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1 **The Impact of Gulf Stream Frontal Eddies on Ecology and Biogeochemistry near**  
2 **Cape Hatteras**

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17

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19

20 **Key Points:**

- 21 • In-depth investigation of a frontal eddy in the Gulf Stream off Cape Hatteras, North  
22 Carolina
- 23 • Continued physical and biogeochemical differences are observed between the eddy and  
24 adjacent water masses even as it begins to shear apart
- 25 • We share a conceptual model of the ecological impact of frontal eddies with a hypothesis  
26 that they supply zooplankton to secondary consumers

27

28

## 29 **Abstract**

30 Ocean physics and biology can interact in myriad and complex ways. Eddies, features found at  
31 many scales in the ocean, can drive substantial changes in physical and biogeochemical fields  
32 with major implications for marine ecosystems. Mesoscale eddies are challenging to model and  
33 difficult to observe synoptically at sea due to their fine-scale variability yet broad extent. In this  
34 work we observed a frontal eddy just north of Cape Hatteras via an intensive hydrographic,  
35 biogeochemical, and optical sampling campaign. Frontal eddies occur in western boundary  
36 currents around the globe and there are major gaps in our understanding of their ecosystem  
37 impacts. In the Gulf Stream, frontal eddies have been studied in the South Atlantic Bight, where  
38 they are generally assumed to shear apart passing Cape Hatteras. However, we found that the  
39 observed frontal eddy had different physical properties and phytoplankton community  
40 composition from adjacent water masses, in addition to continued cyclonic rotation. In this work  
41 we first synthesize the overall ecological impacts of frontal eddies in a simple conceptual model.  
42 This conceptual model led to the hypothesis that frontal eddies could be well timed to supply  
43 zooplankton to secondary consumers off Cape Hatteras where there is a notably high  
44 concentration and diversity of top predators. Towards testing this hypothesis and our conceptual  
45 model we report on the biogeochemical state of this particular eddy connecting physical and  
46 biological dynamics, analyze how it differs from Gulf Stream and shelf waters even in “death”,  
47 and refine our initial model with this new data.

## 48 **Plain Language Summary**

49 Frontal eddies are spinning masses of water (~30km in diameter) that move along western  
50 boundary currents like the Gulf Stream. When they form they carry productive coastal water into  
51 the Gulf Stream and drive upwelling within their cores. Together this leads to an increase in the  
52 amount of phytoplankton within them - much higher compared to surrounding nutrient-limited  
53 Gulf Stream water. On the east coast of the United States one common area of frontal eddy  
54 formation is just off Charleston, SC. Eddies then travel up the coast and dissipate near Cape  
55 Hatteras, NC. In this work we measured a wide range of physical and biological properties of a  
56 frontal eddy just north of Cape Hatteras. We compared these properties within the eddy to the  
57 coastal water on one side and the Gulf Stream water on the other, finding clear differences in  
58 phytoplankton community composition and other physical and chemical properties. Using the  
59 results of these observations together with previous studies we share a simple model for how  
60 frontal eddies may impact phytoplankton, zooplankton, and fish – hypothesizing that they may  
61 contribute to the high diversity and density of top predators off Cape Hatteras.

## 62 **1 Introduction**

63 Circular currents of water, termed eddies, can trap and transport water properties  
64 throughout the ocean, containing and moving hydrographic and biogeochemical properties  
65 laterally as they are advected by major currents and vertically by raising or lowering density  
66 surfaces (McGillicuddy, 2016). Mesoscale eddies, with spatial scales  $O(100\text{km})$  and temporal  
67 scales  $O(\text{months})$ , are often considered the “weather of the ocean” and are a discrete example of  
68 biophysical interaction where physics can strongly influence ocean ecology (Clayton et al., 2013;  
69 Gaube et al., 2014; Lévy, 2008; Mahadevan, 2016; Williams & Follows, 1998).

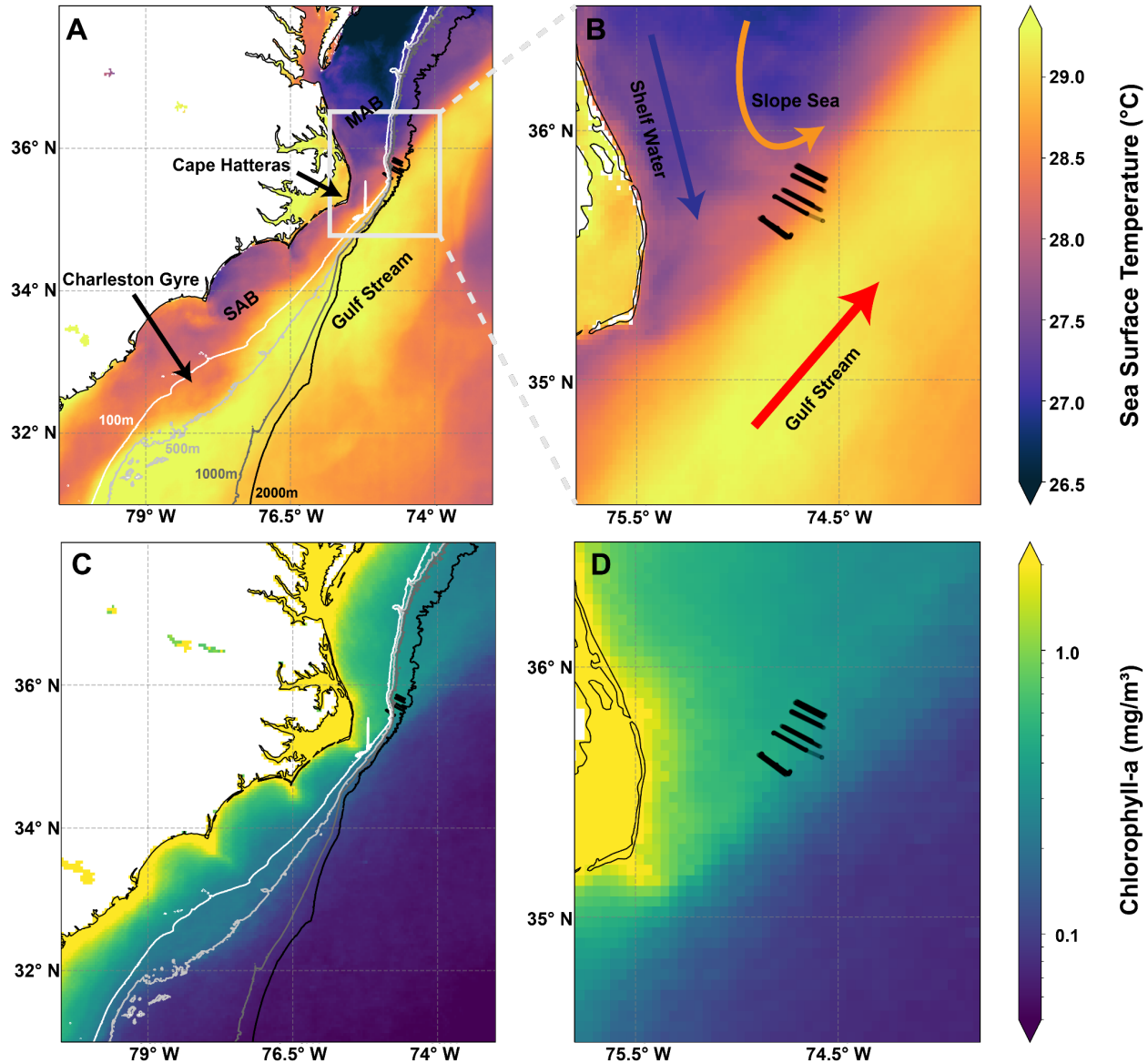
70 The physical processes through which eddies impact ocean ecosystems include trapping  
71 and lateral advection, stirring, upwelling and downwelling, and stratification though the

72 ecological impacts of these processes can be complex and contradictory, for a comprehensive  
73 review see McGillicuddy (2016). As a specific example, cyclonic eddies from western boundary  
74 systems (in the Gulf Stream often called cold core rings) typically have enhanced chlorophyll *a*  
75 (chl-*a*) both from entrainment of more nutrient rich and productive coastal water and enhanced  
76 upwelling due to isopycnal uplift (Gaube et al., 2014), but with strong winds this could be  
77 balanced or even trend negative by wind/eddy Ekman pumping.

78 Given the range of physical and nutrient changes due to eddies, we expect an even more  
79 heterogeneous impact on primary productivity, phytoplankton community composition, and even  
80 higher trophic levels. Generally where the ecosystem is nutrient limited, cyclonic eddies are  
81 associated with increases in phytoplankton size, diversity, and productivity, which lead to  
82 increases in zooplankton populations (Belkin et al., 2022; Landry et al., 2008). For long-lived  
83 eddies (>6 months), modeling work suggests reduced phytoplankton diversity on average due to  
84 competitive exclusion, though individual eddies were widely variable (Lévy et al., 2015). Little  
85 work has been done on secondary consumer responses to eddies, though it is likely that after an  
86 eddy-induced bloom, transfer efficiency increases as the number of trophic links between the  
87 primary consumers and forage fish decreases, e.g. larger phytoplankton such as diatoms  
88 consumed by large zooplankton who are consumed directly by fish (Eddy et al., 2021). Eddy-  
89 driven productivity and biophysical changes can move up the trophic ladder, structuring the  
90 distribution of top predators both due to physiological preferences - anticyclonic eddies deepen  
91 the warmer mixed layer allowing sharks to access deeper prey with less temperature stress  
92 (Braun et al., 2019; Gaube et al., 2018) - and increased prey density. Thus, an increase in  
93 foraging efficiency may explain preferences for eddies in tuna, swordfish, and seabirds  
94 (Arostegui et al., 2022; Haney, 1986; Hsu et al., 2015).

95 One class of eddies that are relatively underexplored are frontal eddies, cyclonic features  
96 that form in the trough of meanders in western boundary currents such as the Gulf Stream, the  
97 Loop Current in the Gulf of Mexico (Maul et al., 1974; Rudnick et al., 2015), the Kuroshio  
98 Current (Kasai et al., 2002), and the East Australian Current (Ribbe et al., 2018). On the U.S.  
99 eastern seaboard, these features are important for production on the outer shelf of the South  
100 Atlantic Bight (T. N. Lee et al., 1991), but they are typically thought to shear apart when the  
101 Gulf Stream narrows and rounds Cape Hatteras, North Carolina shortly before the current  
102 separates from the continental shelf (Figure 1). In this work we investigated a frontal eddy  
103 northeast and downstream of Cape Hatteras, at the Gulf Stream's separation point from the  
104 continental shelf. Our goals in this work were to 1) better understand the evolution of primary  
105 producers and primary consumers within frontal eddies and 2) re-examine the overall ecosystem  
106 impact of frontal eddies throughout their lifetime.

107 Our in-depth in-situ investigation takes place around “the Point” off Cape Hatteras  
108 (Figure 1) using a combination of physical, molecular, chemical, and optical methods to  
109 elucidate the effects of a cyclonic eddy on ocean biogeochemistry. Given that the in-situ  
110 component takes place over just three days - viewed in this work as effectively a single time step  
111 - we use satellite data to complement this in-situ view and investigate the two week-long life of  
112 this eddy.



113

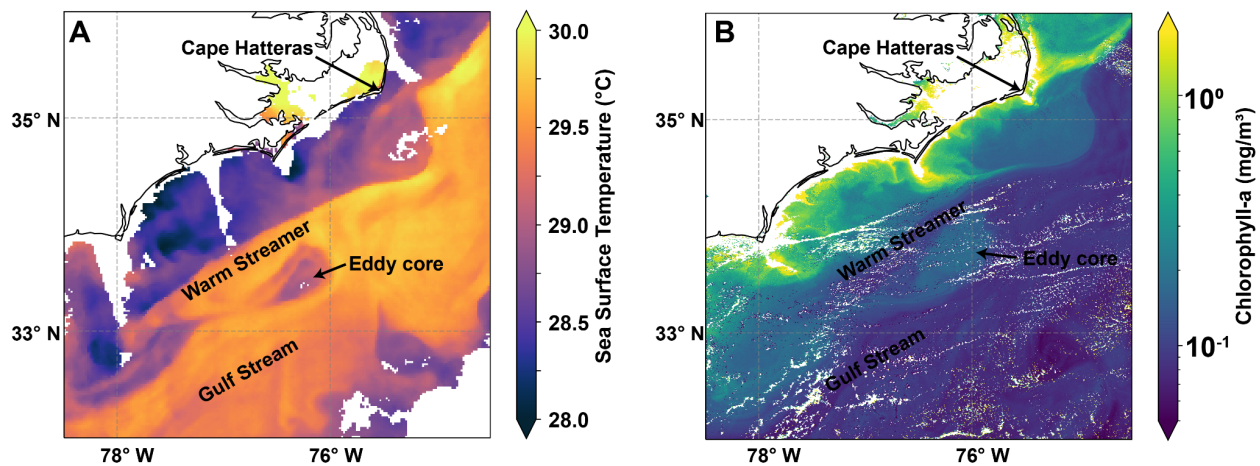
114 **Figure 1.** Study area overview. Panel A shows the broad geographic context using an average  
115 sea surface temperature and chlorophyll-a from August 20th to September 10th, the approximate  
116 lifetime of our eddy. Bathymetry is shown via the 100m, 500m, 1000m, and 2000m contours.  
117 The Gulf Stream is visible as the highest temperature water approximately following the 500m  
118 contour until Cape Hatteras. The Charleston Bump is visible in the 500m contour at  
119 approximately (34° N, 79° W) and the seaward deflection of the Gulf Stream is visible as a  
120 decrease in SST just north of this point. Panel B shows an inset zoom in of our study region with  
121 the nine transects shown in black. Panels C and D show the average chlorophyll-a for the same

122 period. SST is from GOES-16 and chl-a is from the Ocean Colour Climate Change Initiative's  
123 multi-sensor global satellite chlorophyll-a product.

### 124 1.1 A Brief History of Frontal Eddy Research

125 There is a long, though intermittent, history of studying frontal eddies in the Gulf Stream  
126 (von Arx et al., 1955; Pillsbury, 1890; Webster, 1961). Extensive physical surveys describe these  
127 features as cyclonic, cold-core eddies with substantial upwelling through isopycnal uplift (Bane  
128 et al., 1981; Thomas N. Lee et al., 1981). In turn, phytoplankton respond intensely to this  
129 nutrient upwelling, with observed levels of diatom blooms and chl-a 10-100 times greater than  
130 those typically measured in Gulf Stream or outer shelf water (defined as depths from 40-200m  
131 (T. N. Lee et al., 1991)). Menhaden and bluefish migrations to the South Atlantic Bight (SAB)  
132 are suggested to be secondary to this response of primary producers as the high-levels of  
133 phytoplankton provide a consistent food source for higher-level consumers (Yoder et al., 1981).  
134 The Frontal Eddy Dynamics experiment in 1987 intensively surveyed a frontal eddy between  
135 Cape Lookout and Cape Hatteras, providing some of the first evidence that these features  
136 propagate northward and downstream beyond Cape Hatteras, with cross shore and along shore  
137 temperature profiles demonstrating the extent of isotherm doming and continued upwelling  
138 (Glenn & Ebbesmeyer, 1994b). This work suggested that not only did the feature move past  
139 Cape Hatteras, but upwelling continued and a second warm filament formed beyond the cape.  
140 The greatest temperature anomalies from upwelling were measured to occur around ~150m  
141 depth. Later, a longer survey of frontal eddies in the region confirmed the movement of these  
142 eddies north of Cape Hatteras, typically one every 3-7 days, and suggested they are an important  
143 and frequent mechanism for transfer from the SAB and Gulf Stream into the Mid Atlantic Bight  
144 (MAB) slope sea (Glenn & Ebbesmeyer, 1994a). More recent work has demonstrated that Gulf  
145 Stream meanders (including frontal eddies) from the SAB propagate past Cape Hatteras and  
146 slowly decay on their way from the Charleston Bump to The Point (Andres, 2021). Yet beyond  
147 this work and a few others (Churchill & Cornillon, 1991), the literature often views the North  
148 Carolina coast from Cape Lookout northward as a frontal eddy graveyard and thus overlooks the  
149 potential for ongoing ecological impacts of these features.

150



151

152 **Figure 2.** Sea surface temperature (Panel A, SST) and chlorophyll *a* (Panel B, chl-*a*) imagery  
153 annotated to show the structure of the sampled frontal eddy on August 31st, 2021. The warm  
154 streamer is clearly visible as is the cooler and higher chl-*a* eddy core. The chl-*a* image was  
155 acquired 13 hours after the SST image so the eddy is slightly further downstream. Another  
156 frontal eddy is visible downstream off of Cape Hatteras, though the warm streamer has been  
157 pulled into the eddy core and mixed away but is still clearly evident from both the meander in the  
158 stream, the beginning of the formation of a new warm streamer, and the positive chl-*a* anomaly.

159 Frontal eddies form where energy is transferred from the mean flow of the current to  
160 eddy kinetic energy due to instability processes, often influenced by the local bathymetry. In the  
161 northern SAB (Charleston to Cape Lookout, where the eddy in this study formed), this energy  
162 transfer is enhanced by the Charleston Bump which deflects the Gulf Stream offshore (Figure 1).  
163 When small Gulf Stream meanders with positive vorticity pass through this region, this energy  
164 transfer forms mesoscale frontal eddies (see Gula et al 2015 for in depth dynamics). While  
165 typically classified as mesoscale eddies, frontal eddies differ from classic Gulf Stream rings as  
166 they do not detach from the Gulf Stream, but instead remain trapped within the meander of the  
167 current. The main body of the eddy is coastal water entrained by the meander with an upwelled  
168 cold core due to the cyclonic rotation. A shallow warm streamer that flows from the downstream  
169 meander crest upstream and around this entrained coastal water separates the eddy from other  
170 coastal water (Thomas N. Lee et al., 1981). In other regions, specific topographic and current  
171 patterns drive energy transfer but the general mechanism and result are similar e.g. East  
172 Australian Current (Schaeffer et al., 2017), Kuroshio Current (Kimura et al., 1997).

173 Because they are trapped, frontal eddies are subject to shear between Gulf Stream, shelf  
174 waters, and dramatic bathymetry gradients. Frontal eddies are also much less nonlinear than  
175 typical mesoscale eddies (defined as  $U/c$ , the ratio of rotational speed  $U$  to the translational speed  
176  $c$  of the feature). When  $U/c > 1$  the feature is defined as nonlinear, indicating increased  
177 coherence. While a typical Gulf Stream ring might be  $0.2/0.02$  m/s  $\sim 10$ , a frontal eddy could be  
178 approximately  $0.5/0.5$  m/s  $\sim 1$  (Glenn and Ebbesmeyer 1994a), suggesting it is less likely to keep  
179 a coherent structure as it propagates downstream (Chelton et al., 2011). Differences between  
180 frontal eddies and Gulf Stream rings are also described by differences in their Rossby number  
181 ( $Ro = U/fL$ , where  $U$  – characteristic velocity,  $L$  – characteristic length scale,  $f$  – Coriolis  
182 frequency), where a smaller  $Ro$  indicates a more stable eddy (dominated by geostrophic  
183 balance). For our frontal eddy  $Ro = 0.5 / (2.5e-5 * 3e4) = 0.66$  compared to a typical Gulf Stream  
184 ring at the same latitude where  $Ro = 0.2 / (2.5e-5 * 1e5) = 0.008$  suggesting less stability. Rossby  
185 numbers for other frontal eddies such as those in the East Australian Current have been reported  
186 to be similar or higher (0.6-1.9) (Schaeffer et al., 2017). Compared to other mesoscale eddies,  
187 frontal eddies are typically smaller (20-50 km vs. 100+ km), shorter lived (2-3 weeks vs. 6-18  
188 months), and form all year at a higher rate (once every 3-7 days). They often occupy nearly half  
189 or even a majority of the Gulf Stream-shelf edge in the SAB, thus forming an effective and  
190 possibly dominant mechanism for exchange between the Gulf Stream and the shelf (Gula et al.,  
191 2015).

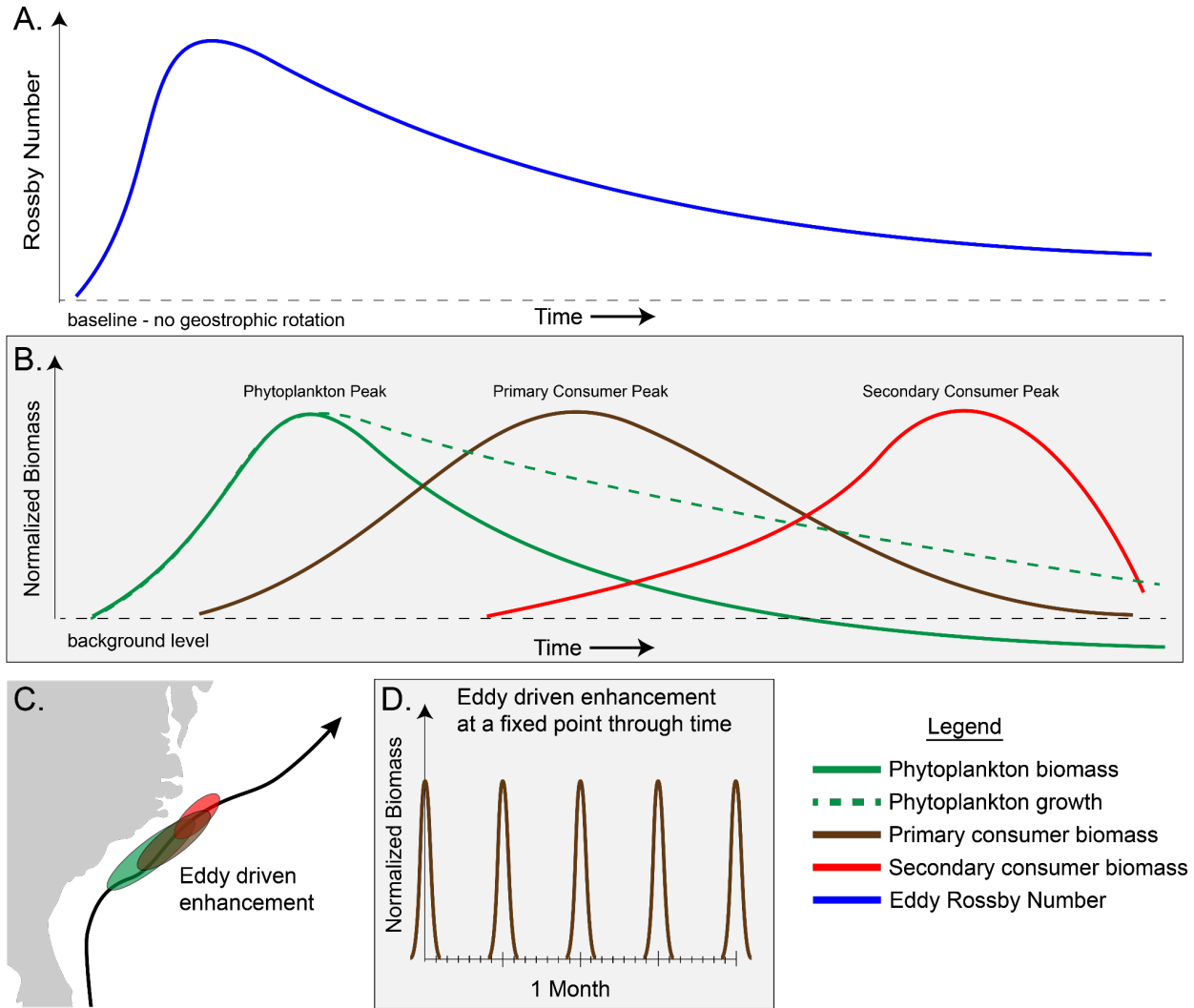
192 Depths of frontal eddies are typically 50-200m (Thomas N. Lee, 1975) along stream  
193 lengths that are 2-3x cross stream. Frontal eddies in this area typically travel at the same speed as  
194 the Gulf Stream meander and are thought to have upwelling on the order of 10 m/day within  
195 200m depth. Important to this upwelling is the deep nutrient core of the Gulf Stream, found  
196 below 100-200m, with concentrations of nitrate  $>10\mu\text{m}$  (Pelegri & Csanady, 1991). Frontal

197 eddies pump the nutrient core up into the euphotic zone via isopycnal uplift driving important  
198 nutrient fluxes into the euphotic zone. For eddies formed around the Charleston Bump, this  
199 generates considerable productivity from Charleston to Cape Hatteras (T. N. Lee et al., 1991).  
200 Recent high resolution modeling ( $dx=150m$ ) shows frontal eddies contain a rich submesoscale  
201 field, localized upwelling, and numerous submesoscale eddies forming on the edge of the frontal  
202 eddy and the Gulf Stream (Gula et al., 2016) with the possibility for major additional biological  
203 implications (Lévy et al., 2018).

204 While the physical and hydrographic dynamics of frontal eddies are reasonably well  
205 understood, how these dynamics impact ecosystem function and composition is not well known.  
206 Most work concludes that these eddies are sheared apart from the Gulf Stream and left stranded  
207 on the outer shelf of the SAB (Lee 1981, 1991), but our work and a few previous studies show  
208 that some of these eddies, though they do experience shear from Cape Lookout to Cape Hatteras,  
209 are still partially coherent and transport their contents to the MAB and possibly far downstream.  
210 In fact, the satellite record shows that a large number of these eddies maintain some coherence  
211 past Cape Hatteras and the remnants of frontal eddies and their warm streamers can often be seen  
212 in SST imagery as far as the Scotian Shelf (Glenn & Ebbesmeyer, 1994a). Some limited work  
213 into the ecosystem implications of frontal eddies in the SAB indicates that the upwelled nutrients  
214 are consumed within 2 weeks and this may drive a zooplankton bloom (McClain & Atkinson,  
215 1985; Paffenhöfer et al., 1987), though that work assumes nitrate was primarily being fluxed  
216 onto the shelf and the eddy was fully dissipating.

217 Based on the literature we developed a simple qualitative conceptual model as a  
218 framework for our study (Figure 3). In this model we expect to see a bloom of phytoplankton  
219 soon after eddy formation, followed by a zooplankton bloom around a week after the  
220 phytoplankton peak, and increased secondary consumers soon after the zooplankton peak. We  
221 expect the biology to lag the physics such that phytoplankton growth above the baseline follows  
222 upwelling by a day or two and terminates soon after upwelling ends. Our study investigates a  
223 single point in time towards the end of the eddy lifetime. Specifically, we examine how physical  
224 and biological properties are spatially structured and differ across the Gulf Stream, frontal eddy,  
225 MAB slope, and MAB shelf waters and use this along with satellite data, and previous work to  
226 understand the natural history of Gulf Stream frontal eddies.





227

228 **Figure 3.** Conceptual model of a frontal eddy from the SAB to the MAB. In Panel A the eddy's  
229 Rossby number is a proxy for geostrophic based upwelling and peaks just after formation and  
230 slowly dissipates as it moves downstream. In Panel B phytoplankton biomass peaks soon (3-5  
231 days) after this peak in upwelling, zooplankton then peaks soon after the phytoplankton peak (5-  
232 7 days), and secondary consumer biomass in the eddy peaks a few days after zooplankton.  
233 Importantly phytoplankton growth is still likely elevated due to upwelling of nutrients even as  
234 standing biomass returns to baseline levels or even below due to grazing. Additionally while  
235 phytoplankton and zooplankton biomass is grown in-place, secondary consumer biomass is not  
236 and instead represents visits. Panel C: while the exact location of these enhancements isn't clear  
237 and is likely variable, this approximately puts the zooplankton enhancement just off Cape  
238 Lookout and Cape Hatteras. Panel D: from a fixed perspective at this peak location, this process  
239 manifests as an enhancement of zooplankton for ~1 day of every 3-7 days year round.

240

### 1.3 Frontal Eddies and the Gulf Stream's separation point

241

242

243

The in-situ focus area for this study is the confluence of the warm and salty SAB, the relatively fresh and cool MAB slope sea water, the even fresher and cooler MAB shelf waters, and the saltiest and hottest Gulf Stream itself (Seim et al., 2022). The anticyclonic rotation of the

244 subtropical gyre, of which the Gulf Stream is the western expression, converges here with the  
245 cyclonic rotation of the slope sea gyre, along with inputs from the MAB shelf water and SAB  
246 shelf water (which typically converge at the Hatteras Front). It is a known biodiversity hotspot  
247 with some of the highest marine mammal diversity in the world (Byrd et al., 2014), major  
248 fisheries for snappers, groupers, tunas, and mackerels, and recreational fishing due to the high  
249 density of major sport fish such as tunas and other billfish.

250 We surveyed a frontal eddy just northeast of Cape Hatteras (Figures 1 and 2) in  
251 September 2021 with a comprehensive set of tools observing the physical, chemical, and  
252 biological status of the region and during both pre-eddy conditions and across the middle of the  
253 eddy.

254 The overall objective of this work is to first investigate the biogeochemical status of this  
255 frontal eddy past Cape Hatteras, where frontal eddies have rarely been sampled, particularly to  
256 see if it contains a different phytoplankton community composition than adjacent waters. Second  
257 we assess if the observations suggest an enhancement of grazers that could be supplying  
258 secondary consumers in this region. And third we use this new understanding to improve our  
259 model of the ecological evolution of eddies from formation to dissolution and their impact on the  
260 outer shelf and Gulf Stream ecosystems where they transit.

## 261 **2 Materials and Methods**

### 262 **2.1 Focal Region**

263 The eddy studied in this work formed off the Charleston Bump on August 25th-26th,  
264 moved past Cape Hatteras on Sept 4th, was surveyed on Sept 5th, 6th, and 7th and moved rapidly  
265 downstream and was dissipating, but still apparent by Sept 9th.

### 266 **2.2 Ship transects**

267 Transects on the R/V Shearwater transited the North Wall of the Gulf Stream in approx  
268 10-15 km lines with five data intensive day time transects and four less data intensive night time  
269 transects. Transects were planned to cross the front between the shelf and eddy or shelf and Gulf  
270 Stream water. In this work we collected nine transects, five in the daytime with a more intensive  
271 approach, and four at night (Figures 1, 4 and S1).

### 272 **2.3 Temperature and Salinity**

273 Temperature and salinity were collected with a SeaBird SBE38 Thermosalinograph  
274 collected via the Shearwater's flow through system from an intake at approximately 1.5m depth.  
275 This data was logged once per second.

### 276 **2.4 Chl-a sampling**

277 In-situ chl-a was measured by filtering 100 mL of seawater onto combusted 0.7  $\mu\text{m}$  GF/F  
278 filters, extracting in 100% methanol for 48 hours, and reading fluorescence on a chlorophyll  
279 calibrated Turner 10AU fluorometer equipped with Welschmeyer filters (Johnson et al., 2010).

280

## 281 2.5 Flow cytometry

282 Duplicate whole seawater samples were collected from the ship's flow through system at  
283 1m depth, fixed with net 0.125% glutaraldehyde and stored at -80 °C until processing.  
284 Prokaryotic phytoplankton populations were enumerated using a Becton Dickinson  
285 FACSCalibur Flow Cytometer and categorized as previously described (Johnson et al., 2010).  
286 Bacterioplankton were quantified using SYBR Green-I on the Attune NxT acoustic flow  
287 cytometer (Life Technologies) (Marie et al., 1997).

## 288 2.6 Nutrients

289 Nutrients were collected by filtering duplicate ~50mL samples through 0.22  $\mu\text{m}$  Sterivex  
290 filters which was stored at -80 °C until analysis at the UCSD Nutrient Analysis facility  
291 (<https://scripps.ucsd.edu/ships/shipboard-technical-support/odf/chemistry-services/nutrients>)  
292 where a Seal Analytical continuous-flow AutoAnalyzer-3 was used to measure silicate, nitrate,  
293 nitrite, phosphate, and ammonia using the analytical methods described by (Atlas et al., 1971;  
294 Gordon et al., 1992; Hager et al., 1972).

## 295 2.7 Optical and CDOM

296 Hyperspectral absorption ( $a$ ), attenuation ( $c$ ), and the volume scattering function (VSF) at  
297 120 deg and 470, 532, and 650 nm were measured continuously (4 Hz, 4 Hz, and 1 Hz  
298 respectively) for the duration of this work.  $a$  and  $c$  were measured at 81 wavelengths 399 to 736  
299 nm using a WetLabs ACS spectrophotometer and VSF was measured at 120 deg at 470, 532, and  
300 650 nm using a WetLabs ECO-BB3 which was converted to backscattering ( $b_b$ ) measurements.  
301 Both instruments were manually switched between running 0.2  $\mu\text{m}$  filtered sea water and total  
302 ("normal") sea water the rest of the time. Filtered seawater was run before and after each transect  
303 and absorption, attenuation, and backscattering during the filtered period were linearly  
304 interpolated and subtracted from the total sea water values to get the particulate  $a$  ( $a_p$ ),  $c$  ( $c_p$ ), and  
305  $b_b$  ( $b_{bp}$ ). This setup allows retrieval of particulate optical properties independently from  
306 instrument drift and biofouling (Slade et al., 2010). This data was collected using Inlinino  
307 (Haëntjens & Boss, 2020), an open-source logging and visualization program, processed using  
308 InlineAnalysis (<https://github.com/OceanOptics/InLineAnalysis>) following (E. Boss et al., 2019).  
309 Colored dissolved organic matter (CDOM) was also measured with a Seapoint Ultraviolet  
310 Fluorometer logged on a DataQ DI-2108 to Inlinino. (See supplemental material for more  
311 detailed processing overview)

312 These inherent optical properties (i.e., absorption, attenuation, and backscattering) and  
313 products calculated from them were used as proxies for a range of particulate properties.  $\gamma$ ,  
314 which is estimated as the spectral slope of  $c_p$ , is a strong proxy for particle size distribution with  
315 a higher  $\gamma$  indicating smaller average particle sizes (Emmanuel Boss et al., 2001). Scattering is  
316 driven primarily by particle concentrations, and backscattering is sensitive to both particle  
317 refractive index and concentrations, thus the backscattering ratio (i.e. backscattering to  
318 scattering) normalizes concentration and varies primarily with refractive index, serving as a  
319 proxy for particle composition (Twardowski et al., 2001). A proxy for phytoplankton size  
320 (HH\_G50) based on anomalous dispersion in the narrow chl- $a$  absorption band around 676 nm is  
321 also reported (Houskeeper et al., 2020). The last optical proxy we used is phytoplankton pigment  
322 concentrations derived from a gaussian decomposition of the particulate absorption spectrum  
323 following (Chase et al., 2013). This approach uses a series of gaussians placed at the same

324 location as various pigment absorption peaks and minimizes the difference between a spectrum  
325 constructed of these gaussians with the measured spectrum. This gives the approximate  
326 concentration of a range of pigments that can be used as a proxy for various phytoplankton  
327 taxonomic groups.

## 328 2.8 Underway Profiling

329 Profiles were conducted with a Rockland Scientific VMP-250 which collects S, T,  
330 chlorophyll-a fluorescence, turbidity (via optical backscatter at 880nm), and turbulence. This  
331 instrument was operated in a tow-yo mode on a winch which allowed it to freefall and then be  
332 quickly reeled back in and repeated. Profiles were deployed to roughly 100m depth  
333 approximately every 500-800m along track. Only downcasts were used.

## 334 2.9 O<sub>2</sub>/Ar-based Net Community Production

335 Net Community Production (NCP), a measure of the net production minus net respiration  
336 in the system, was estimated by continuously measuring O<sub>2</sub>/Ar ratios in the seawater using  
337 Equilibrator Inlet Mass Spectrometry. Briefly, the biological oxygen supersaturation in the  
338 mixed layer was calculated following:

$$339 \quad \Delta \left( \frac{O_2}{Ar} \right) = \left[ \frac{\left( \frac{O_2}{Ar} \right)_{meas} - 1}{\left( \frac{O_2}{Ar} \right)_{sat}} \right]$$

340 where  $(O_2/Ar)_{meas}$  is the ratio of O<sub>2</sub> and Ar measured in the seawater and  $(O_2/Ar)_{sat}$  is the ratio of  
341 O<sub>2</sub> and Ar in the air. Mixed layer depth (MLD) was calculated using a change of 0.1kg m<sup>-3</sup> from  
342 the surface density based on VMP-250 profiles. MLD was interpolated linearly to get to 2-  
343 minute average ML. MLD was fairly consistent in the shelf, slope, eddy, and Gulf Stream water  
344 types and thus night time MLD was based on day time MLDs and water type. NCP was  
345 calculated following:

$$346 \quad NCP = \Delta \left( \frac{O_2}{Ar} \right) \times O_{2sat} \times \rho \times k$$

347 where  $O_{2sat}$  represents the saturated oxygen concentration ( $\mu\text{mol kg}^{-1}$ ) ([Garcia and Gordon 1992](#)),  
348  $\rho$  represents the density of the seawater ( $\text{kg m}^{-3}$ ), and  $k$  represents the weighted gas transfer  
349 velocity ( $\text{m d}^{-1}$ ) calculated following ([Wanninkhof, 2014](#)) and ([Reuer et al., 2007](#)), with  
350 modifications from ([Teeter et al., 2018](#)). NCP is reported here in units of  $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ . 6-  
351 hour wind speed data were downloaded from the ERA 5 REanalysis dataset  
352 (<https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5>). More detailed NCP  
353 calculation methods can be found in ([Cassar et al., 2009](#)).

## 354 2.10 ADCP

355 Ocean velocity data was collected using a Nortek Signature 500 VM Acoustic Doppler  
356 Current Profiler. This instrument operates at 500kHz and collects horizontal current vectors and  
357 acoustic backscatter. From this, current speed, direction, and shear were calculated along with  
358 backscatter strength. Vertical profiles of these measurements were binned in 1m increments from  
359 ~1 to 60m depth.

360

## 361 2.11 Satellite data

362 We used multiple ocean-observing satellites to provide context for the vessel-based  
363 sampling. Chl-a products were derived from the European Commission Copernicus programmes  
364 Sentinel-3's Ocean and Land Color Instrument (OLCI) and the Ocean Colour Climate Change  
365 Initiative's multi-sensor global satellite chl-a product (Sathyendranath et al., 2019). The OLCI  
366 data was used to track chl-a within the eddy over its lifetime. Sea surface temperature products  
367 were from the Geostationary Operational Environmental Satellite 16 (GOES-16). OLCI Level 2  
368 and obtained from <https://codas.eumetsat.int>, OC-CCI chl-a was version 5.0 eight day composites  
369 from <https://www.oceancolour.org/>, and GOES-16 hourly SST was acquired from  
370 <https://cwcmom.aoml.noaa.gov/erddap/griddap/goes16SSThourly.html>.

## 371 2.12 Delineating the water masses based on Salinity and Temperature

372 Analysis is primarily based on a continuous view of water properties, given the amount  
373 of turbulent mixing occurring along the front, but we also divide water masses into discrete  
374 categories of shelf, slope, eddy, and Gulf Stream based on temperature and salinity. That  
375 delineation is done by categorizing all water where Shelf < 34 PSU, 35.75 PSU > Slope > 34  
376 PSU, 28.2 C > Eddy > 35.75 PSU, and Gulf Stream > 28.2 °C as shown by the T-S diagram in  
377 Figure 4 and 5.

## 378 2.13 Eddy Microbiome

379 A companion study was conducted which focused on the microbiome of the eddy and  
380 adjacent water masses (Gronniger et al., 2023). This companion work ran 16SrRNA gene  
381 sequencing on the same water samples as our flow cytometry and nutrient analysis and compares  
382 the genetic makeup of microbes across the physical structures we studied. The results of  
383 Gronniger et al (2023)'s work are summarized and included in the discussion of this study for  
384 context.

## 385 3 Results

386 Our data indicate multiple distinct water masses and clear transitions between the shelf,  
387 slope, eddy, and Gulf Stream water (Figure S2). While most biogeochemical properties shift  
388 gradually and monotonically across water types, some measured parameters cluster into four  
389 distinct groups matching the independent discrete T-S based definitions (Figure 5). Salinity and  
390 temperature increase from shelf to slope to eddy to Gulf Stream, while CDOM, phytoplankton  
391 size, *Synechococcus*, and bacteria all decrease along this continuum. Physically, the eddy water  
392 is similar to Gulf Stream salinity, but is slightly cooler in temperature and thus denser. After  
393 classifying water masses based on T and S more nuanced patterns are visible (Figure 6). At first  
394 glance, the eddy appears to be on the continuum between slope and Gulf Stream water or, at  
395 times, indistinguishable from the Gulf Stream. This is true for most of the optical proxies.  
396 Measurements of  $c_p$  are similar in the shelf, slope, eddy, and Gulf Stream waters (Figure S4).  $c_p$   
397 is dominated by  $b_p$  in all water masses, though  $a_p$  is a substantially larger proportion of  $c_p$  in the  
398 400-500nm range in the shelf compared to eddy and Gulf Stream water (Figure S5) as we might  
399 expect given the higher chl-a concentrations on the shelf. The backscattering ratio at 440nm  
400 (representative of refractive index and thus composition) generally decreases marginally as we  
401 move offshore, indicating slightly more organic relative to inorganic particles. Phytoplankton  
402 size (via HH\_G50) decreases monotonically with CDOM as we move offshore, though

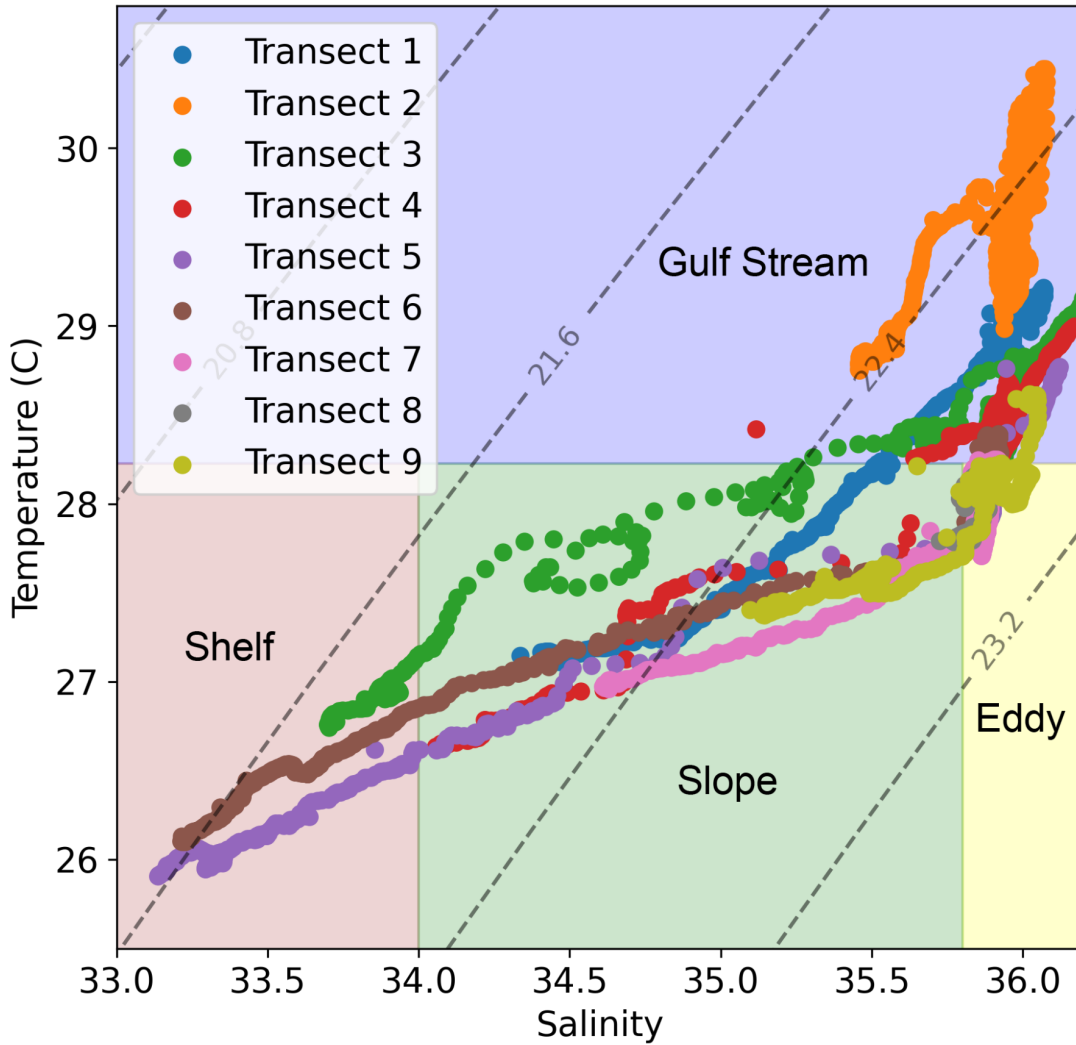
403 surprisingly  $\gamma$  (negatively correlated with the particle size distribution) decreases as we move  
404 offshore, indicating larger particles offshore compared to inshore, in contrast to HH\_G50 trends.

405 A few properties however reveal the eddy as distinct from the Gulf Stream, with depleted  
406 nitrate and silicate compared to the Gulf Stream water, enhanced non-phycoerythrin containing  
407 picocyanobacteria compared to all other water masses, the highest bacteria to chl-a ratio, and  
408 lowest volumetric NCP (Figures 5 and 6). In the eddy  $c_p$ (460), and  $b_{bp}$ (440), and  $\gamma$  are marginally  
409 lower compared to Gulf Stream (Figures 5 and 6).

410 Profiling data shows a MLD of  $\sim 10$ m for shelf and slope water with eddy or Gulf Stream  
411 water underlying that shallow shelf/slope water and a second thermocline around  $\sim 30$ -50m. The  
412 MLD for the eddy ranges from approximately 30-50m and Gulf Stream is the same range from  
413 35-55m. Calculating MLD at the front at these scales is often problematic given the intense  
414 mixing and turbulence across the front, so these exact depths should be interpreted with caution.  
415 We observe a fairly consistent cold and fresh intrusion (Figure S8) moving from the shelf to the  
416 Gulf Stream and converging with the Gulf Stream that could be of Arctic or northern slope origin  
417 given the temperature ( $<15^\circ\text{C}$ ) and salinity (33-33.5 PSU, comparable to shelf). While not the  
418 focus of this study, this cold and relatively fresh layer has intense structuring of both chl-a  
419 fluorescence and echosounder volume backscatter.

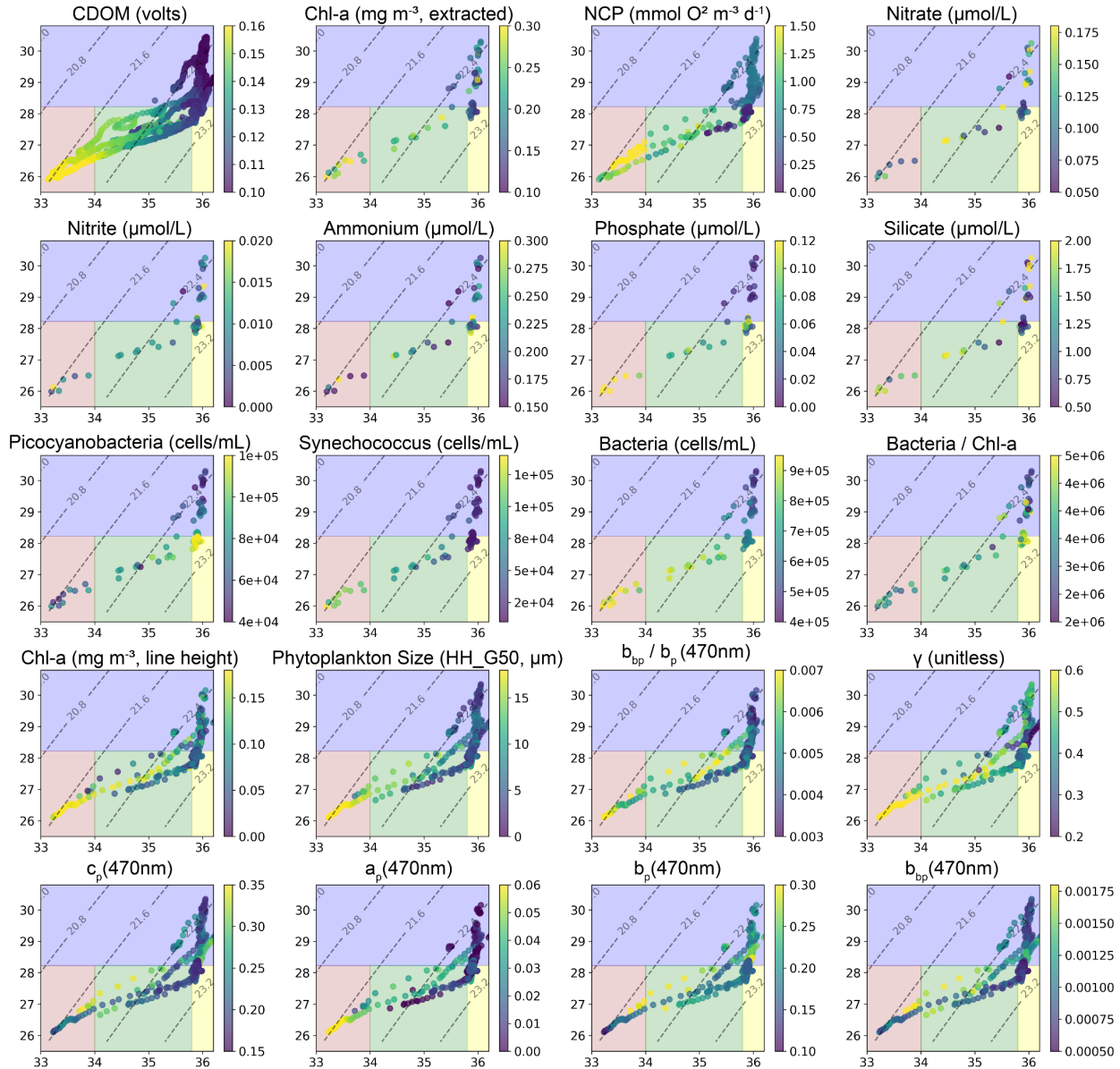
420 ADCP data supports conclusions from profiling and surface categorizations, showing  
421 faster current speeds in the Gulf Stream water vs eddy water and cyclonic rotation in Transect 9  
422 (T9, Figure 8). Echosounder data from the ADCP shows fairly consistent backscatter responses  
423 in Gulf Stream and Eddy water and much stronger backscatter in the shallow shelf water (Figure  
424 9). This acoustic backscatter data also shows a thin layer at the thermocline of the eddy that isn't  
425 apparent in the Gulf Stream water (Figure 8).

426 Looking back over the satellite record indicates a monotonic decrease in chl-a at each  
427 observation time step from eddy formation until our survey work (Figure 7).



428

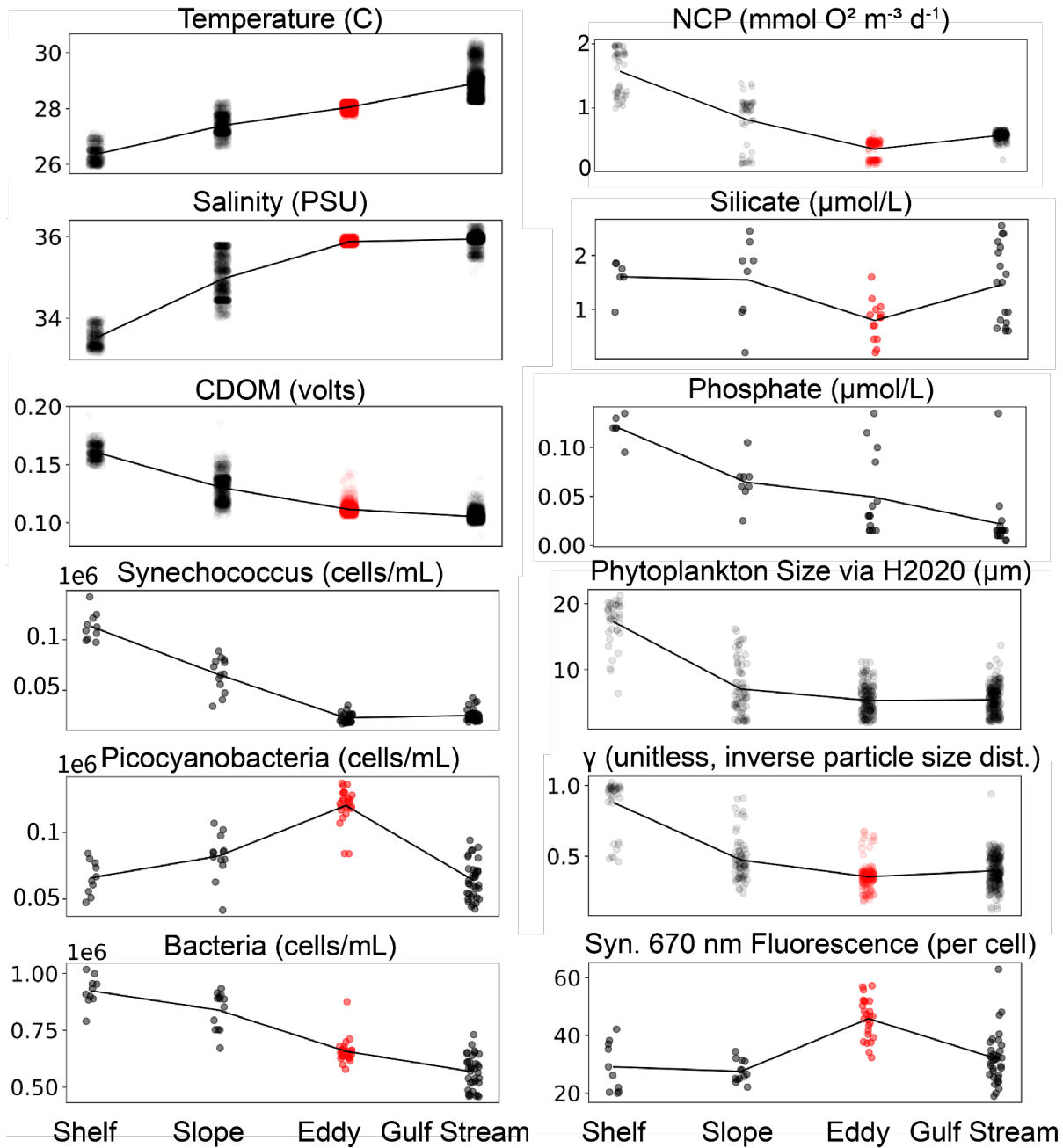
429 **Figure 4.** All nine transects are plotted together on a Temperature-Salinity diagram. Isopycnals  
430 are shown with dashed gray lines across the plot. The reddish section with low temperature and  
431 low salinity is the shelf water, green is the slope water, yellow is the eddy, and blue is the Gulf  
432 Stream.  
433



434

435 **Figure 5.** Measured parameters are shown on these T-S diagrams with salinity on the x-axis and  
 436 temperature on the y-axis. CDOM shows the expected general trend of decreasing dissolved  
 437 organic matter as you move from the shelf (colder and fresher) to the Gulf Stream (hotter and  
 438 saltier). While many properties show a general increase or decrease from the Gulf Stream to the  
 439 shelf - with the eddy simply near the middle or resembling the Gulf Stream properties - a few  
 440 properties stand out in the eddy from either side. These are namely elevated picocyanobacteria,  
 441 elevated bacteria/chla ratio, depleted silicate, and depleted nitrate.  
 442

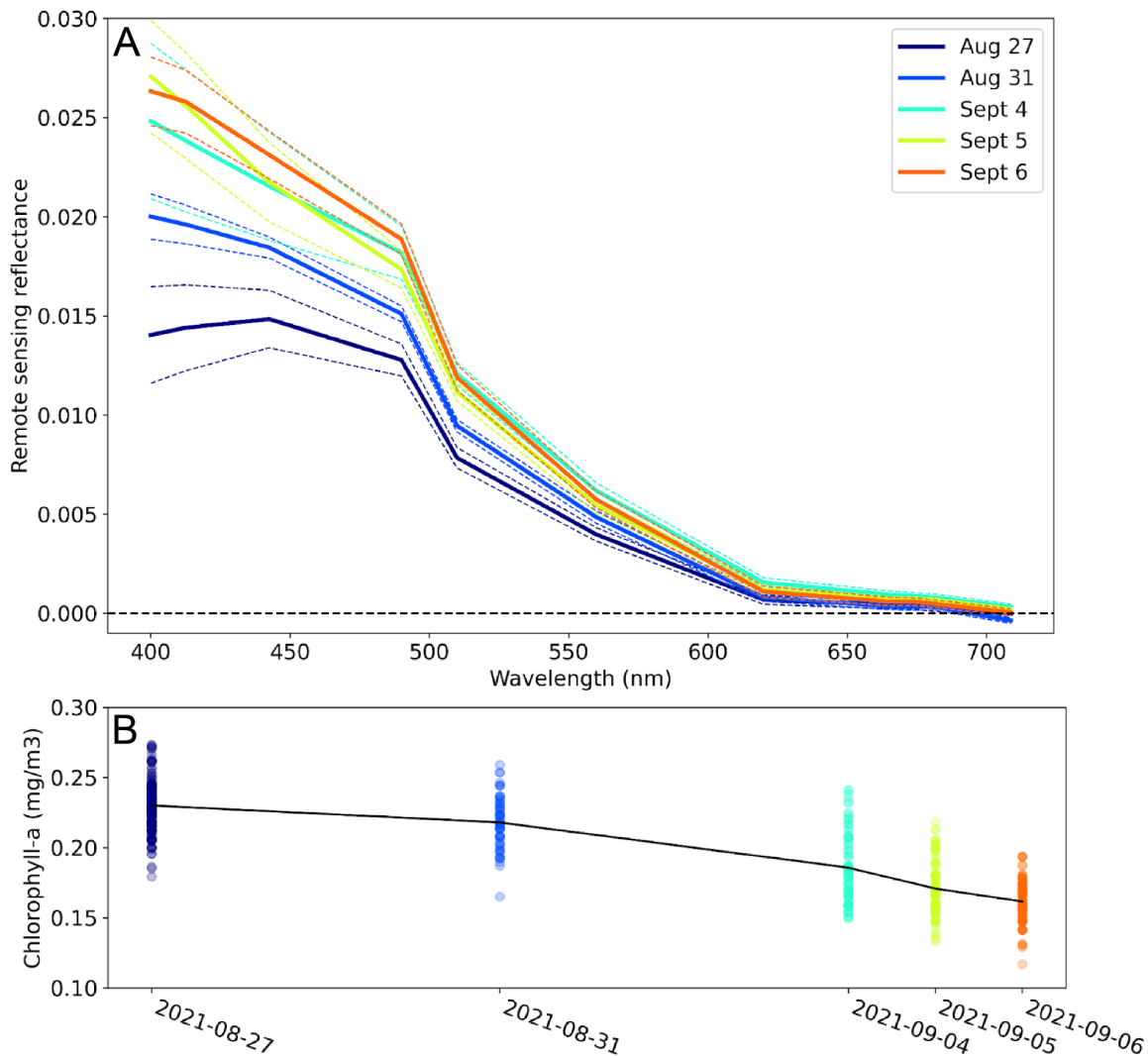




443

444 **Figure 6.** Subset of measured surface variables after classifying water masses into discrete  
 445 groups (shelf, slope, eddy, and Gulf Stream) based on temperature and salinity properties. Red  
 446 color in the eddy samples indicates it is statistically different from all other water masses  
 447 (Welch's T-test with a p value < 0.05). Some variables are simply a continuum through these  
 448 water types, monotonically decreasing as T or S increases (e.g. CDOM, bacteria, PO<sub>4</sub>) and some  
 449 properties are notably different in the eddy and could not be a simple product of mixing (e.g.  
 450 picocyanobacteria, NCP, fluorescence per cell). A few variables including NO<sub>2</sub>, NH<sub>4</sub>, and NO<sub>3</sub>  
 451 are not statistically different between any water mass (e.g. NO<sub>3</sub> ~0.1  $\mu\text{mol/L}$  in all water masses).

452 Not shown here, but fluorescence per cell is nearly identical for non-phycoerythrin containing  
453 picocyanobacteria.



454

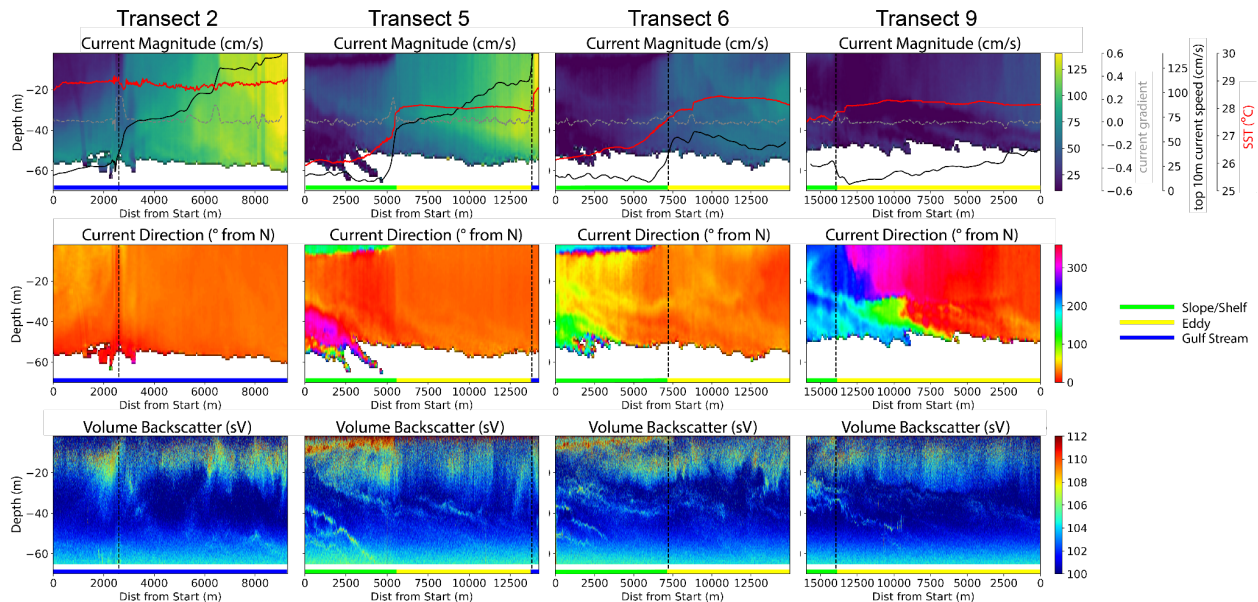
455 **Figure 7.** A. Shows median R<sub>rs</sub> spectra of the eddy from the Sentinel-3 OLCI sensor over the  
456 lifetime of the feature. This shows an increase in the blue wavelengths over time from the  
457 formation of the eddy up until the last day it was coherent and not cloudy. Dashed lines show  
458 standard deviation of spectra within the eddy. Black dashed line demarcates and R<sub>rs</sub> value of 0.  
459 B shows chl-a concentration (calculated via the Hu et al 2012 ocean color index) decreasing  
460 monotonically throughout the observational period, the colors represent the same dates as in the  
461 top panel and the black line connects the means of each time step. All satellite data used in this  
462 figure shown in Figure S1.

463

464 The VMP data reveals the physical structure across all transects, with a general trend of  
465 fresher and less dense shelf/slope water sitting on top of the eddy/Gulf Stream water in a thin  
466 layer 5-20m and under this water is eddy or Gulf Stream water (Figure S8). Then where the

467 shelf/slope water ends at the surface the eddy/Gulf Stream water reaches the surface. The peak in  
468 chl-a fluorescence from VMP data is typically around 30-50m, just below the thermocline.

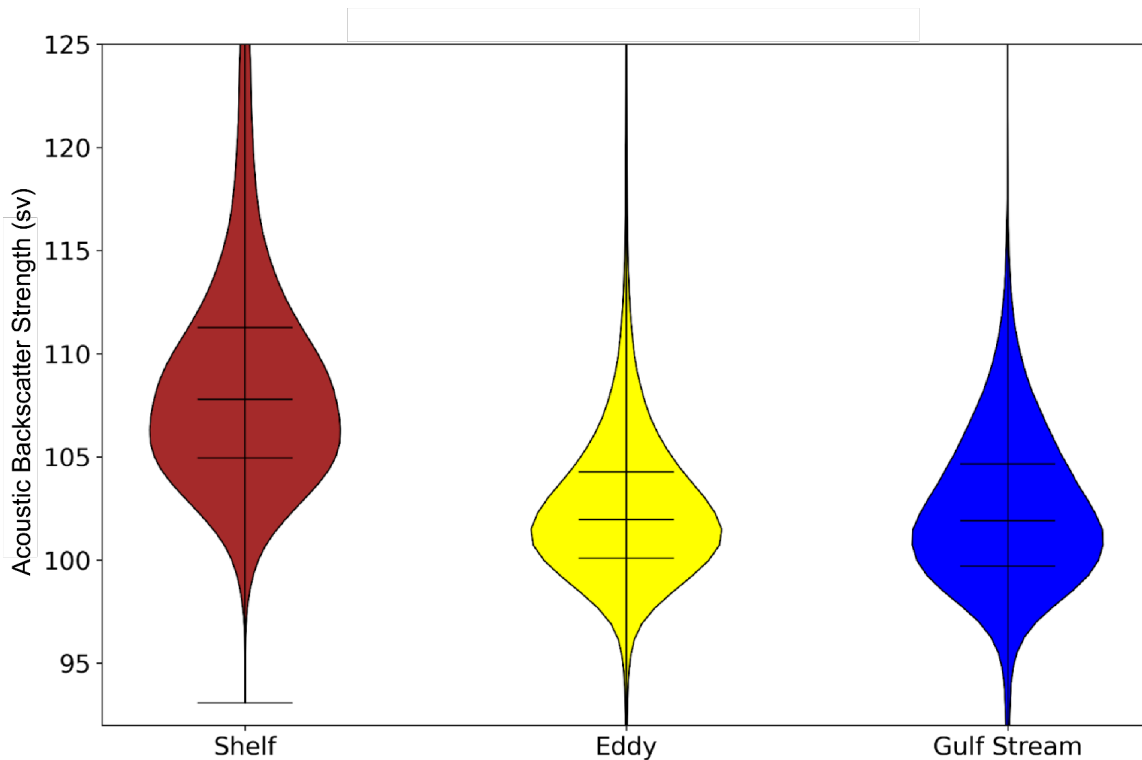
469 On the last transect of the cruise, T9, the ADCP indicates we crossed the entirety of the  
470 eddy near the middle of the feature and we see strong evidence for continued rotation (Figures 8  
471 and S7), though at relatively low speed ( $10\text{-}40\text{ cm s}^{-1}$ ) compared to the Gulf Stream transects (T2,  
472  $150\text{ cm s}^{-1}$ ). The ADCP also shows clear structuring of acoustic backscatter (representative of  
473 zooplankton and small fish). The highest values of acoustic backscatter are in the shelf water.  
474 Within the Gulf Stream and eddy water we observe high backscatter from the surface down to  
475  $\sim 35\text{ m}$  (effectively the mixed layer) and then comparatively low backscatter from  $\sim 35$  to  $\sim 60\text{ m}$ .  
476 From 60m and deeper the data is overwhelmed by noise. As these different water masses are  
477 layered physically, so are the backscatter responses. For example in Transect 6 (T6), around  
478 4000 m into the transect laterally, there is highly scattering shelf water from 0-8 m, then eddy  
479 water with backscatter that eventually decreases further around 30 m, followed by 3-4 thin  
480 backscattering layers of 1-3 m, first at the thermocline where the eddy ends and then above and  
481 below the cold water intrusion.  
482



483

484 **Figure 8.** Current magnitude and direction from the ship-based ADCP are shown in the top two  
485 rows and the third row shows volume backscatter from the echosounder on the ADCP. The  
486 vertical dashed black line is the front as defined by the peak gradient in current, the red line is  
487 sea surface temperature as measured by the ADCP, the black line is current speed, and the grey  
488 line is the current gradient. Current magnitude (top panel) shows clear delineations between shelf  
489 water and the eddy and the eddy and the Gulf Stream. The acoustic backscatter data (bottom  
490 panel) shows the most intense backscatter in the shelf water with some possible structuring from

491 the eddy and strong thin layers from the cold water intrusion below the eddy. Note T2 data is  
492 only from half of the transect due to an instrument error.



493

494 **Figure 9.** Acoustic backscatter strength across water masses from the ADCP. This is the  
495 distribution of acoustic backscatter in the mixed layer for the shelf (down to 10m), eddy, and  
496 Gulf Stream water (both averaged down to 40m). Means are respectively 108.97, 102.56, and  
497 102.34 for the Shelf, eddy, and Gulf Stream water. ADCP measurements were not collected in  
498 the slope water and thus are not represented here.

#### 499 **4 Discussion**

500 Given the frequency of frontal eddies traveling along the Gulf Stream past Cape Hatteras,  
501 it was our goal to understand their state after passing Cape Hatteras and the possible  
502 biogeochemical impacts in the MAB. Using this information, we assess if they could help  
503 explain the productivity of “the Point” of Gulf Stream separation from the continental shelf and  
504 broadly how they may be impacting the MAB.

##### 505 **4.1 Eddy history**

506 The satellite record (Figures 7 and S1) indicates a formation and evolution of the  
507 observed frontal eddy in line with observations from previous studies and recent modeling  
508 (Glenn & Ebbesmeyer, 1994b; Gula et al., 2016; T. N. Lee et al., 1991) and suggests that this  
509 eddy is a typical example of a frontal eddy in this region. The eddy formed off the Charleston  
510 Bump (Figure 1) driving a chl-a and SST anomaly within a Gulf Stream meander. The satellite  
511 data does not show a time-evolving surface bloom compared to the initial shelf waters, but the

512 eddy does initially have higher surface chl-a than the Gulf Stream water. Over the course of two  
513 weeks there is a gradual decrease in chl-a either from die off or mixing with Gulf Stream water.  
514 This lack of a satellite-visible increase in chl-a when compared to the initial shelf conditions  
515 could be due to enhancement of growth occurring at a depth below that detectable by satellite,  
516 from a concomitant increase of grazers, or limited upwelling. We suggest it is a combination of  
517 enhancement at depth and then grazers based on previous work on frontal eddies in the SAB and  
518 across the globe (Glenn & Ebbesmeyer, 1994a; Gula et al., 2016; Kasai et al., 2002; Yoder et al.,  
519 1981). The satellite record shows the eddy had been coherent for two weeks at the time of our in-  
520 situ observations.

#### 521 4.2 Physical status during cruise

522 During our cruise the eddy was still mostly coherent with consistent physical properties  
523 across the feature and continued cyclonic rotation, which, while weak, would likely be driving a  
524 negative SSH anomaly and upwelling within the eddy, possibly still enhancing productivity.  
525 However, higher resolution and deeper sampling within the water column would be needed to  
526 reveal the eddy's core and any stimulation of primary producer biomass.

527 On T6 we observe what is likely the remains of the frontal eddy's warm streamer that has  
528 been pulled into the body of the eddy (Figure S2 for a detailed description of each transect along  
529 with S and T). It is apparent from the surface to ~30m depth where temperature and salinity are  
530 higher than the rest of the eddy and cell counts from flow cytometry are closer to the Gulf  
531 Stream. Salinity and temperature in this warm streamer are intermediate between Gulf Stream  
532 and eddy, likely representative of the intense mixing that occurs in frontal eddies (Gula et al.,  
533 2016), especially past Cape Hatteras where they begin to dissipate.

#### 534 4.3 Ecological observations

535 In spite of predicted upwelling at depth, in general the eddy has more oligotrophic  
536 conditions compared to the other water masses, with lower silicate and  $\text{NO}_3$  in the eddy  
537 compared to Gulf Stream and slope waters and enhanced non-phycoerythrin containing  
538 picocyanobacteria (a group which contains *Prochlorococcus*) compared to other water masses  
539 (Figure 6). While cyclonic eddy dissipation will relax the isopycnal uplift, causing downwelling  
540 (see Figure 5 in McGillicuddy, 2016), it is unclear exactly how this process works within frontal  
541 eddies and if the timeline matches for this to help explain the more oligotrophic conditions.  
542 Combined with the nutrient data which reveals lower silicate and  $\text{NO}_3$  in the eddy compared to  
543 Gulf Stream and slope waters, this suggests a shift to a microbial loop dominated system. The  
544 highest bacteria to chl-a ratio occurs within the eddy, suggestive of post-bloom conditions  
545 (Buchan et al., 2014). NCP is another variable in support of post-bloom conditions with the  
546 lowest volumetric NCP being measured in the eddy, slightly lower than the Gulf Stream  
547 conditions and substantially lower nearer the core of the eddy on the final study day (Figure 5).

548 A companion study (Gronniger et al., 2023), focused on the eddy microbiome, was  
549 undertaken on the same flow-through surface samples and similarly reveals differences in  
550 microbial community composition between water masses. This companion study found that the  
551 eddy harbored higher abundance of *Prochlorococcus* and lower abundances of *Synechococcus*  
552 and *Pelagibacteraceae*. However, despite differences between the Gulf Stream and eddy  
553 microbiomes, including higher abundances of *Prochlorococcus* in the eddy and higher  
554 abundances of the nitrogen-fixer *Trichodesmium* in the Gulf Stream (see also Figure 6), the eddy

555 is most similar to the Gulf Stream relative to the other water masses, suggesting that assembly of  
556 the eddy microbiome is primarily determined by environmental filtering in these warm, low  
557 nutrient waters. Gronniger et al (2023) clustered the microbiome data and compared this to the  
558 physical delineations which showed that the discrete physical classes used here do not fully  
559 reflect microbiome clusters, likely due to the intense submesoscale dynamics in this region.

560 Fluorescence per cell via flow cytometry is highest in the eddy and in frontal regions  
561 (Figure 6). This was not our expectation considering higher fluorescence per cell can be  
562 indicative of either more nutrients or more pigments per cell. We thus would expect the slightly  
563 lower nutrient conditions in the eddy to result in lower fluorescence per cell. Because higher  
564 fluorescence per cell can also indicate cells physiologically acclimatized to lower light levels,  
565 this may indicate mixing from depth in these regions or higher nutrient uptake rates, not reflected  
566 in free nutrient concentrations (Figure 6).

567 Acoustic backscatter shows substantial structure in all water masses (Figure 8). As  
568 expected, the shelf water, which had the highest chl-a values, has the highest acoustic  
569 backscatter. The Gulf Stream and eddy water are not statistically different with respect to  
570 backscatter (Figure 9), though in all eddy transects there is a clear thin layer of enhancement in  
571 backscatter around the thermocline of the eddy that does not appear in the Gulf Stream water  
572 (Figure 8). Given the limited number of samples, it is possible this difference is related to other  
573 factors and not the dynamics of the eddy itself. The cold water intrusion also appears to drive  
574 thin layers in acoustic backscatter above and below the feature. Interestingly, the peak in chl-a  
575 fluorescence from the VMP data is sometimes shifted down by ~15m from the acoustic  
576 backscatter peak. This could be due to grazing decreasing biomass and thus fluorescence, non-  
577 photochemical quenching of fluorescence in the better-lit upper layer, the relatively high  
578 1000kHz sampling frequency not picking up on the grazers consuming the phytoplankton, or  
579 actual partitioning in habitat. While some combination of these various factors is the most likely  
580 explanation, this is nonetheless a surprising finding. It is unlikely quenching is drastically  
581 different at 35m vs 45m and could suggest that in this region standing phytoplankton biomass  
582 (here proxied by chl-a) is not a good representation of productivity.

#### 583 4.4 Particle Size Surprises

584 One interesting note from this work is the divergence of  $\gamma$  (proxy for mean particle size)  
585 from typical patterns.  $\gamma$ , which is sensitive to particles in the size range from approximately 3-30  
586  $\mu\text{m}$  (Emmanuel Boss et al., 2001), generally corresponds to chl-a concentration, based on the  
587 commonly found relationship that higher chl-a corresponds to larger phytoplankton. Thus, we  
588 would expect a decrease in mean particle size as we move from coastal water (high chl-a and  
589 larger particles) to oligotrophic water (low chl-a and smaller particles) (Emmanuel Boss et al.,  
590 2013; Buonassissi & Dierssen, 2010). In this study, we instead see an increase in particle size  
591 and a decrease in chl-a as we move from shelf water further offshore into the eddy and Gulf  
592 Stream (Figures 5 and 6).

593 In general, most particles in the open ocean are phytoplankton or detritus. The observed  
594 increase in the mean particle size offshore is unlikely to be indicative of phytoplankton based on  
595 HH\_G50 which shows decreases in phytoplankton size offshore - following expectations of a  
596 positive relationship between chl-a and phytoplankton size. The particles driving  $\gamma$  are therefore  
597 unlikely to be live phytoplankton. The backscattering ratio decreases marginally as we move  
598 offshore suggesting the particles influencing  $\gamma$  are relatively more organic, just not chl-a

599 containing. Another relevant piece of evidence,  $b_p$  is not only spectrally flatter in the Gulf Stream  
600 (driving  $c_p$  to be flatter and lower  $\gamma$ ), but actually higher overall, indicating higher particle  
601 concentrations.

602 So more particles, larger average particle sizes, and particles that are similarly or  
603 relatively more organic than those inshore. This leads us to the conclusion that it is either due to  
604 an enhancement of small heterotrophs or possibly detritus and non-algal particles within the eddy  
605 and Gulf Stream waters. This could be suggestive of grazer enhancement in the eddy, though  
606 again this is not specific to the eddy. It could also be due to an accumulation of buoyant particles  
607 near the front.

608 The relative consistency of  $\gamma$  and HH\_G50 between eddy and Gulf Stream waters  
609 suggests whatever process is influencing this divergence from expectations is not an eddy  
610 specific phenomenon, or if it is, that the resultant particulate impact is mixed into Gulf Stream  
611 waters and is possibly persistent between eddies.

#### 612 4.5 Impact of frontal eddies on grazers

613 While relevant studies investigating consumer response to frontal eddies are rare,  
614 previous work shows that copepods and doliolids increase substantially in response to  
615 phytoplankton enhancement in frontal eddies. In this case these zooplankton exhibited minimal  
616 vertical migration, with maxima near the thermocline, suggesting they would likely be entrained  
617 in the frontal eddy and move with it north of Cape Hatteras (Paffenhöfer et al., 1987). The  
618 timeline of this increase in zooplankton is variable across taxa, but in this work, the authors  
619 found zooplankton increased dramatically from five days to two weeks after peak chl-a  
620 concentration, and peak chl-a concentration was approximately a week after eddy formation.  
621 Similar work has shown that copepods, which are slower to respond, may persist for a few  
622 weeks, and doliolids which respond within days, were also found to decrease faster, persisting  
623 for 7-9 days (Deibel, 1985). This work was done on the southern half of the SAB (with eddy  
624 generation around Florida and dissipation just upstream of the Charleston Gyre) and may have  
625 different characteristics than the northern section of our study, but if we assume similar  
626 responses, zooplankton abundance should peak right when the eddy is passing Cape Hatteras.

627 Our acoustic data does not support an enhancement of zooplankton and small fish  
628 biomass in the eddy compared to Gulf Stream water at the time of our measurements (Figure 9).  
629 The variability of some transects adds substantial uncertainty to these comparisons and we don't  
630 have a "pure" Gulf Stream endmember for comparison. Modeling shows substantial diapycnal  
631 mixing between these eddies and the Gulf Stream (Gula et al., 2016), possibly contributing to the  
632 lack of clear distinction in acoustic backscattering between these water masses. We do see  
633 structuring of acoustic backscatter (i.e. zooplankton and fish) with a clear partitioning at the  
634 thermocline of the eddy and an increase just below it which is not observed in the Gulf Stream  
635 data. This could be an indicator of upwelling and higher growth. Adding to the complexity we  
636 observe a large vertical migration via acoustic backscatter into the shelf and eddy water from  
637 around 250 m depth. Considering our eddy has spent two nights off the shelf there is a possibility  
638 a large amount of the potential grazer biomass enhancement has already been consumed by fish  
639 in this migrating layer. To fully parse this out would require a Lagrangian observation approach  
640 over the full lifetime of the eddy.

641 In much of the previous work on frontal eddies the assumption was that these eddies  
642 decayed onto the outer shelf of the SAB, and an ongoing question was that if there is such a  
643 substantial input of nutrients due to upwelling why is the outer shelf of the northern SAB not  
644 more productive in higher trophic levels? We suggest based on our work and previous studies  
645 that a large amount of this new production could be moving into grazer biomass, and while some  
646 of this may occur on the outer shelf edge in the SAB, these features are still typically being  
647 carried by the Gulf Stream into the MAB where they could contribute to the high productivity of  
648 “the Point”. Even where there are subsurface intrusions far up onto the shelf of the SAB due to  
649 frontal eddy upwelling this water is quickly entrained into the Gulf Stream’s northward flow, and  
650 while some of this may stay on the SAB shelf long enough for the grazers to die off or be  
651 consumed themselves, most of it is north of Cape Hatteras within 1-2 weeks, shown both by our  
652 work and previous studies (Glenn & Ebbesmeyer, 1994a). This is a match in time for grazers to  
653 have bloomed following the initial phytoplankton bloom and occurs frequently enough to sustain  
654 elevated levels of secondary consumers. Previous work that did consider the entrainment of  
655 carbon into the Gulf Stream from these processes framed it as a generic export process rather  
656 than explicitly a potential enhancement of zooplankton being delivered directly into the mouths  
657 of hungry fish in the MAB e.g. (T. N. Lee et al., 1991). In this sense the northern SAB could be  
658 thought of as the breadbasket of the southern MAB with frontal eddies providing the fertilizer.

#### 659 4.6 A refined conceptual model

660 Using insights from this work we both place our study into the context of the initial  
661 conceptual model (Figure 3) and refine that model based on our new understanding.

662 We begin with the meander at the Charleston Bump which drives the Gulf Stream further  
663 offshore. Due to this injection of vorticity the Charleston Gyre exists, and periodically (~3-7  
664 days) drives the creation of a frontal eddy and a warm streamer of Gulf Stream water which  
665 encloses this newly formed frontal eddy, partitioning it from the shelf water. We have no in-situ  
666 data during this period, but previous work all supports upwelling due to the cyclonic rotation and  
667 isopycnal uplift as well enhancement (compared to Gulf Stream water) from trapping during  
668 eddy formation (Glenn & Ebbesmeyer, 1994b; T. N. Lee et al., 1991; Yoder et al., 1981). This  
669 combination of productive shelf water and upwelling creates a chl-a anomaly well above the  
670 mean. Upwelling slowly decreases as the eddy dissipates energy as it moves downstream (Gula  
671 et al., 2015). The enhancement in phytoplankton growth enables an increase in grazer  
672 populations, which peaks between Cape Lookout and Cape Hatteras, and sustains an enhanced  
673 level of secondary consumers, possibly contributing to the high level of top predator populations  
674 in this region. By the time the eddy is just north of Cape Hatteras the physics may still be driving  
675 some upwelling but the phytoplankton community has switched to gleaners, possibly in a  
676 microbial loop. This is where we place our study, around the secondary consumer peak and after  
677 phytoplankton biomass has shifted below the baseline. After this shift to smaller cells such as  
678 *Prochlorococcus*, the transfer efficiency to fish and top predators is likely to be substantially  
679 lowered, adding on to the decrease in available phytoplankton (Eddy et al., 2021).

680 Our data shows the eddy from this study has depleted Si compared to Gulf Stream and  
681 slope water suggesting a possible recent diatom bloom. It has the highest ratio of bacteria : chl-a  
682 and lowest NCP again suggestive of post-bloom conditions. The eddy also has a higher ratio of  
683 mean particle size : chl-a indicating either an enhancement of micro grazers along with the  
684 picocyanobacterial or more detritus per unit chl-a. Both flow cytometry and molecular



685 sequencing show a different community composition dominated by picocyanobacteria and  
686 particularly *Prochlorococcus* - again suggestive of a switch to the microbial loop. Thus we  
687 hypothesize the eddy arrives at Cape Hatteras with enhanced grazer biomass due to the previous  
688 phytoplankton bloom and that these grazers are consumed by the large migrating layer we  
689 observed.

690 Within the SAB frontal eddies are thought to have a dominant impact on nitrogen fluxes  
691 on the outer shelf (T. N. Lee et al., 1991) - with a huge impact on the ecology of the SAB outer  
692 shelf. Based on our observations, frontal eddies do not appear to supply phytoplankton into the  
693 MAB, but are possibly an efficient shuttle of grazers into the highly productive southern MAB  
694 which is thought to have some of the highest marine mammal diversity in the world and is a  
695 productive fishing ground (Byrd et al., 2014).

696 Given the complexity and dynamic nature of this region we can only hypothesize the  
697 impact of frontal eddies on the overall ecosystem of the SAB and MAB (see supplemental  
698 material for extended caveats). In future studies we need a Lagrangian survey approach over the  
699 entire lifetime of the eddy. With acoustic backscatter and discrete net tow samples we could  
700 identify the density and type of zooplankton within the eddy. In this work we focused on surface  
701 samples but a large component of the frontal eddy driven enhancement may be below the  
702 thermocline as it is lifted into a more favorable light environment. A fleet of autonomous assets  
703 would facilitate a more synoptic view of the eddy. A survey design similar to (Zhang et al.,  
704 2021) with AUVs and gliders to assess the full physical and biogeochemical status could enable  
705 a test of our hypothesis. This could be an ideal exercise for high resolution modeling to examine  
706 the MAB ecosystem with and without frontal eddies.

#### 707 4.7 Broader Context

708 A similar process may be happening just upstream (south) of the Charleston Bump,  
709 where the timeline matches up for the enhancement of grazers after frontal eddy enhancement  
710 from Miami to Charleston and possibly complemented by a longer duration stay in the Gyre.  
711 Even more generally, anywhere a western boundary current follows the continental shelf and the  
712 system is nutrient limited frontal eddies may be a reliable mechanism for increasing primary  
713 production and transfer efficiency to higher trophic levels.

## 714 5 Conclusions

715 We show in this work that frontal eddies do in fact often get advected north past Cape  
716 Hatteras, can still have cyclonic rotation, and have nutrient profiles and phytoplankton  
717 community compositions distinct from adjacent water masses even in dissipation. We  
718 hypothesize they may be well timed to supply zooplankton to secondary consumers between  
719 Cape Lookout and Cape Hatteras. Synthesizing previous literature we share a simple conceptual  
720 model for the ecosystem impact of frontal eddies and place our study within that model and add  
721 refinements. Given the frequency of frontal eddies moving along the Gulf Stream this may be a  
722 mechanism for substantial enhancement of phytoplankton, zooplankton, and secondary  
723 consumers - particularly at the highly productive separation point of the Gulf Stream jet. We  
724 suggest further work on frontal eddies in the Gulf Stream and other western boundary currents to  
725 see if this is a general phenomenon.

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## 737 Open Research

738 The code to recreate this analysis are available at <https://doi.org/10.5281/zenodo.7685135>  
739 (Gray, 2023) and all data used in this study is available at  
740 <https://doi.org/10.5281/zenodo.7680135> (Gray et al., 2023). All code is shared with an MIT  
741 License for free reuse. We have provided multiple Jupyter Notebooks that go from raw or  
742 initially processed data to the nearly complete figures shown in the paper. The python  
743 environment used can be easily and exactly reproduced using the pangeo-notebook a Docker  
744 image <https://github.com/pangeo-data/pangeo-docker-images/tree/master/pangeo-notebook> as  
745 detailed in the Github repo.

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