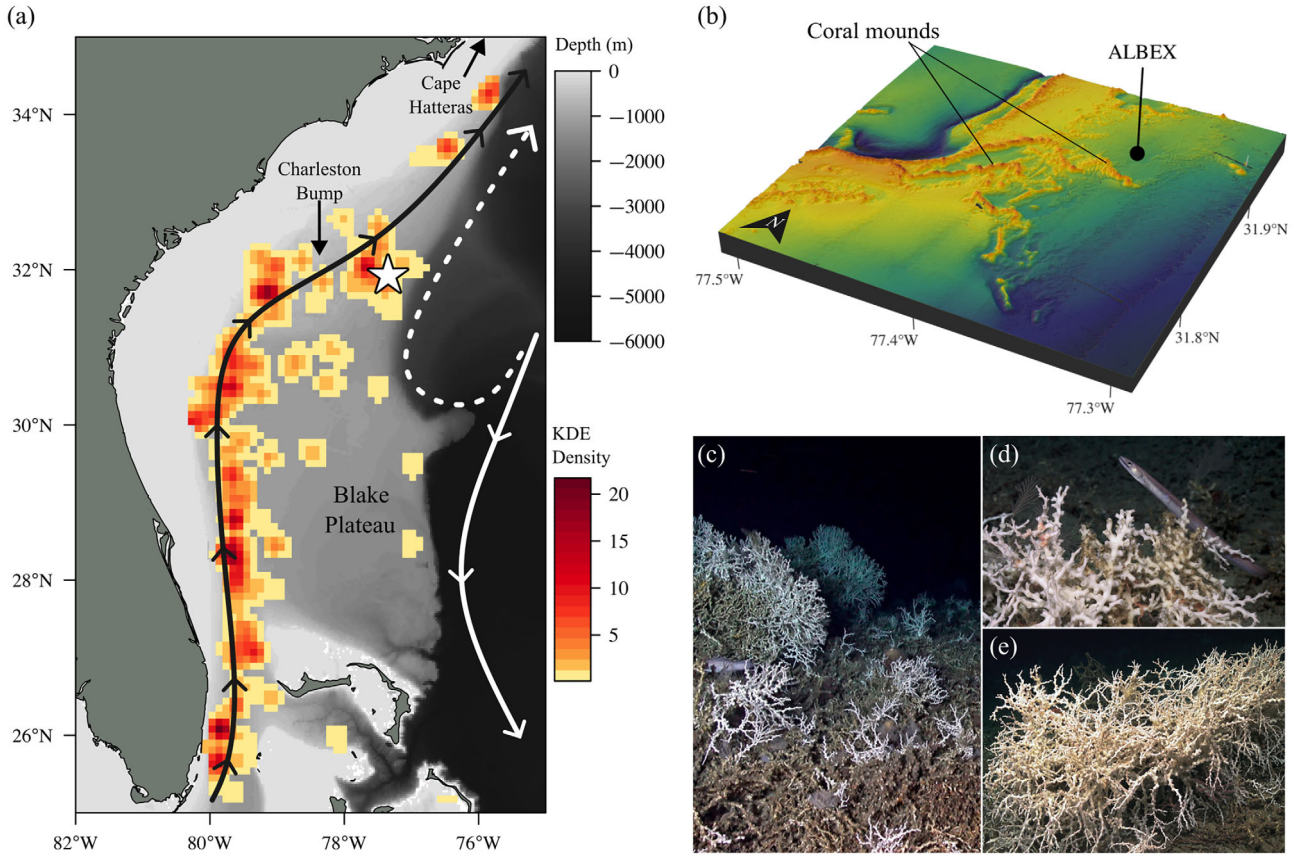

Fig. 1. *Desmophyllum pertusum* along the US shelf. (**a**) 15 arc-second bathymetry (GEBCO 2021) with kernel-density estimation (KDE) of *D. pertusum* location records (NOAA DSCRTP 2021; OBIS 2021). The white star indicates the location of the Richardson Reef Complex. The solid black line represents the 5-yr (2017–2021) mean surface path of the Gulf Stream. The solid white line shows the approximate path of the Deep Western Boundary Current, while the dashed white line shows the redirection of the upper layers of this current (approx. 1000 m depth), approximated from Chomiak et al. (2022). (**b**) Three-dimensional topography of the Richardson Reef Complex and location of the ALBEX lander. The color scale indicates depth, which has also been vertically exaggerated 2.8× for visual purposes. The areas of raised relief, shown in red/orange colors, are comprised of coral mounds and ridges. (**c**) *D. pertusum* mounds in the Richardson Reef Complex, with living coral (white) growing over dead structure. (**d**) Coral structure forms complex habitat for associated fauna, including fish and invertebrates. (**e**) Live *D. pertusum* in the bush stage of colony growth. Images (**c**–**e**) are from *Jason-2* dives at Richardson Reef Complex during the *RB1903* cruise.

Some of the most remarkable ecosystems influenced by the Gulf Stream include cold-water coral reef communities, predominantly formed by scleractinian corals such as *Desmophyllum pertusum* (formerly *Lophelia pertusa* Linnaeus, 1758). Home to various associated species including deep-sea sponges and a variety of other fauna, cold-water corals generate complex three-dimensional structures that serve as multi-functional habitat that supports rich benthic assemblages and provides essential habitat for fish species within the South Atlantic Bight (Reed et al. 2006; Buhl-Mortensen et al. 2010). To date, the distribution of cold-water corals, in particular *D. pertusum*, has been attributed to certain depths and the presence of hard-bottom features as well as broad scale environmental conditions. Geographic analyses and short-term observational or experimental studies have provided valuable descriptions of time-averaged conditions within cold-water coral reef areas, and delineated environmental ranges for *D. pertusum*, particularly with respect to temperature, salinity, dissolved oxygen content (Dodds et al. 2007; Davies et al. 2010; Davies and Guinotte 2011; Lunden et al. 2014).

At a regional scale, cold-water corals have been found in areas where surface productivity is enhanced and current speeds and food particle supplies are elevated due to topographic influences, ocean currents, internal mixing, or a combination of these processes (Mienis et al. 2007; Davies et al. 2009; Soetaert et al. 2016). However, in situ observations suggest that the environmental conditions within cold-water coral reefs are more variable than previously recognized (Hanz et al. 2019; Hebbeln et al. 2020; Gómez et al. 2022). In the Pacific, scleractinian reefs have been observed below the aragonite saturation horizon, where habitats are expected to be unsuitable for coral growth (Baco et al. 2017; Gómez et al. 2018). Observations of *D. pertusum* reefs along the southwestern African shelf have found populations existing in relatively high temperatures (regularly reaching up to 13.2°C) and

near-hypoxic dissolved oxygen concentrations (< 1 mL^{-1}) (Hanz et al. 2019; Hebbeln et al. 2020; Wienberg et al. 2023). Similar environmental conditions have been observed in *D. pertusum* reefs within the Mediterranean basin, with mean temperatures > 13°C and high salinity relative to Atlantic reefs (Freiwald et al. 2009). Yet experimental trials have shown that exposing cold-water corals to higher temperatures results in reduced metabolic function, cellular, and behavioral stress responses, reduced recovery from co-stressors, and in cases of prolonged exposure, mortality (Dodds et al. 2007; Brooke et al. 2013; Lunden et al. 2014; Dorey et al. 2020; Weinnig et al. 2020; Gómez et al. 2022).

Patterns of deep-sea biodiversity and niche functioning have long been qualified by a classical assumption of environmental stability, which is observable at a broad scale (e.g., the range gradients of temperature and organic material that decrease and narrow with increasing depth; Rex and Etter 2010). However, these concepts have been necessarily revised as pervasive evidence of complex environmental heterogeneity and temporal variability in the deep-sea have emerged. Observations by Mienis et al. (2014) using benthic landers at *D. pertusum* reefs in the Cape Lookout area of the Blake Plateau captured large fluctuations in temperature, with increases of up to 9.5°C over 24 h, reaching short-term peaks of 15.2°C (relative to < 10°C for most of the observation period), along with corresponding elevations in salinity, current speed, and other physical parameters. It has been thought that this variability in temperature may confer significant stress for corals (Guihen et al. 2012), as rapid temperature changes of this magnitude result in significantly higher metabolic demands in *D. pertusum* as well as decreased feeding rates (Gómez et al. 2022). However, reefs in this region also experience occasional pulses of enhanced chlorophyll and particulate matter that may create short-term food abundance as organic carbon supplies are temporarily elevated, potentially offsetting the impacts of thermal stress (Mienis et al. 2014; Maier et al. 2023). The paradox that corals persist, and even thrive, in apparently suboptimal conditions for survival has thus led to an emerging hypothesis that site-specific ecological benefits (e.g., increased food supply) may compensate for environmental stress, allowing corals a wider environmental niche than previously thought (Hebbeln et al. 2020). The dynamic influence of the Gulf Stream upon the deep benthos thus provides an opportunity to better understand how corals and cold-water reef communities tolerate environmental variability and conditions outside their assumed preferred ranges, which remains an evolving question.

The current study seeks to evaluate this hypothesis at a regional scale by determining whether ecological tradeoffs between environmental stress (e.g., increased temperature and variability) and mitigating offsets (e.g., enhanced food particles) exist by describing the oceanographic mechanisms that ultimately control the distribution of cold-water coral communities. We have done so using a case study from the Richardson Reef Complex, a deep reef site comprised of living coral and coral carbonate mounds that stretch across more than 200 km of the Blake Plateau (Gasbarro et al. 2022; Cordes et al. 2023). Long-term observations of temperature, current flow, and suspended particulates captured by a benthic lander at this site were collected to explore how specific Gulf Stream behaviors impacted bottom conditions. Based on documented thermal asymmetries of the current's structure within the region (Hazelworth 1977; Heiderich and Todd 2020), we expected to observe pulses of warm, chlorophyll-rich water at the reef during periods in which the Gulf Stream intruded onto the reef. We also expected to see the replacement of this warm stream-entrained water by cross-shelf upwelling of colder deeper water masses originating beyond the shelf, driven by offshore meandering (Atkinson 1977). These findings were further contextualized by comparing the distribution of *D. pertusum* presence records throughout the South Atlantic Bight with a time-averaged location of the Gulf Stream, with the hypothesis that cold-water corals are clustered along the offshore margin of the Blake Plateau where the Gulf Stream influence may be maximized. We add to the growing body of work that shows how large-scale oceanographic features can create complex environmental patterns that are important to deep-sea habitats and show how high levels of environmental variability may not be as detrimental to the distribution of cold-water corals as previously believed.

Materials and methods

Study region and reef site

The Richardson Reef Complex is one of many cold-water coral reef sites documented within the South Atlantic Bight (Cordes et al. 2023), lying along the northeastern edge of the Blake Plateau where it narrows towards Cape Hatteras (Fig. 1). Here, near-continuous carbonate mounds are populated by both living *D. pertusum* in the bush stage of colony growth (Fig. 1e), dead coral reef structures and coral rubble (Fig. 1c), as well as abundant octocorals (*Plumarella* spp., *Lateothela grandiflora*, *Pseudodrifa nigra*, and others), other scleractinian species (*Madrepora oculata*, *Enallopsammia rostrata*), and sponges (Cordes et al. 2024; Sowers et al. 2024). Underwater surveys of the area have documented abundant mobile fauna associated with the reef structure as well (e.g., Fig. 1d). Spanning depths between 750 and 900 m, the reef extends across several miles of hard-bottom swales and mound ridges, bordered by a deeply eroded substrate to the west and the Blake Escarpment slope to the east (Fig. 1b). Within the complex, the habitat consists of hard substrate and coral rubble interspersed with areas of thin sediment within swale-like depressions (Cordes et al. 2024).

Oceanographic setting

South of Cape Hatteras, the Gulf Stream flows parallel to the continental shelf against relatively cold, fresh, slow-

moving shelf water at its northern wall. This boundary results in strong vertical gradients of temperature, salinity, and other physical parameters across the stream front that extend to its deepest components (Hazelworth 1977), such that cross-front temperature differences at 800 m on the Blake Plateau can exceed 8°C (Heiderich and Todd 2020). Although Gulf Stream speeds are strongest at the surface, velocities of up to 50 cm s^{-1} and temperatures up to 11°C can extend to the Blake Plateau seafloor (~ 700–1000 m) causing fluctuations in benthic environmental conditions depending on the position of the Gulf Stream (Hazelworth 1977; Lee and Waddell 1983; Heiderich and Todd 2020). As the Gulf Stream meanders offshore, displacement within inshore troughs drives upwelling of cold, deep water that supplies nutrients to the photic zone (Lee et al. 1991). Meandering is locally amplified by the Charleston Bump, a bathymetric terrace located west of the Richardson Reef Complex (Fig. 1a) between the shelf and northern Blake Plateau (Lee and Waddell 1983; Lee et al. 1991; Gula et al. 2016).

Lander deployment

Near-bed environmental data was collected in 2019 as part of the Deepwater Atlantic Habitats II DEEP SEARCH (DEEP Sea Exploration to Advance Research on Coral/Canyon/Cold seep Habitats) collaborative research program funded by the Bureau of Ocean Energy Management. The benthic lander ALBEX (Autonomous Lander for Biological Experiments) (Duineveld et al. 2004), was deployed within the Richardson Reef Complex (31.899°N, 77.353°W) during research cruise *RB1903* at a depth of 830 m on April 13, 2019, approximately 1 km north of a dense mound of abundant live *D. pertusum* as well as some *M. oculata* and *E. rostrata* stony corals and various octocoral species. The lander was equipped with a Nortek Aquadopp single-point current meter with a side-facing head and a Wetlabs combined fluorometer and turbidity sensor measuring fluorescence and optical backscatter. All instruments sampled at 15-min intervals with sampling volumes approximately 1 m above bottom until the lander was recovered on October 23, 2019 (193-d deployment). Environmental time series derived from the sensors on the lander included: temperature, horizontal and vertical components of velocity, acoustic backscatter, optical backscatter, fluorescence, and pressure. Both acoustic and optical backscatter were used for detection of suspended particulate matter/turbidity, where acoustic backscatter is sensitive to detection of larger particles and optical backscatter is sensitive to detection of small particles with signal decay at increasing particle size (Haalboom et al. 2021). Acoustic backscatter was calculated from current meter data as the average signal amplitude for each sample time point. Raw data for both optical backscatter and fluorescence were calibrated to standard units of nephelometric turbidity units (NTU) and chlorophyll concentration (μg L^{-1}), respectively, using manufacturer calibration conversions. Acoustic and optical backscatter are hereafter referred to collectively or individually as turbidity. Chlorophyll/fluorescence signal is assumed as a metric of the flux of fresh phytodetritic material from the surface. To account for erroneous measurements of suspended material sticking to the sensor faces, outliers greater than 10 standard deviations above the mean were removed for both the optical backscatter and fluorescence time series, amounting to 36 and 22 data points, respectively.

Data analysis

All analyses were performed using R statistical software (v4.3.1, R Core Team 2023). A cross-wavelet transform was performed for temperature and chlorophyll to determine whether signals were correlated at any times during the deployment period using the R function "xwt" in the "biwavelet" package (v0.20.21, Gouhier et al. 2021), with a Morlet wavelet selected as the mother wavelet. Cross-wavelets are frequently used to visualize agreement of time-series signals, including biogeophysical time series, and in some cases can determine causality in the time-frequency space (Grinsted et al. 2004). As it is used for this analysis, cross-wavelet power represents a correlation in signal response between temperature and chlorophyll signals, which we hypothesized would be linked to Gulf Stream intrusion. For comparisons to daily gridded surface altimeter data, daily means (00:00–24:00 UTC) from the lander time series were calculated for each parameter. Net displacement of the current over the deployment period was calculated as $\sqrt{(\sum N)^2 + (\sum E)^2}$ and the angle of displacement was calculated as $\tan^{-1}\left(\frac{\sum N}{\sum E}\right)$, where N and E are the north and east velocity components, respectively. Raw values of horizontal speed and pressure from the current meter were used in harmonic analyses of least squares (HAMELS) to assess presence of tidal periodicity using the "oce" package and "tidem" tool in R (v1.8-1, Kelley and Richards 2023). Though this method is commonly used with sea surface height data to evaluate tidal patterns in coastal areas, current velocity and pressure have been used in deeper settings for similar purposes of examining internal tides.

Surface data and Gulf Stream position

The position of the Gulf Stream was mapped along the US shelf using publicly available gridded daily geostrophic surface velocity (0.25° resolution) and level 4 sea surface temperature (0.01° resolution) from Copernicus Climate Change Service (CCCS 2018, 2019). Both datasets provided daily grid cell averages, with the daily geostrophic surface velocity centered around 12:00 UTC and daily sea surface temperature averages at 00:00 UTC. For each day of the lander deployment period, raster data containing layers with the zonal/eastward (u) and meridional/northward (v) components of absolute geostrophic velocities (m s^{-1}) were used to calculate surface horizontal speed and vector direction for each grid cell (horizontal speed $= \sqrt{u^2 + v^2}$; direction $\theta = \tan^{-1}\left(\frac{u}{v}\right)$). Surface velocity above the reef site was extracted from the grid cell closest to the Richardson Reef

Complex (31.875°N, −77.375°W). The estimated proximity of the Gulf Stream to the reef site was derived for each day by the following steps: coordinate points of the cell centroids which contained the highest geostrophic speed values along all northwest–southeast diagonals (roughly perpendicular to Gulf Stream flow) were isolated within the study region; coordinates were then connected into a spatial line with a kernel smoothing function using a width equal to twice the mean distance between adjacent points. The distance between the reef and closest point along the spatial line for each day was derived using the "geosphere" R package and "dist2Line" tool (v1.5–18, Hijmans 2022).

Desmophyllum pertusum records and spatial processing

In addition to the Richardson Reef Complex case study, *D. pertusum* records throughout the South Atlantic Bight were analyzed in relation to the 5-yr mean location of the Gulf Stream. A total of 4842 presence records of *D. pertusum* (extent: longitude −83 to −68°W; latitude 20–5°N) were obtained from the Ocean Biodiversity Information System (OBIS 2021) and the National Oceanic and Atmospheric Administration's Deep-sea Coral Data Portal (NOAA DSCRTP 2021). Points were filtered to include only records with a reported coordinate accuracy of less than 1 km and with depths accurate to within 100 m of spatially merged 15 arc-second gridded bathymetry depth values (GEBCO 2021). A common limitation in deep-sea spatial ecology is the potential for sampling bias due to survey limitations and lack of absence records. To mitigate sampling bias, the remaining 2494 records were subsampled to 500 by iteratively selecting data points that were maximally dispersed from their preceding sites, starting with a randomly selected point, a spatial thinning technique which reduces the effects of intensive sampling within small regions while maintaining the maximum distribution of records (Aiello-Lammens et al. 2015). A visual reference of the distribution of spatially thinned sites is also provided in Fig. 1a as a 10-km resolution kernel-density estimation (KDE) with a bandwidth of 20 km.

Five years (2017–2021) of daily geostrophic current data (CCCS 2018) were used to estimate the mean Gulf Stream path and the variability of stream meandering. The mean path was identified in a similar manner to the daily path locations, first by isolating the coordinates of raster cell centroids that had the highest 5-yr mean velocities along (relatively cross-stream) northwest-to-southeast diagonals, then connecting these points into a kernel-smoothed spatial line (bandwidth equal to twice the mean distance of adjacent points). The minimum distance between the 5-yr mean Gulf Stream path and each *D. pertusum* record was then calculated, with points on the shoreward side (north/west) of the stream assigned a negative value and points on the offshore side (south/east) of the stream assigned a positive value. In addition, the mean and standard deviation of current speed for the location of each coral record were also extracted from the 5-yr summary geostrophic current data. Density distributions of *D. pertusum* records were then plotted against site depth and each of these location-derived metrics (distance between site and time-averaged Gulf Stream location, mean surface current speed, standard deviation of surface current speed).

Results

Richardson Reef Complex environmental characteristics

Time series of environmental parameters at the Richardson Reef Complex revealed high variability during periods in which the Gulf Stream approached the site (Fig. 2). Though most reef temperatures were between 4°C and 6°C (mean: 5.03°C), peaks of up to 10.82°C were detected on May 4, May 27, August 12–14, and September 4, and September 8–10, while the lowest temperatures (minimum: 4.13°C) were observed on May 6, May 20–21, and August 25–26 (Fig. 2a). The rates of change in temperature were substantial, with a maximum hourly change of 3.74°C during events that lasted between 13.25 and 34.75 h, the longest of which occurred between September 8 and September 10 (Fig. 2a). Chlorophyll concentration was generally very low throughout the deployment (0.00–0.15 mg L^{-1}), though sporadic increases occurred around the same time periods as those observed for temperature peaks (Fig. 2b). During high-temperature periods (defined as when 12-h mean temperature was > 6.34°C, equivalent to two standard deviations above mean temperature), mean chlorophyll was 11% higher than during the rest of the deployment (6-month mean: 0.08 mg $L^{-1} \pm 0.01$ SD). Fine and large-particle turbidity were also 34% and 50% higher, respectively, during temperature peaks than during nominal temperature conditions (Fig. 2c,d). Both turbidity parameters showed moderate elevations that lasted well-beyond the elevated temperature windows with frequent fluctuations throughout the observational period (Fig. 2c,d). Near-bottom horizontal currents at Richardson Reef Complex ranged from 0 (multiple time points) to a maximum 51.3 cm s^{-1} on May 4 (6-month mean: 7.1 cm $s^{-1} \pm 5.4$ SD). The highest current speeds occurred in early to mid-May and in early August (Fig. 2f). Although constituents of both diurnal (K_1, O_1) and semi-diurnal (M_2, S_2, N_2) frequencies were detected in the pressure time series, current speed showed no significant fit to any major astronomical tides (Supplementary Table S1). Additional environmental statistics for the reef are summarized in Supplementary Table S2.

Surface currents above the reef

The Gulf Stream meandered approximately 80 km laterally onshore and offshore along the South Atlantic Bight, with frontal edges lengthening and contracting throughout the study period (Fig. 4; Supplementary Fig. S1). Surface velocity above the reef was highest on August 3 when the Gulf Stream was less than 11 km northwest of the reef (Fig. 2g,h). Twice during the deployment, the stream was directly over the reef (May 7 and July 19), but at no point did the Gulf Stream

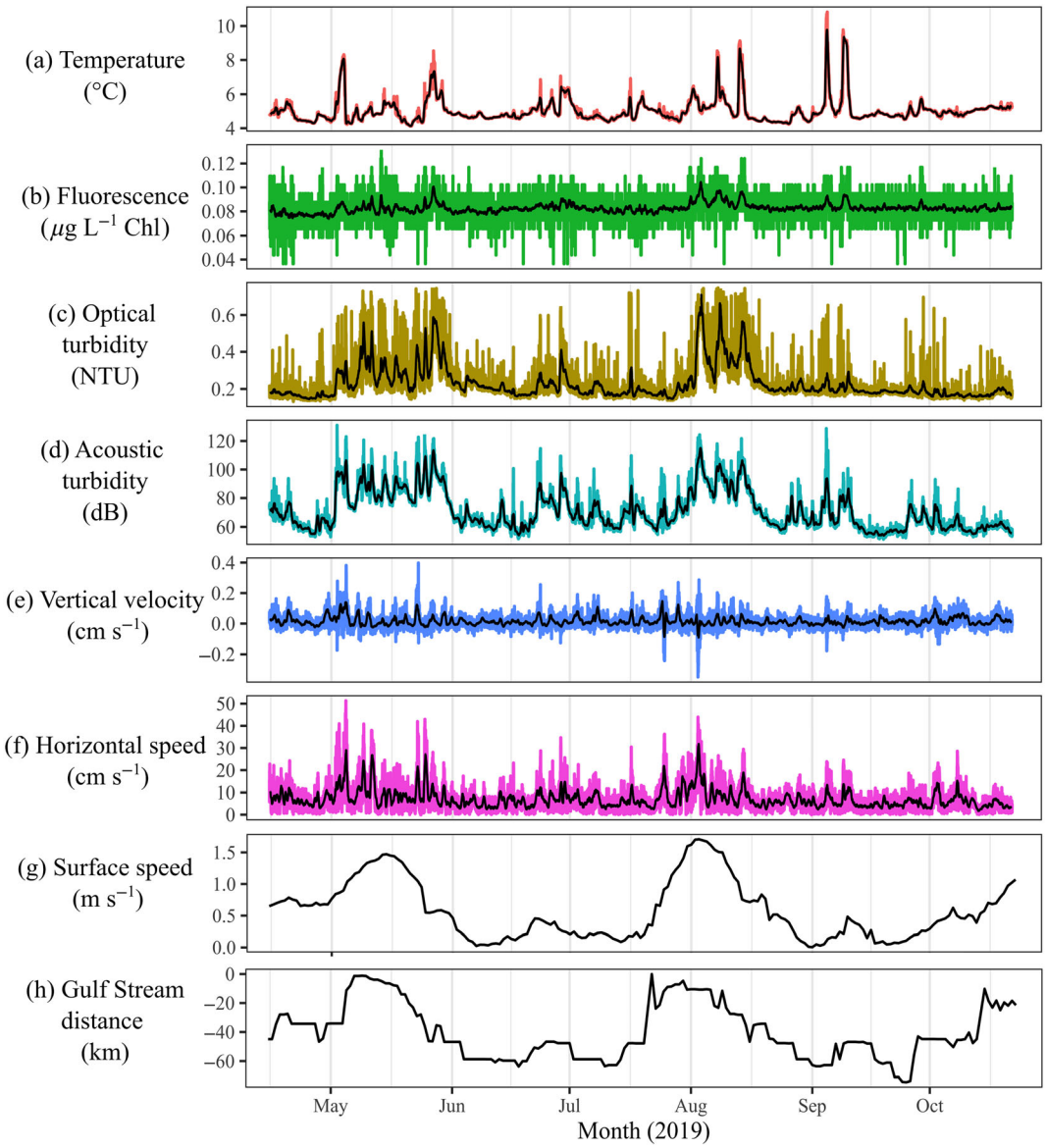

Fig. 2. Time series of major environmental parameters recorded by the benthic lander at Richardson Reef Complex (**a**–**f**), where colored lines are raw (15-min interval) data and 12-h moving averages are overlaid in black; (**g**) geostrophic surface current speed directly above the reef site; (**h**) Minimum distance (subtracted from 0) between the reef site and the instantaneous position of the Gulf Stream at surface (inshore/northwest of the reef). A value of zero indicates that the Gulf Stream is directly above the reef site, while lower values indicate its position further inshore.

meander further offshore of the reef site. Surface currents were generally an order of magnitude faster than those observed at reef depths (mean surface speed: 0.45 m s^{-1} compared with 0.071 m s^{-1} at the reef). Unlike the west-northwestern trends in the net displacement of flow at the reef, surface currents above the reef trended northeast (net displacement: 8790 km at 38°; 6-month mean velocity: 57.9 cm s^{-1} ± 46.2 SD at 46°) with the exception of a period between May 30 to July 25 during which surface currents slowed considerably and reversed direction toward the southwest before resuming northeasterly flow (Fig. 3b). This time frame corresponded to a period where the Gulf Stream had moved relatively far inshore (Fig. 2g,h; Supplementary Fig. S1). Multiple instances of eddy and eddy-filament formation at the surface were observed within the frontal edges of the Gulf Stream as it meandered, with some eddies remaining for up to 5 d (Fig. 5; Supplementary Fig. S1; July 30, cold-core cyclonic eddy ca. −78.00°W, 32.25°N; August 11, warm-core anticyclonic eddy ca. −77.25°W, 33.25°N).

Meandering behavior by the Gulf Stream appeared to drive sequential changes in the environmental conditions at the reef site. At the onset of offshore stream movement, direct

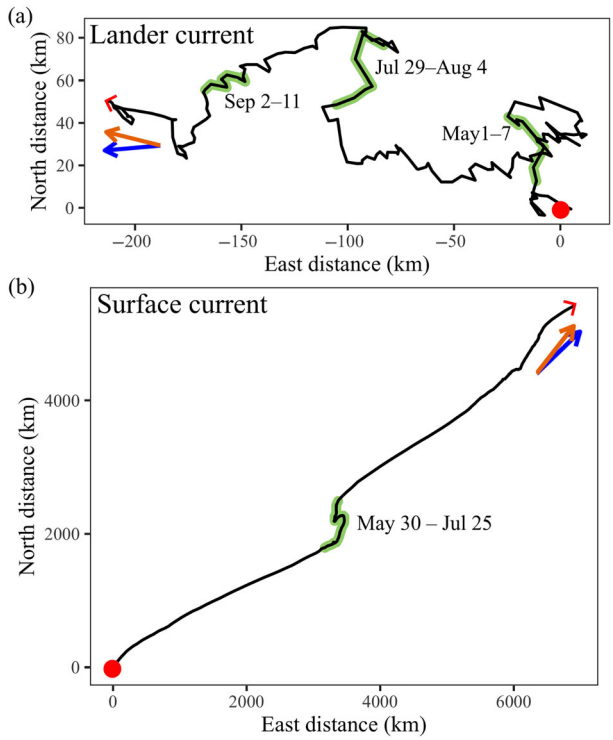

Fig. 3. Progressive vector diagrams of velocity over the 6-month observational period for (**a**) near-bed currents at the Autonomous Lander for Biological Experiments (ALBEX) lander site, averaged by day to match the resolution of surface currents, and (**b**) surface currents above the lander site. Red circles indicate the start of measurements on April 15 and red arrows indicate the end point on October 23 (2019). Arrows near the end points show the angles of net displacement (orange) and time-averaged flow directions (blue). Time frames of interest (referenced in-text) are outlined in green.

intrusion of warm waters and high particulates (including chlorophyll) washed over the reef site and near-bed currents flowed generally north-northeast, matching the surface current direction. One clear example of this pattern was observed at the beginning of early May (Fig. 4). Starting May 1, the Gulf Stream began a lateral offshore meander toward the Richardson Reef Complex, from an initial state of near-linear northeasterly flow well inshore of the reef (Fig. 4a). Over the following 6 d, the stream position shifted offshore and became sinuous, flowing east and then curving northnortheast to pass directly over the reef (Fig. 4a). At depth, the offshore movement between May 1 and May 4 corresponded with environmental signatures of deep Gulf Stream intrusion to the reef, wherein temperature increased by nearly 4°C (4.48–8.25°C), chlorophyll increased by 0.06 mg L^{-1} (0.05–0.11 mg L^{-1}), and turbidity increased as the stream approached the reef (Fig. 4b). During this time, the near-bed current at the reef redirected from north-northwest toward the north-northeast, presumably influenced by northerly flowing deep Gulf Stream component approaching the reef (Fig. 4b). As the stream's offshore position stabilized, high temperatures at the reef site were replaced by a cold, deeper water mass that was upwelled over the shelf break at high speeds (51 cm s^{-1}), in pronounced redirection of flow towards the northwest (Figs. 3a, 4). Reef temperature rapidly decreased to 4.25°C while chlorophyll concentrations returned to preintrusion levels within a single day (May 4). These strong upwelling currents coincided with short-term turbidity pulses as the Gulf Stream remained in the vicinity of the reef site for a week or longer, possibly driven by the interplay between deep Gulf Stream components and upwelling currents. When the Gulf Stream began to meander back inshore between May 15 and June 1, upwelling ceased and a secondary intrusion of deep Gulf Stream waters occurred, again characterized by rapid increases in temperature, chlorophyll, and turbidity, mirroring the initial intrusion at the onset of the meandering event (Fig. 4b).

In late July and early August, another offshore meander event appeared to drive a very similar pattern in environmental responses at the reef, with some additional features. During this event, a cyclonic eddy became apparent within the Gulf Stream front northwest of the reef site on July 29 and remained visible at the surface until August 4 (Fig. 5a). The formation of the cold-core eddy introduced a unique signature where chlorophyll continued to increase during the cold-water upwelling phase from 0.08 mg L^{-1} (the intrusion-event maximum on August 1) to 0.12 mg L^{-1} on August 3 (Fig. 5b). Also distinctive of the eddy event was the behavior of current direction at the reef. As reef temperature ramped during Gulf Stream intrusion on July 29, the current redirected from the north-northwest to the northeast, flowing moderately at 5–15 cm s^{-1}. Flow then appeared to loop back south and then westward on August 1 (coinciding with the temperature decrease and pulse of chlorophyll), then redirected again towards the north on August 2 (Fig. 5c). This looping motion, along with sharp oscillations in vertical velocity, including the strongest downward currents of the study period, indicated a period of increased turbulence. Correspondingly, reef site turbidity became significantly elevated in this period. Although the looping motion followed a roughly anticyclonic direction, this event could be a result of eddy-driven turbulence deep in the water column or could be attributed to especially active upwelling currents.

Other oceanographic features

In addition to local Gulf Stream meanders and frontal eddies, surface patterns revealed the presence of mesoscale eddies and the passage of a significant storm during the deployment period. In mid-May, a large cyclonic mesoscale eddy entered the region from the east and moved slowly west until reaching an approximately stable position south-southwest of the reef by August 1 where it remained until late September (just offshore of the Gulf Stream center; approx. center: 30.00°N, 78.25°W) (Supplementary Fig. S2). In addition, the close passage of Hurricane Dorian between the

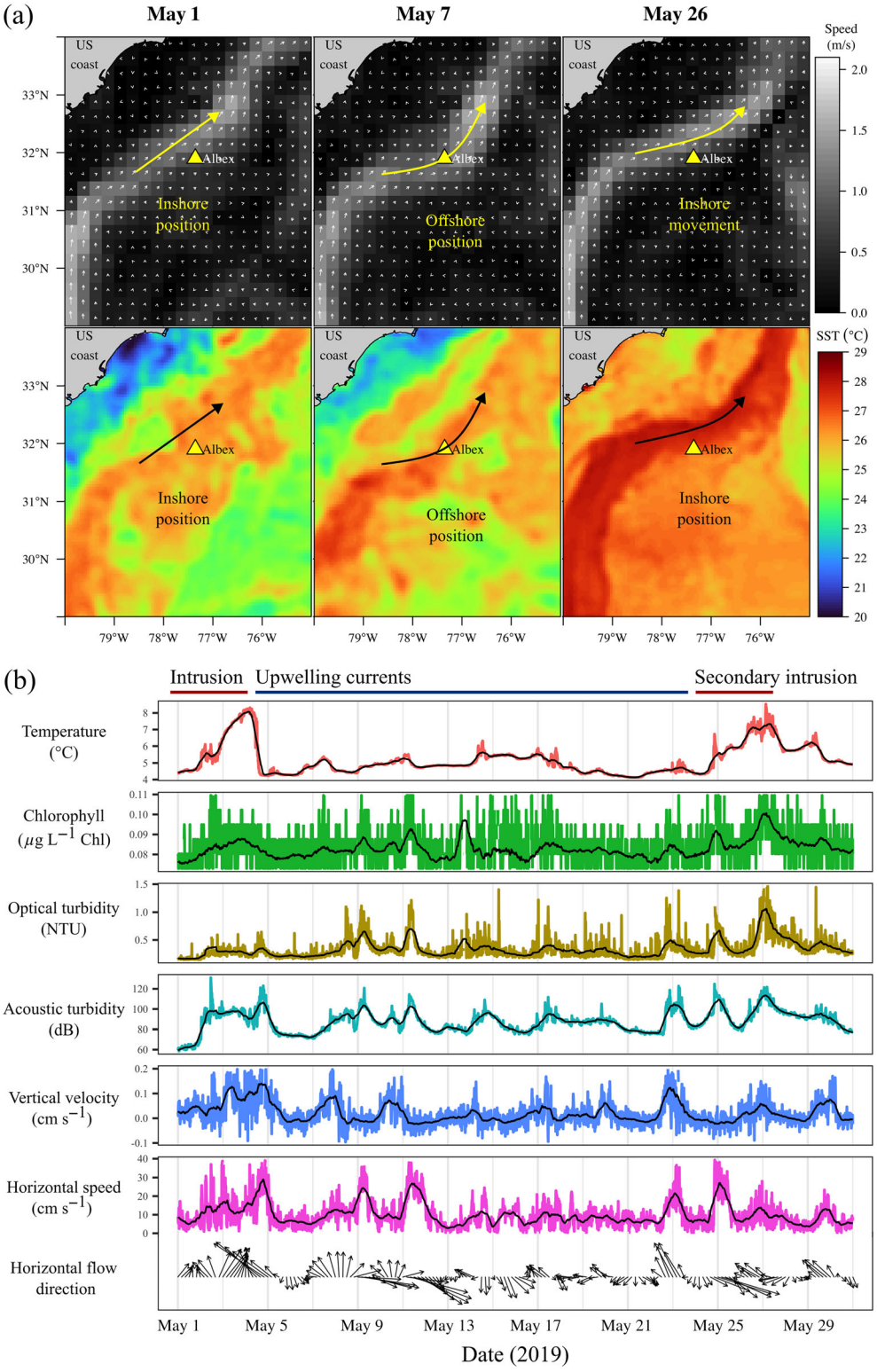

Fig. 4. An offshore meander event observed between May 1 and May 7 and the environmental responses at the Richardson Reef Complex. (**a**) Map panels showing surface current speed (top row) and sea surface temperature (SST, bottom row); (**b**) time series window of environmental conditions at the reef site, where colored lines are raw (15-min interval) data and 12-h moving averages are overlaid in black. Warm temperatures and north/northeasterly flow characterize the Gulf Stream intrusion phase (May 1–3) and are followed by rapid cooling, high current speeds veering west during postintrusion upwelling, and a secondary intrusion as the Gulf Stream began to move back inshore.

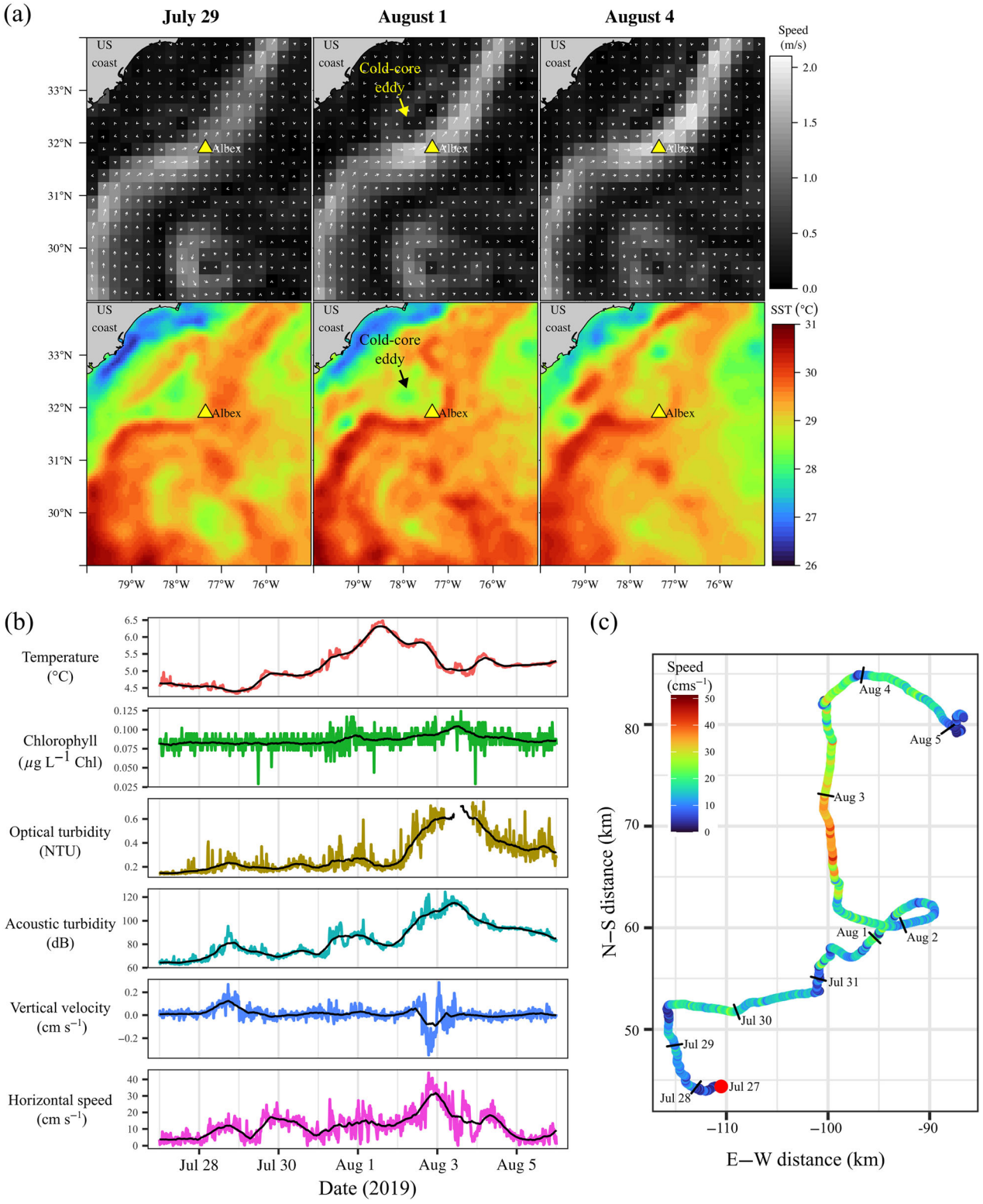

Fig. 5. An offshore meander event with cold-core eddy formation observed between July 29 and August 4 and the environmental responses at the Richardson Reef Complex. (**a**) Map panels showing surface current speed (top row) and sea surface temperature (SST, bottom row); (**b**) time series window of environmental conditions at the reef site, where colored lines are raw (15-min interval) data and 12-h moving averages are overlaid in black; (**c**) progressive vector diagram of currents (1 m above bottom) during this time frame. Warm water flows northeast during the intrusion phase (August 1) and is followed by cooling (August 2–3) and secondary peaks in chlorophyll and turbidity (August 3).

coastline and the study site (passing within 2° of latitude and longitude of the reef) as a Category 3 hurricane between September 4 and September 6 (Supplementary Fig. S3a) coincided with temperatures that reached observed maximum (September 4; 10.82°C) as well as substantial increases in turbidity and chlorophyll (Supplementary Fig. S3c). The influxes of warm turbid waters and surface-derived material to the reef site at 830 m depth suggests that the storm caused significant mixing throughout the water column. However, bottom currents remained relatively moderate (up to 20 cm s^{-1}) relative to the currents observed during intrusion events. These patterns appeared again several days after (September 10–11), suggesting a potential secondary effect of storm-related disturbances after the storm had passed.

Cross-wavelet transform

To examine the relationship between reef site temperature and potential food supply, it was necessary to distinguish the time-varying relationship in raw signals for these parameters, the strength of which depended on the Gulf Stream's relative position. This was accomplished via the cross-wavelet transform of reef site temperature and chlorophyll signals (Fig. 6). Essentially, this statistic indicates the changes in correlational power between temperature and chlorophyll through time (May–October), the relative phase of the relationship (in-phase or antiphase; leading or lagging), and the periods (hours to weeks) over which the relationship is strongest. There was a clear link between high power and the proximity to the Gulf Stream, meaning that the correlation between temperature and chlorophyll became stronger as the Gulf Stream meandered toward the reef site, with chlorophyll signal phase-matched with or occasionally leading temperature (Fig. 6). In particular, Gulf Stream intrusions during May and August showed significant power over periods of approximately 2–10 d, roughly the same duration of intrusions themselves (Fig. 6). Moreover, signal agreement was also significant, albeit lower, during weak or distant offshore meandering events, as in late June and early September compared with major meandering events, and during the passage of the Hurricane Dorian in early September (Supplementary Fig. S3). Longer periods (1–1.5 months) also showed high power, possibly a reflection of the lower-frequency meander cycles or due to potential edge effects of the period length approaching duration of the time series.

Desmophyllum pertusum records and relation to the Gulf Stream

Of the 500 spatially thinned *D. pertusum* records within the region, 91% of records were located within 50 km of the 5-yr Gulf Stream position, with 49% of all records located within 0–30 km on the offshore side of the stream (Fig. 7a,d). We used the variability (standard deviation) of surface current speeds as a proxy to understand how active the Gulf Stream was across the region (Fig. 7b). Sites were also clustered along regions of the Gulf Stream that had moderate to high meandering variability (Fig. 7b,e). Site depths ranged from

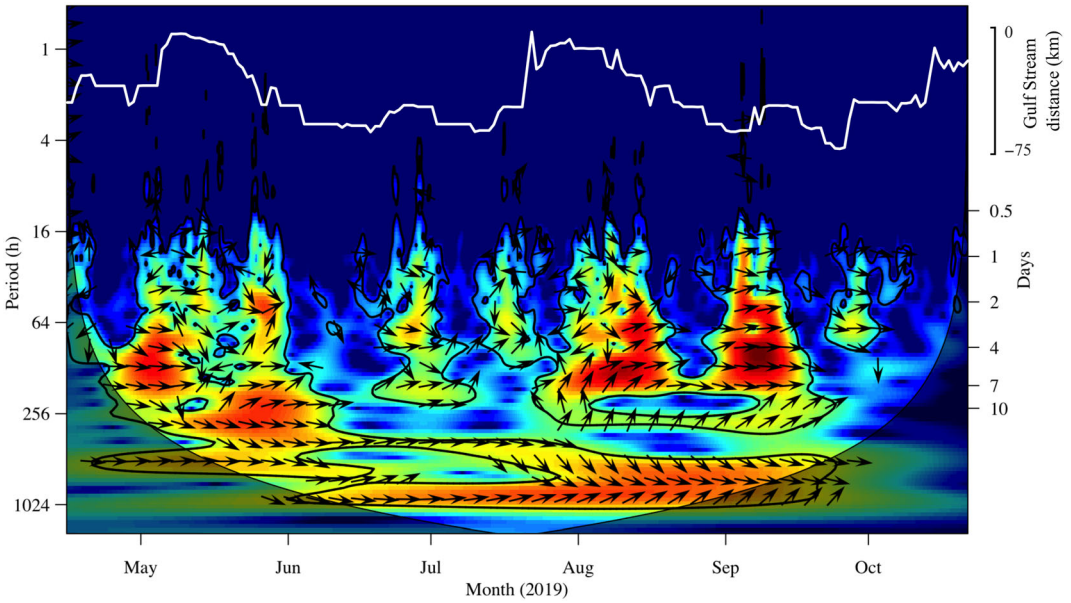

Fig. 6. Cross-wavelet transform of temperature and chlorophyll concentration using 12-h rolling mean values. The color scale indicates combined power signal of the two series in time-frequency space, with low-to-high power in blue-red rainbow scale. The relative phase of temperature with respect to chlorophyll is shown as arrows, with in-phase pointing right and antiphase pointing left, and the lead and lag of phases pointing up and down, respectively. Contoured areas within black lines indicate 5% confidence interval. Significant power occurred at periods between approximately 2.5–10 d only during Gulf Stream meanders near the site. The dark shaded region represents values that are inaccurate due to edge effects. The distance of the Gulf Stream (km) to the reef site is overlaid in white.

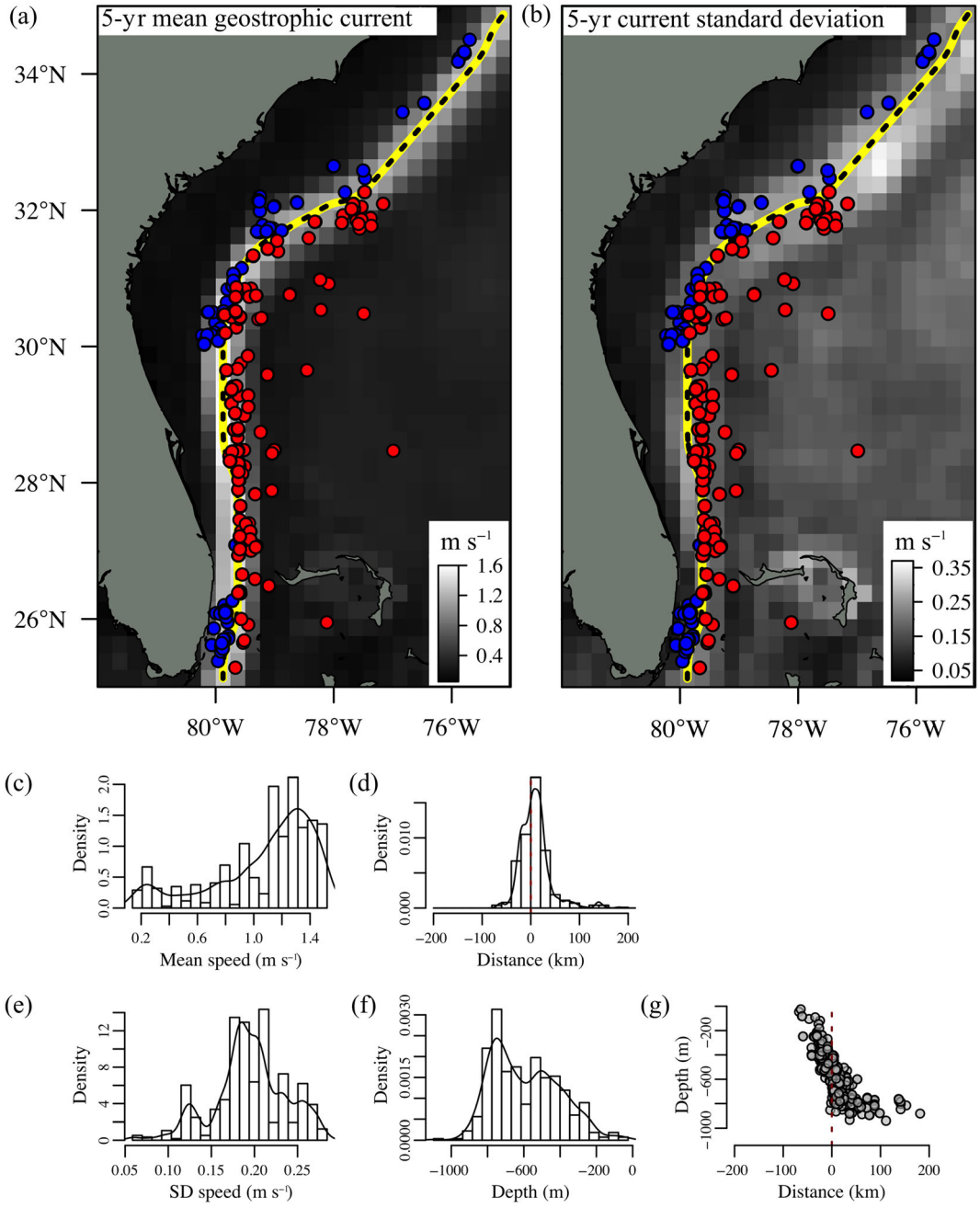

Fig. 7. Distribution of *Desmophyllum pertusum* presence observations (subset within the South Atlantic Bight after 10 sites north of Cape Hatteras were removed, $n = 500$) overlain on (**a**) mean surface current speed and (**b**) standard deviation of surface current speed. The yellow dashed line is the smoothed center line of the Gulf Stream. Red dots indicate offshore sites and blue dots indicate shoreward sites (relative to the Gulf Stream). (**c**–**f**) Probability density histograms of sites as a function of the following variables: (**c**) mean surface current speed, (**d**) distance from Gulf Stream, (**e**) standard deviation of surface current speed, and (**f**) seafloor depth. (**g**) Distance from Gulf Stream vs. site depth.

47 to 1098 m and were distributed bimodally with highest density around the 500 m depth bin and the 760–800 m bins (Fig. 7f). Depth and distance of *D. pertusum* records from the Gulf Stream were themselves linked (Fig. 7g), a relationship that is intrinsic to the parallel flow of the Gulf Stream to the continental shelf slope that drops off between approximately 200–800 m depth. For this reason, it is impossible to separate the effects of depth vs. proximity to the Gulf Stream on the distribution of coral sites. However, areas where mean surface currents were high (1.25–1.52 m s^{-1}) and variable (0.17–0.22 m s^{-1} SD) contained the highest density of sites (42% and 55%, respectively) (Fig. 7c,e). Together, these factors

suggest that coral distribution is greatest in areas where the Gulf Stream is actively meandering.

Discussion

Six months of high-resolution near-bed observations found a vibrant *D. pertusum* reef complex to persist within a highly variable and sometimes extreme physical setting, similar to other cold-water coral reefs described within the region (Mienis et al. 2014; Gasbarro et al. 2022; Cordes et al. 2023). While extrema of some environmental parameters may theoretically stress corals (e.g., thermal stress, smothering, feeding inhibition), conditions at the reef site were highly dynamic such that extreme conditions were rarely sustained for more than 1–2 d, and occurred with corresponding increases in food supply, potentially mitigating the impacts of stressors. We discuss the mechanisms and near-benthic environmental responses to offshore meandering including direct intrusion of warm, Gulf Stream-entrained water to the site, cross-shelf upwelling of cold, turbid currents, and vertical transport of chlorophyll and particulates during stream front activity.

Offshore meandering

The stream's offshore meanders towards the Richardson Reef Complex were bookended by phased intrusions of warm Gulf Stream-entrained waters onto the reef along with pulses of chlorophyll. During intrusion, high temperatures could confer an increase in coral respiration rates and other metabolic demands (e.g., Dodds et al. 2007; Gómez et al. 2022). However, high-temperature intrusion events were coupled with pulses of organic material, suggesting that metabolic demands from thermal stress may be partially offset by enhanced food supply. The upwelling of nutrients into the mixed layer due to the offshore meander allow the exchange of nutrients that would stimulate an additional supply of organic material transported from surface waters (Lee et al. 1991; Pascual et al. 2015). Though only a small fraction of organic carbon reaches the deep seafloor, amplified production at the surface can result in short-term pulses of this material into the deep benthos, similar to fluxes observed during seasonal upwelling events such as spring blooms (Maier et al. 2023). Flux of organic material can be further augmented by subduction where frontal eddies locally modify the depth of the mixed layer (Lee and Nurser 2012). Gómez et al. (2022) posited that additional food supply may not be enough to offset thermal stress in *D. pertusum* because high temperatures were associated with nearly threefold declines in feeding rates in laboratory trials that were designed to capture the temperature ranges of reefs on the Blake Plateau. However, these findings were a result of 7-d exposure to a near-maximum temperature for the region (14°C) that far exceeded the durations of in situ temperature events, which were sustained for no longer than 1–2 d before rapid cooling. In this view, it could be argued that the environmental variability observed at the reef site is a mitigating factor with respect to thermal stress in corals because it may prevent the aggravated effects of prolonged exposure to high temperatures. Furthermore, excess phytodetritus that goes uncaptured because of reduced feeding still presents an energetic subsidy to cold-water corals if it is captured within the faunal reef filter that traps and recycles organic material into bio-available forms (Maier et al. 2020, 2023). As opportunistic feeders, corals can efficiently exploit this recycled material, including dissolved organic material and bacterial biomass (Mueller et al. 2014).

Moreover, we highlight at least one instance (e.g., August 3) in which additional pulses of chlorophyll continued to occur after the dissipation of warm temperatures, an event that coincided with the sustained presence of a cyclonic frontal eddy northwest of the reef site (Fig. 5a). This marked a departure from the temperature–chlorophyll relationship that was apparent during intrusion phases and may be a result of intense vertical exchange between the mixed layer and nutrients upwelled within deep eddy fronts (Gula et al. 2016). Even if food pulses during direct intrusion were insufficient to meet the metabolic demands of the accompanying temperature spikes, a single short-term pulse of plankton or highly concentrated organic carbon supplied to the reef may sustain up to 17% of a coral's yearly carbon budget in stored lipid reserves (Maier et al. 2023). In the absence of thermal stress, normal feeding rates would allow better assimilation of this material that may then be stored in coral tissue to help offset future food-limited periods (Gómez et al. 2022; Maier et al. 2023).

The postintrusion phase, characterized by rapid cooling and especially strong currents, can be attributed to a deep-water mass being pulled cross-shelf toward the inshore troughs created by Gulf Stream meanders. Lee and Waddell (1983) described a similar phenomenon for near-bed velocities on the outer edge of the Blake Plateau at 30°N, wherein prolonged (42 d) currents reaching > 30 cm s^{-1} flowed mostly westward and southward, while sites further inshore generally experienced northeasterly flow in alignment with the Gulf Stream. The authors suggested that the anomaly could be explained by the temporary influence of a deep undercurrent, identifiably the cold, fast-moving upper layers of the Deep Western Boundary Current. Although this current generally flows southward, redirection of flow towards the north and/or cross-shelf direction can occur within the current's upper layers at depths of approx. 1000 m between latitudes of 30°N and 36°N, where the two currents approach a crossover region near Cape Hatteras (Fig. 1a) (Chomiak et al. 2022). This is consistent with the strong north/northwesterly currents observed during the Gulf Stream meander events at the Richardson Reef Complex (e.g., August 2, May 4; Figs. 3a, 4, 5) and suggests that meandering induces these currents to move further inshore as they are upwelled over the slope of the Plateau. The presence of strong currents is a well-established predictor of suitable habitat for *D. pertusum* because currents can increase particle transport, interact with reef topography to induce

downwelling of organic material from the surface, cause resuspension and recycling of locally deposited organic carbon, and prevent sedimentation of polyps by removing accumulated sediments (e.g., Mienis et al. 2007; Davies et al. 2009; Maier et al. 2023). Although we expected that currents would become elevated during direct stream intrusion, velocities were higher during the cold-water upwelling phase than during intrusion, suggesting that upwelling currents are an especially important component of the ecological influence of the Gulf Stream. Although the current speed maxima seen during Gulf Stream intrusion and upwelling were much higher than current speeds suggested as optimal for feeding by coral polyps under experimental conditions (< 7 cm s^{-1}) (Purser et al. 2010; Orejas et al. 2016), dense coral colony structure and/or near-bottom topography like that at the Richardson Reef Complex can significantly alter near-bed currents to allow for more efficient particle capture (Mienis et al. 2019).

Upwelling currents and intrusion were also linked to large increases in turbidity, likely a result of sediments resuspended by currents interacting with the seabed as opposed to fresh material advected onto the reef (Mienis et al. 2014). The ecological result to corals was a significant supply of particulates, comprised of a low fraction (0.05–8%) of organic carbon (Mienis et al. 2014) delivered via temporarily elevated currents. At concentrations > 50 mg L^{-1}, suspended particulates can pose a threat to coral polyps in the form of burial/oxygen depletion, reduced feeding ability, and/or energetic costs to remove excess sediment (Brooke et al. 2009; Larsson and Purser 2011). Though some negative sedimentation effects remain possible, these lethal concentrations far exceed the turbidity levels recorded at the Richardson Reef Complex (based on generic backscatter conversion rates from Sehgal et al. 2022). While polyps can self-clean particulates from their tissue surface to an extent, smothering can be reversed with current speeds that are strong enough to wash suspended matter away from a reef, a process that can also be mediated by reef structure and the hydrographic features of a site (Mienis et al. 2019). Furthermore, *D. pertusum* can survive burial conditions for 1–2 d (nonlethal effects notwithstanding) (Brooke et al. 2009; Allers et al. 2013), thus this risk is likely mediated by the short duration of the sedimentation events. Even so, the same enhanced currents that were associated with the delivery of particulates may also have allowed at least partial removal from the reef within 2 d of peak concentrations (Figs. 4, 5), followed by more complete flushing as the Gulf Stream eventually meandered back inshore away from the study site.

Other oceanographic influences

Large-scale cold-water coral distribution patterns are linked to topographies that generate internal tides, which locally enhance flow speed and particle transport (van der Kaaden et al. 2024). However, the relative influence of tides can be superseded by the presence of strong boundary currents like those found in other regions of the Atlantic (Schulz et al. 2020). Though tidal frequencies were detected at the Richardson Reef Complex, the effects of tides on near-bottom currents were either masked or significantly altered by the influence of the Gulf Stream. We attribute this to the possibility of the stream front acting as partial filter of tidal propagation to the open ocean; at higher latitudes, movement of internal tidal waves into the Gulf Stream front at oblique angles can cause reflection of those waves back toward shore and energetic scattering between tidal modes (Kelly and Lermusiaux 2016). Furthermore, nontidal oscillations were observed in near-bed currents speeds at subhourly frequencies (e.g., Fig. 2e,f). The amplitudes of these oscillations were highest when the Gulf Stream was actively intruding onto the site (Figs. 2, 4), and thus are perhaps linked to high-frequency internal waves within the Gulf Stream, especially prevalent near the Charleston Bump (Todd 2017).

Notably, the two most extreme temperature elevations during the deployment were not linked to the proximity of the Gulf Stream but rather to the passage of Hurricane Dorian (Supplementary Fig. S3). At the time of publication, no studies have captured the passage of a major hurricane directly over a deeper cold-water coral reef site. While significant, the environmental response at the Richardson Reef Complex was consistent with studies in other systems that have shown hurricanes can induce intense water column turbulence and turbidity via vertical mixing and upwelling over short timescales (e.g., Scrosati 2020). Nearshore tropical cyclones have intensified in the last 40 yr, and model simulations predict this trend to accelerate in the coming years in response to rising ocean surface temperatures (Balaguru et al. 2024). Though the corals on the Blake Plateau already experience a quasi-stochastic regime, increased exposure to storm impacts could imbalance the environmental relationships that allow their survival. For instance, extreme heat shocks at reefs like those seen during the passage of Dorian may be sustained for longer under slower-moving storms in the future, exacerbating the risk of prolonged thermal stress (Brooke et al. 2013; Gómez et al. 2022) or storm-induced turbidity flows may form deep nepheloid layers that alter existing trophic structures (Ziervogel et al. 2016). These scenarios and others are possible pathways toward an environmental tipping point for cold-water corals in the region.

Another distinctive presence in the region was the cyclonic mesoscale eddy that persisted over several months (Supplementary Fig. S2). While its effects upon environmental conditions on the reef were not qualitatively obvious in lander time series signatures, the eddy's size, duration, and proximity to the Gulf Stream upstream of the reef suggest that the effect would be non-trivial. Mesoscale eddies influence the supply of organic material the seafloor via vertical exchange of nutrients that stimulates new production as well as lateral advection of phytoplankton (McGillicuddy and Robinson 1997). As a cyclonic cold-core eddy, upwelling of deep water within the

core might also have contributed to locally cooled temperatures at the reef site (Castelao 2014). These dynamics and how they impact the corals at depth remain hypothetical, as water column data in the study region during this period is lacking. At a minimum, we posit that the presence of the eddy in the region and its interactions with the Gulf Stream front likely contributed additional variability to the environmental profile of the Richardson Reef Complex.

Distribution of *D. pertusum* records

Given the observed effects at the Richardson Reef Complex, it was hypothesized that the Gulf Stream may be a major driver of conditions that support the persistence of cold-water coral reefs throughout the region, in conjunction with other important habitat variables such as depth, substrate, and bathymetric features. Support for this hypothesis was shown in the distribution patterns of *D. pertusum* records throughout the South Atlantic Bight, where there was clear clustering of reefs distributed within 50 km of the 5-yr mean Gulf Stream position and especially within its offshore edge (Fig. 7a,d). Moreover, clustering of coral records within areas of moderate-high surface current variability (Fig. 7e) emphasizes the importance of Gulf Stream processes and associated mechanisms as a potential driver of coral distribution and not just the proximity of corals to the center stream alone. High site density found along the offshore margin relative to the inshore side of the Gulf Stream might be explained in part by the cross-shelf distance reached by upwelled water masses during meanders. Cross-shelf upwelling, bringing cold, deep-sourced water onto the shelf postintrusion, was an ecologically important phase of Gulf Stream meandering because it truncated high-temperature events that were intrinsic stream intrusion and brought swift currents and suspended particulate matter (Fig. 4). However, this process varies by season; during non-winter months, upwelling on the shelf extends further inshore than during winter months (Atkinson 1977; Hazelworth 1977). Therefore, for reefs along the inshore edge of the Gulf Stream, seasonal reduction of upwelling could mean longer temperatures elevations and diminished particle advection.

While the distribution of cold-water corals in many regions is controlled by more predictable tidally driven regimes (e.g., Mienis et al. 2007; van der Kaaden et al. 2024) or unidirectional flows (e.g., Correa et al. 2012), the Blake Plateau environment appears to be dominated by low-frequency Gulf Stream meanders that exert substantial environmental variability amid interactions between the stream front, eddies, and upwelled water masses. If examined with the older notion of a narrow ecological niche for cold-water corals, this habitat otherwise appears unpredictable and biologically inhospitable, yet hundreds of coral reefs have been documented in the region (Stetson et al. 1962; Reed et al. 2006; Sowers et al. 2024). We present a push-pull effect between deep stream intrusion and cold upwelling from beyond the shelf break, together driving dynamics of metabolic stress and food supply to corals in its path. This mechanism appears to be ecologically self-mitigating, as the metabolic effects of high temperatures on Richardson Reef Complex are rapidly offset by the upwelling of colder water from greater depths and regular coupling with pulses of organic material. Therefore, despite the extreme variability, the conditions at the Richardson Reef Complex may be well-balanced from a biological perspective for reef-building corals.

Conclusions

As collective knowledge of cold-water coral reefs expands, certain cold-water coral populations have been found to tolerate conditions that were previously considered extreme. While the Blake Plateau is unique, deep-sea habitats are found beneath large ocean currents, including major boundary currents, throughout the world (Schulz et al. 2020). The present study demonstrates the value of longer-term monitoring and high-quality data acquisition to improve upon earlier niche baselines and discern how cold-water coral reefs function across a breadth of physical–ecological regimes. Long-term in situ Eulerian studies with high temporal resolution using lander or mooring deployments can more intricately capture dynamic bottom conditions at subhourly timescales to interpret the effects of important oceanic processes. Furthermore, to anticipate coral responses to our changing climate, an improved understanding of the linkages between coral physiological responses and their environment is urgently needed. While cold-water corals on the Blake Plateau may be well-adapted to temperature variability, heat shocks of more than 12°C have been recorded on *D. pertusum* reefs in the North Atlantic within the last two decades, raising questions of how local populations may fare if these patterns continue (Guihen et al. 2012). Following historically stable periods, ocean-scale Atlantic Meridional Overturning Circulation processes have weakened in the last two centuries (Caesar et al. 2021). With a mechanistic understanding of how Gulf Stream processes influence reefs, our findings may help forecast the ways in which presently suitable habitats will change under future fluctuations of large-scale circulation patterns. The authors are hopeful that the evidence presented here demonstrating environmental resilience of cold-water corals is emblematic of many lessons to come.

Data availability statement

Lander data used in this analysis is available at https://doi.org/10.5281/zenodo.12117392. Other data sources are publicly available via the OBIS and NOAA DSCRTP (coral occurrence records) and Copernicus Climate Change Service (SST and geostrophic velocity) websites as referenced.

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Conflict of Interest

The authors of this study declare no conflicts of interest.

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