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Seabird affinities for Gulf Stream frontal eddies: Responses of mobile marine consumers to episodic upwelling

by J. Christopher Haney[1,2]

ABSTRACT

This study combined ship-board counts of seabirds with satellite hydrography to determine whether Gulf Stream frontal eddies influenced spatial and seasonal patterns of apex consumers on the southeastern United States continental shelf and slope. Stratified sampling indicated seabird densities at eddies were 7–15× higher than in resident shelf and Gulf Stream water, ranging from 2.31–10.91 birds km^{-2} compared to 0.15–1.51 birds km^{-2} in noneddy regions. At any given time eddies covered 3–17% of the outer shelf and upper slope, yet 28–59% of total seabird numbers in this domain aggregated within areas influenced by eddies.

Gulf stream eddies consist of an upwelled, nutrient- and phytoplankton-rich cold-core and an oligotrophic warm filament entrained from the Gulf Stream. Seabird densities within eddy cold-cores were 4–21× higher, ranging from 2.91–16.35 birds km^{-2} compared to 0.16–3.70 birds km^{-2} in the warm filament. Seabird abundances within eddy cold-cores were higher (a) near the frontal boundaries between water masses, and (b) within older upwelled (upstream) cold-core water as opposed to recently upwelled (downstream) cold-core water.

Eddy size accounted for 99%, 94%, and 98%, respectively, of the between-eddy variation in seabird abundance, biomass, and minimum daily food requirements per unit area. Between-eddy differences in seabird density, biomass, and food requirements showed no relationship to eddy age.

The frequency and the extent of satellite-detected, near-surface upwelling originating from eddies on the outer shelf and upper slope decreased during late summer and early fall. Total seabird density (pooled species' abundances) showed no relationship to this seasonality. However, taxa that are particularly dependent on upwelling (Family Hydrobatidae: *Oceanites* and *Oceanodroma*) exhibited declines in abundance that correlated with seasonal decreases in near-surface upwelling. Seabird patchiness within the outer shelf and upper slope was greatest during months of frequent eddy upwelling, indicating that small-scale seabird distribution within domains may be affected by upwelling seasonality.

Eddies influence seabird distribution and abundance at space scales of 10–50 and 50–150 km, and at time scales of 2–14 and 30–180 days. Seabird responses to environmental heterogeneity caused by eddies give strong circumstantial evidence for energy transfer beyond primary producers at these episodic upwelling features.

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1. Introduction

The continental shelf off the southeastern United States is unique in its proximity to a major western boundary current, the Gulf Stream. No slope water mass exists and the Gulf Stream front interacts directly with outer shelf water via variations in the mean flow caused by northward propagating wavelike meanders and cold cyclonic frontal eddies (Lee and Brooks, 1979; Lee *et al.*, 1981). Within the South Atlantic Bight (Cape Hatteras to Cape Canaveral), these features form and degrade during 2- to 14-day periods, have along- and cross-shelf dimensions of 100–200 and 20–50 km, respectively, and propagate along the frontal boundary from south to north at speeds of 35–45 km d^{-1} (Pietrafesa and Janowitz, 1979; Lee and Brooks, 1979; Blanton *et al.*, 1981; Lee *et al.*, 1981; Lee and Atkinson, 1983).

Eddies cause a net flux of nutrients onto the shelf, and eddy-induced upwelling is the largest single nitrate source for the outer shelf (40–200 m) domain (Lee *et al.*, 1981). Previous studies showed that: (a) this upwelling is the most significant process determining phytoplankton productivity on the outer shelf, (b) outer shelf productivity is higher than originally thought, (c) a significant proportion of upwelled nutrients is used by phytoplankton, and (d) episodic upwelling causes highly productive but short-lived phytoplankton blooms throughout the year (Dunstan and Atkinson, 1976; Atkinson *et al.*, 1978; Bishop *et al.*, 1980; Yoder *et al.*, 1981b; Yoder *et al.*, 1983). Upwelling, high nutrient concentrations, and phytoplankton growth may occur either near the surface or intrude below the shelf mixed layer (Blanton *et al.*, 1981; Atkinson *et al.*, 1984; Yoder *et al.*, 1985).

Yoder *et al.* (1981b) hypothesized that eddy-related phytoplankton blooms were important in the food chain dynamics of the outer shelf. Subsequent studies have shown that zooplankton (Paffenhöfer *et al.*, 1984) and demersal fishes (Atkinson and Targett, 1983) respond to subsurface or intrusion-type upwelling. However, the question of whether near-surface productivity in the cold-core of Gulf Stream eddies is transferred to higher trophic groups has not been resolved. Is the biomass associated with eddy cold-cores removed from a fixed position on the outer shelf by downwelling (Yoder *et al.*, 1983), or is it removed by northward advection (Lee *et al.*, 1981)? If rapid removal of biomass by downwelling predominated, then little or no carbon flux to higher trophic groups could occur on the outer shelf.

The behavior of highly mobile marine consumers like seabirds could give an indication of whether carbon flux beyond the producer level occurs at eddies. Although feeding on a variety of prey and foraging at several trophic levels (Ashmole, 1971), seabirds share the common trait of apex positions in marine food webs. Trophically-influenced use by seabirds of physically-differentiated marine habitats is especially apparent at surface oceanographic features in tropical water masses (Diamond, 1978; Pocklington, 1979; Haney, 1986). Seabirds in the South Atlantic Bight are primarily surface foragers, and are dependent upon prey concentrated at or very near the ocean surface (Haney and McGillivary, 1985a,b). Seabird affinities for oceanographic

Table 1. Summary of seabird count effort (number of 15-minute counts and surface area censused) on the South Atlantic Bight outer shelf (40–200 m) and upper slope (201–400 m), 1982–1985.

	Season				
	Jun–Aug	Sep–Nov	Dec–Feb	Mar–May	Total
Number of counts	454	280	68	404	1,206
Surface area censused (km^2)	449.9	335.5	72.1	449.9	1,357.4

features are more likely to be trophically-influenced compared to other apex consumer taxa. Mesoscale distributional patterns of fishes, for example, may be attributed to nontrophic causative factors such as behavioral thermoregulation at heterothermal features (Magnuson *et al.*, 1980; 1981), or to constraints on dispersal arising from circulation processes (Olson and Backus, 1985).

The purpose of this investigation was to examine if and how mesoscale patterns of seabird distribution were affected by Gulf Stream frontal eddies. The following questions were addressed: (1) Is seabird abundance greater at eddies? (2) Is seabird abundance influenced by the within-eddy variance in biomass distribution, particularly between the warm filament and cold-core? (3) Does seabird abundance show any relationship to variation in eddy size and age? (4) Does eddy-induced, near-surface upwelling display any seasonal pattern, and do seasonal seabird abundances correspond to this pattern?

2. Methods

Counts of seabirds were made from research vessels on the outer shelf and upper slope (OSh/USl) domain between 29 and 33N in the South Atlantic Bight. For the period November 1982 to June 1985, 1,206 counts censusing 1,357 km^2 were made during all seasons (Table 1). At least one cruise was made each month except January.

Density estimates of seabirds were derived using a 0.3 km, 90° sector band transect and 15-minute count period (Tasker *et al.*, 1984; Haney and McGillivary, 1985a). Ship position was recorded at the beginning and end of each count. The surface area censused in each count was then determined by multiplying the distance traveled (in km) by 0.3. Seabirds were differentiated to species or to the lowest possible taxon.

Comparisons of seabird densities at eddies to resident shelf or Gulf Stream water, and comparisons of densities within or between eddies were accomplished by plotting counts on daily satellite charts of sea surface temperature (VHRR; Gulf Stream System Flow Charts, prepared by Dr. S. Baig, NOAA/NESS, Miami, Florida). On 1 and 2 August 1984, continuous and consecutive seabird counts were made at an eddy mapped simultaneously with ship-board sea surface temperature (SST) measure-

Table 2. Summary of seabird count effort and date, location, age (in days), and size (km²) of seven Gulf Stream frontal eddies studied between 3 May 1983 and 2 August 1984.

Date	Number	Location*	Age[+]	Size[†]	Number of counts	Surface area censused (km²)
3 May 1983	83-5	31° 45′ N 79° 20′ W	10	2,323	50	37.6
17–18 June 1983	83-6B	31° 35′ N 79° 35′ W	4	2,926	82	81.3
12 July 1983	83-7	32° 30′ N 78° 00′ W	4	16,067	30	18.2
12 October 1983	83-10	33° 00′ N 77° 00′ W	9	7,556	25	32.4
9 May 1984	84-5	29° 40′ N 80° 00′ W	2	1,324	16	17.8
11 May 1984[♦]	84-5	29° 00′ N 80° 10′ W	4	2,865	9	12.5
1–2 August 1984	84-8	31° 40′ N 79° 20′W	6	2,381	66	61.4

*Geographic center of eddy cold-core.
[+]Number of days since propagation was initially detected.
[†]Surface area (km²) of eddy cold-core.
[♦]The eddy on 11 May 1984 was identical to the 9 May 1984 eddy, but was sampled two days later.

ments. Relative age (in days) of eddies at the time of sampling was determined by consulting previous charts for initial eddy propagation. Because the charts had temporal resolution of 24 to 48 hours, absolute age was underestimated. Eddy size was estimated using the areal coverage of the upwelled eddy cold-core. The cold-core surface area was computed using the formula for an ellipse:

$$S_E = \pi ab, \tag{1}$$

where S_e is the area of the cold-core, a is the cross-shelf cold-core radius and b the along-shelf cold-core radius (both in km). A planimeter was used to measure the radii from Gulf Stream charts. Dates, locations, age, size, and seabird sampling effort at each of seven eddies are summarized in Table 2.

Monthly upwelling indices based on eddy frequency, size, and percent coverage of the 200 m isobath were derived using 274 1982–1985 Gulf Stream System Flow Charts. Monthly indices were standardized for between-month differences in number of available charts by expressing frequency, size, and coverage as a function of satellite map days (SMD; Haney, 1985a; Haney and McGillivary, 1985b). Since upwelling

below the mixed layer is not satellite-detected, these indices were representative only of the near-surface component of eddy upwelling.

Green's (1966) coefficient of dispersion (G_c) was used to measure the monthly within-domain dispersion of seabirds on the outer shelf and upper slope. The index is independent of sample mean, size, and total sample number, and ranges from 0 for maximum evenness to 1 for maximum patchiness (Elliott, 1977):

$$G_c = \{(s^2/\overline{x}) - 1\}/\Sigma x - 1 \tag{2}$$

where s^2 is the monthly between-count variance in seabird density, $\overline{x}$ is the monthly mean density, and Σx is the total number of seabirds per month.

Comparisons of mean seabird densities between eddy-influenced and resident shelf and Gulf Stream waters, between different eddies, and between water masses within eddies (Fig. 1) were all evaluated with Mann-Whitney U-tests or Student's t-tests for samples of unequal sizes (Snedecor and Cochran, 1980). Mann-Whitney tests were used when the number of seabird counts in one or both samples was ≤ 10. Student's t-tests were used when counts from both samples exceeded 10. Before t-tests were made, an F-test for equality of variances was performed. When variances between samples were statistically different, the alternate t' statistic (Aspin, 1949) and approximate degrees of freedom for t' were used (Satterthwaite, 1946). Correlation (r) and linear regression of nontransformed data were used to compare seabird abundance, biomass, and food requirements per unit area to eddy size and age. Spearman's rank correlation (r_s) was used to test for significant relationships between eddy age and seabird abundance, and for relationships between seasonal upwelling frequency and seasonal seabird abundance. Statistical significance was declared when the null hypothesis was rejected at the 5% probability level.

3. Results

a. Eddy influence on outer shelf/upper slope seabird abundance. Seabird abundances were consistently higher at eddies than elsewhere within the OSh/USl domain. Mean densities were 7 to 15 times greater within eddies compared to resident shelf and Gulf Stream water (Table 3). On 12 July 1983, seabird density was 10.91 birds km^{-2} at eddy 83-7 compared to 1.51 birds km^{-2} in resident shelf and Gulf Stream water. Differences in densities between the two regions were highly significant ($t' = 5.07$, $df = 31$, $\alpha < 0.005$). At eddy 84-8 on 1 and 2 August 1984, eddy seabird density was 2.31 birds km^{-2} versus 0.15 birds km^{-2} at shelf areas not under eddy influence. Density differences were again highly significant ($t' = 6.28$, $df = 74$, $\alpha < 0.005$).

The effect of Gulf Stream frontal eddies was also apparent when the relative proportions of OSh/USl seabird numbers aggregated at the eddy were compared to the relative proportion of this domain under eddy influence. Total numbers of seabirds were estimated with the stratified densities given in Table 3, and then contrasted with the ocean surface area under influence of the eddy's cold-core within the region
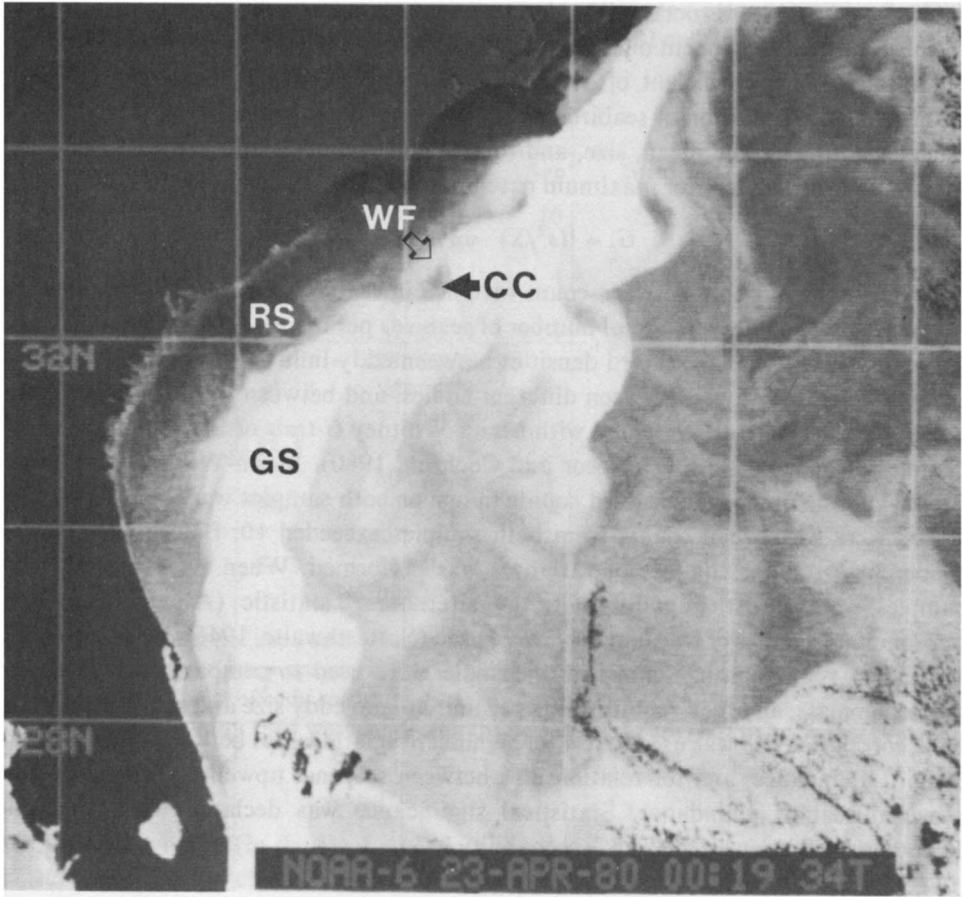
Figure 1. NOAA-6 satellite VHRR atmospherically-corrected thermal image of the Gulf Stream on 23 April 1980 at 0019 UT. Light hues indicate warm waters and dark hues cold. Water mass designations: RS = resident shelf water; GS = Gulf Stream water; WF = eddy warm filament; CC = eddy cold-core. (Image prepared by Otis Brown and Bob Evans of the University of Miami.)

bounded by 29 and 33N and the 40 and 400 m isobaths. The total number (N_T) of OSh/USl seabirds can be represented as

$$N_T = D_E(S_E) + D_S(S_S) \qquad (3)$$

where D_E is the eddy seabird density, D_S is the resident shelf/Gulf Stream seabird density, S_E is the total ocean surface area under influence of the eddy's cold-core, and S_S is the remaining OSh/USl ocean surface area. The relative percentage of the OSh/USl domain under eddy influence is thus given by

$$S_E/(S_E + S_S). \qquad (4)$$

Table 3. Seabird abundances at Gulf Stream frontal eddies compared to resident shelf and Gulf
Stream water.

Eddy number	Eddy density	Resident shelf/ Gulf Stream density	Factorial increase
83-7	10.91	1.51	7.2
84-8	2.31	0.15	15.4

$(S_E + S_S)$ was measured as 95,506 km^2. The proportion of total seabird numbers at the
eddy is

$$N_E/N_T \tag{5}$$

where $N_E = D_E(S_E)$.

Results from calculations based on data listed in Tables 2 and 3 and Eqs. (3), (4),
and (5) indicated that disproportionate numbers of OSh/USl seabirds aggregate at
eddies. On 12 July 1983, eddy 83–7 covered 17% of the OSh/USl (16,067 km^2), and
59% of seabirds were eddy-associated. On 1 and 2 August 1984, eddy 84-8 covered
<3% of the OSh/USl domain (2,381 km^2), yet 28% of seabirds were aggregated within
the region under eddy influence.

b. The influence of within-eddy heterogeneity. The amplified, unstable Gulf Stream
frontal waves that cause the formation of cyclonic cold-core eddies, and the water
masses associated with eddies, are readily identified by remote sensing radiometry
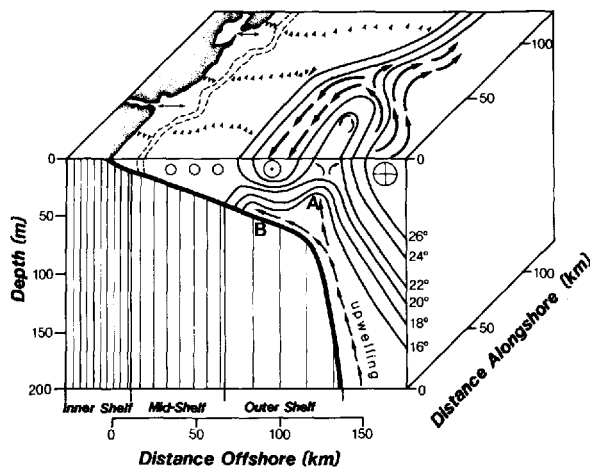(Fig. 1). Eddies consist of a southward-flowing warm filament or streamer of shallow

Figure 2. Schematic representation of a Gulf Stream frontal eddy on the Georgia continental
shelf. Eddy-induced upwelling may be either near-surface (A) or subsurface (intrusion-type;
B).

Table 4. Between-water mass comparisons of seabird densities at three Gulf Stream frontal
eddies.

Eddy number	Warm filament density	Cold-core density	Factorial increase
83-5	0.16	3.49	21.8
83-7	3.70	16.35	4.4
84-8	0.63	2.91	4.6

(15–20 m deep), near-surface Gulf Stream water separated from the main body of the
Gulf Stream by a cold upwelled core (Figs. 1 and 2; Lee *et al.*, 1981). The eddy warm
filament is differentiated from the cold-core by its shingle shape (Fig. 1), higher
surface temperature (Lee *et al.*, 1981), lower nitrate (Dunstan and Atkinson, 1976)
and chlorophyll levels (Yoder *et al.*, 1981b). Mean currents are southward west of the
cold-core in the warm filament (Lee and Atkinson, 1983). Vertical circulation in the
eddy warm filament is controlled primarily by downwelling (Pietrafesa and Janowitz,
1980).

Compared to eddy warm filaments, seabird densities were 4–21× greater in the
nitrate- and phytoplankton-rich cold-core (Table 4). On 3 May 1983, counts ($n = 7$;
6.26 km^2 censused) in the warm filament of eddy 83-5 gave a mean seabird density of
0.16 birds km^{-2} compared to 3.49 birds km^{-2} in the cold-core ($n = 23$ counts;
16.32 km^2). Density in the eddy cold-core was significantly greater ($P < 0.01$,
Mann-Whitney U-test, $N = 7, 23, Z = 3.41$). Within eddy 83-7 on 12 July 1983,
seabird density in the cold-core ($n = 21$ counts; 10.41 km^2) was 16.35 birds km^{-2}
versus 3.70 km^{-2} in the warm filament ($n = 9$ counts; 7.83 km^2). Seabird abundance
was again significantly greater in the cold-core ($P < 0.05$, Mann-Whitney U-test, $N = 9, 21, Z = 2.40$). Seabird density within the cold-core of eddy 84-8 on 1 to 2 August
1984 was 2.91 birds km^{-2} ($n = 43$ counts; 44.7 km^2) compared to 0.63 km^{-2} in the
warm filament ($n = 20$ counts; 20.8 km^2), again significantly higher ($t' = 4.37$,
$df = 57, \alpha < 0.005$).

Between 1 and 2 August 1984, SSTs were measured from the R/V *Blue Fin* at an
eddy off Georgia (Fig. 3). Seabird counts were conducted concurrently, allowing
detailed, fine-scale mapping of seabird abundances with respect to within-eddy
heterogeneity (Fig. 4). During the two day period, 86 seabird count transects were
made while the vessel was underway, and SSTs were recorded simultaneously on a
thermosalinograph chart recorder.

The "shingle" thermal pattern recorded between 1 and 2 August 1984 (Fig. 3) had
the characteristic SST signature of cyclonic cold-core frontal eddies (Lee *et al.*, 1981).
The August 1984 eddy (eddy 84-8) had a similar configuration to an eddy studied in
April 1980 off Florida (Lee and Atkinson, 1983), although absolute SSTs were much
higher at eddy 84-8. Cold-core SSTs at the April 1980 eddy were 22°C, 4° cooler than
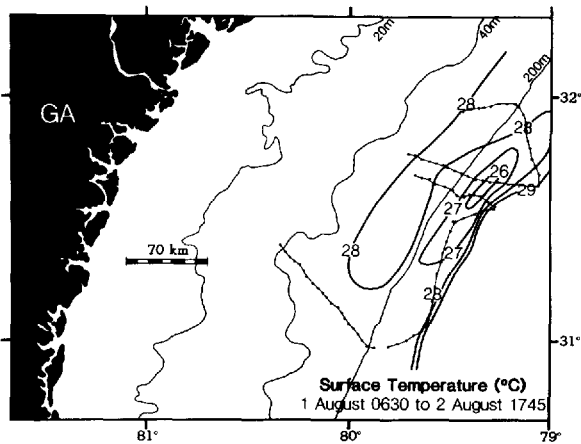
Figure 3. Ship-measured surface temperature (°C) at an eddy on 1 August (0630 hours) to 2 August (1745 hours) 1984. Dots represent stations where temperature was recorded and connecting lines indicate seabird counting transects.

the August 1984 eddy cold-core. However, the SST gradients between cold-core and Gulf Stream water at the two features were identical (3°C at both features). The between-eddy differences in absolute SSTs can be attributed to seasonal heating of outer shelf waters. Solar inputs are greatest in summer (June and July), and shelf waters reach maximum temperatures in August and September (Atkinson *et al.*, 1983) when eddy 84-8 was sampled.

Seabird abundances at and near eddy 84-8 were lowest in resident shelf water (Fig. 4; lower right), in the eddy warm filament (Fig. 4; upper left and right), and in the downstream (north) portion of the eddy cold-core. Eddies propagate along the Gulf Stream frontal boundary from south to north, and the downstream part of the cold-core contains the most recently upwelled water (J. Miller, pers. comm.). A comparison of seabird densities along the two east-west sections of the cold-core between the 28° isotherm (Fig. 3) gave densities of 3.63 birds km^{-2} along the upstream section versus 1.49 birds km^{-2} along the downstream section. Density differences between the two sections were statistically significant ($P < 0.05$, Mann-Whitney U-test, $N = 10, 10, Z = 2.23$).

Additional within-eddy variability in seabird abundance occurred (Fig. 4). Densities were greater along the eastern (offshore) portion of the cold-core where SST gradients were higher. Seabirds display similar small-scale (1–5 km) affinities for the Gulf Stream front in the absence of eddies (Haney and McGillivary, 1985a).

c. *Consequences of between-eddy variability for seabirds.* The eddies studied varied in age as well as areal coverage or size (Table 2). Between-eddy variations in seabird
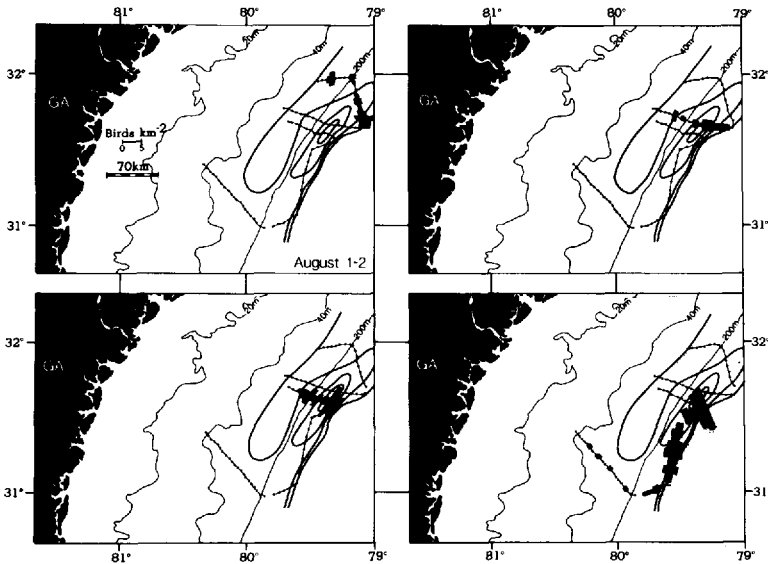
Figure 4. Small-scale variability in seabird abundance associated with a Gulf Stream frontal eddy on 1 to 2 August 1984. Bar widths normal to the cruise track indicate relative abundance. Data are separated by cruise track for clarity.

abundances were examined with respect to these two variables. Between 17 and 20 June 1983, seabird abundances were also compared at two adjacent eddies that differed in their cross-shelf positions.

Between 13 and 27 June 1983, an unusually long series of Gulf Stream charts was available because of continuous cloud-free conditions (Fig. 5). During this two-week period, three eddies (83-6A-C) formed between 29 and 33N. On 19 June, seabird counts ($n = 23$) at an eddy (83-6B) with a cold-core centered on or shoreward of the 200 m isobath were compared to counts ($n = 55$) at an eddy (83-6C) with a cold-core 20 km seaward of the 200 m isobath. No significant differences in seabird densities between the on- and off-shelf eddy were detected (3.25 versus 3.88 birds km^{-2}; $t = 1.17$, $df = 76$, $P > 0.05$).

No correlation between eddy age at time of sampling and eddy-specific seabird density was apparent ($r = 0.136$, $df = 5$, $P > 0.05$; $r_s = 0.371$, $df = 5$, $P > 0.05$). Sampling at eddies was conducted during an extended seasonal time span (May to October), however, a period when seabird abundances change phenologically (Haney, unpubl. data). Because of this bias, a more valid comparison would be of the same eddy sampled at two different intervals. Eddy 84-5 (Table 2) was sampled on both 9 and 11 May 1984, but no significant differences in seabird abundances occurred between the two sampling dates ($P > 0.05$, Mann-Whitney U-test, $N = 9, 16, Z = 0.93$).

Seabird density showed a strong positive relationship to between-eddy variation in
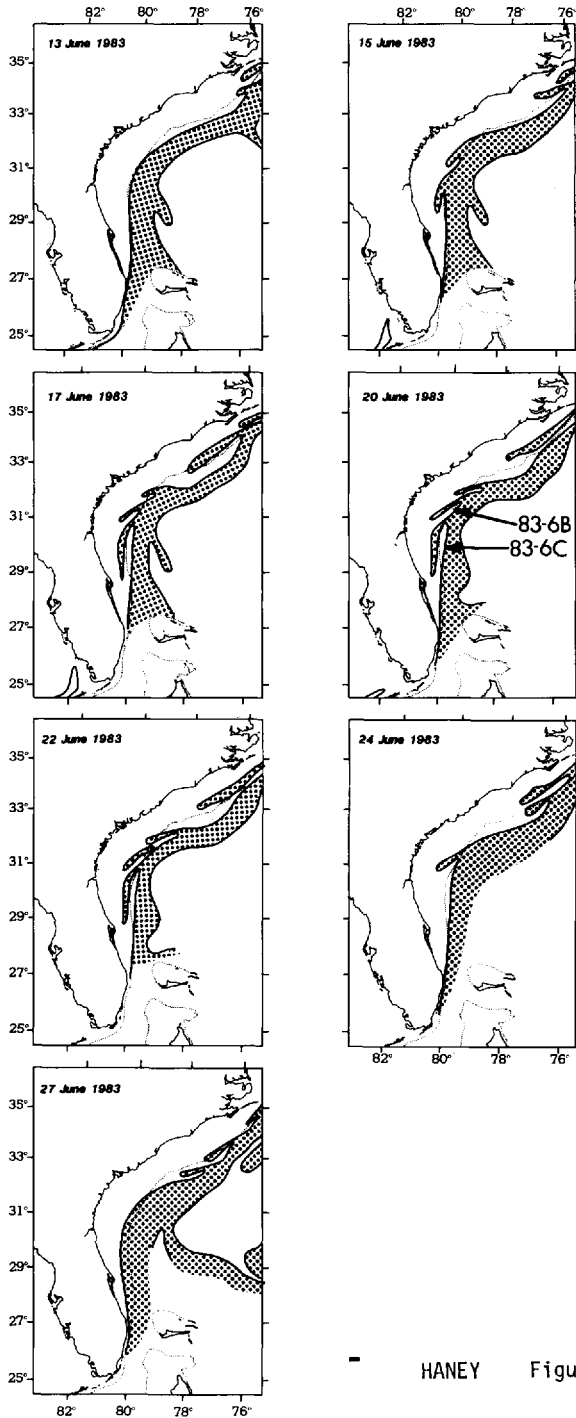
Figure 5. Time series showing the formation and degradation of Gulf Stream frontal eddies, 13–27 June 1983. Data originated from NOAA Gulf Stream System Flow Charts derived from VHRR satellite composites. Three eddies (83-6A-C) formed between 29 and 33N latitude during the two-week period.
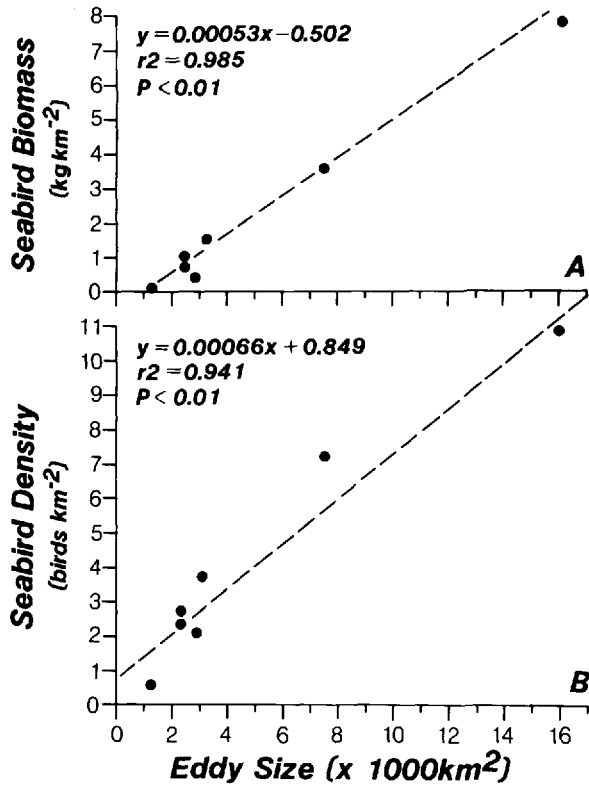
Figure 6. Comparison of seabird biomass (A) and abundance (B) to eddy size for seven eddies studied 3 May 1983 to 2 August 1984 (Table 2).

size (Fig. 6; $r = 0.970$, $df = 5$, $P < 0.001$). Between-eddy seabird densities ranged from 0.62 birds km^{-2} at eddy 84-5 on 9 May 1984 to 10.91 birds km^{-2} at eddy 83-7. The variance in seabird density between the smallest and largest eddy differed by a factor of 17.

To account for possible differences in the distribution of species abundances between eddies, seabird biomass per unit area was calculated for each eddy using species-specific body weights given in Table 5. The seabird biomass per unit area for each eddy was computed by

$$\left(\sum_{i-1}^{n} F_i M_i\right) / S_E \tag{6}$$

where F_i and M_i are, respectively, the total numbers and body mass in kg of the ith species, n is the number of species at the eddy, and S_E is the area of the eddy cold-core (Eq. 1).

Table 5. Body mass (kg), standard metabolic rates (SMR; kcal d^{-1}), and food requirements (2.5SMR) of seabird species observed at seven Gulf Stream frontal eddies (Table 2).

Species	Body mass*	SMR	Daily food requirements kcal d^{-1}	Daily food requirements g C d^{-1}
Pterodroma hasitata[+]	0.40	40	100	5.6
Calonectris diomedea[+]	0.88	71	178	9.9
Puffinus gravis[+]	0.84	69	173	9.7
Puffinus puffinus[+]	0.45	44	110	6.1
Puffinus lherminieri[+]	0.32	34	86	4.8
Oceanites oceanicus[*]	0.04	8	19	1.1
Oceanodroma leucorhoa[*]	0.05	9	22	1.2
Oceanodroma castro[*]	0.05	9	22	1.2
Sula dactylatra[+]	1.80	120	299	16.7
Stercorarius pomarinus[+]	0.70	61	151	8.4
Stercorarius parasiticus[+]	0.45	44	110	6.1
Larus atricilla[+]	0.30	33	82	4.6
Larus argentatus[+]	1.00	78	196	10.9
Sterna maxima[+]	0.45	44	110	6.1
Sterna hirundo[+]	0.14	19	47	2.6
Sterna paradisaea[+]	0.14	19	47	2.6
Sterna anaethetus[+]	0.10	14	36	2.0
Sterna fuscata[+]	0.17	22	54	3.0
Chlidonias niger[+]	0.06	10	26	1.5

*Body masses were mean values obtained from Clapp *et al.* (1982), Clapp *et al.* (1983), and Cramp (1977, 1983).

[+]Nekton-feeding species.

[*]Zooplankton-feeding species.

Seabird biomass per unit area, as calculated by Eq. 6, was also significantly correlated with eddy size (Fig. 6; $r = 0.979$, $df = 5$, $P < 0.001$). Biomass ranged from 0.12 kg km^{-2} at eddy 84-5 on 9 May 1984 to 7.89 kg km^{-2} at eddy 83-7. Seabird biomass per unit area differed by a factor of 66 between the smallest and largest eddy (Table 6).

For endothermic vertebrates, basal metabolism is proportional to weight raised to a power of 0.75 (Lasiewski and Dawson, 1967; Kendeigh, 1970). This allometric scaling was used to examine energetic (food) requirements of seabirds as a function of eddy size. Daily seabird energetic requirements were estimated as 2.5× standard metabolic rate (SMR) based on previous studies (MacMillen and Carpenter, 1977; Weathers and Nagy, 1980; Schneider and Hunt, 1982). SMR is given by

$$SMR = 78.3M^{0.733} \tag{7}$$

where SMR = kcal d^{-1} and M = body mass in kg. To calculate the per unit area

Table 6. Comparisons of seabird density, biomass, and daily food requirements per unit area (km^2) at seven Gulf Stream frontal eddies.

Eddy	Density (birds km^{-2})	Biomass (kg km^{-2})	Food requirements kcal km^{-2} d^{-1}	g C km^{-2} d^{-1}
83-5	2.61	0.89	229	12.9
83-6B	3.69	1.52	348	19.5
83-7	10.91	7.89	1,638	91.7
83-10	7.18	3.58	799	44.7
84-5	0.62	0.12	34	1.9
84-5*	2.16	0.40	121	6.8
84-8	2.33	0.70	179	10.0

*Eddy 84-5 was sampled on two different dates (Table 2).

energetic requirements of seabirds for each eddy, the formula

$$\left[\sum_{i-1}^{n}F_i(2.5\mathrm{SMR}_i)\right]/S_E \qquad (8)$$

was used. F_i and SMR_i are, respectively, the total numbers and standard metabolic rate of the ith species, n is the number of species per eddy, and S_E is the eddy surface area (Eq. 1). Energetic requirements were also calculated in terms of grams of carbon using conversion factors listed in Schneider and Hunt (1982).

The results from energetic computations [Eqs. (7) and (8)] indicated that eddy size accounted for a very high percentage of the between-eddy variation in daily seabird energetic requirements (Fig. 7). Food requirements in terms of both kcal ($r = 0.966$, $df = 5$, $P < 0.005$) and grams of carbon ($r = 0.992$, $df = 5$, $P < 0.005$) were significantly correlated with eddy size. Between-eddy daily seabird food requirements varied from 34 to 1638 kcal km^{-2} d^{-1} (1.9 to 91.7 g C km^{-2} d^{-1}). These rates differed by a factor of 48 between the smallest and largest eddy.

Thus, seabird abundance, biomass, and energy requirements showed strong positive relationships to eddy size. A linear regression model accounted for 94%, 99%, and 98–99% of the respective between-eddy variance in these three measurements.

c. Upwelling seasonality and its influence on seabirds. Eddy-related upwelling showed a pronounced seasonal pattern, with the near-surface component most prominent in late fall, winter, and spring (Fig. 8A–C). Eddies covered a greater proportion of the OSh/USl domain between January and June (14–24%) and October and December (13–17%) compared to the July to September period (0–6%). Eddy size ranged from 10,000–55,000 km^2 SMD^{-1} during late fall, winter, and spring versus 0–3,000 km^2 SMD^{-1} July through September. Eddy frequency was also lowest in summer (0–0.3 eddies SMD^{-1}) compared to other seasons (0.7–1.5 eddies SMD^{-1}).
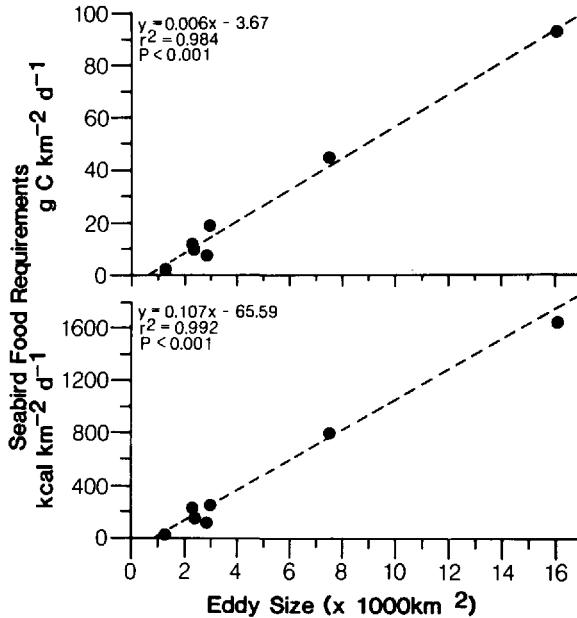
Figure 7. Seabird food requirements as a function of eddy size. Food requirements were calculated from species-specific metabolic rates and then summed for each of the seven eddies studied between 3 May 1983 and 2 August 1984 (Tables 2 and 5).

Seabird density varied seasonally on the OSh/USl (Fig. 8E), but did not correlate with any monthly upwelling index (r and r_s values with P values > 0.05). Monthly seabird densities ranged only from 1.5 to 5.0 birds km^{-2}, with peaks in July, October, and November caused primarily by shearwaters (*Calonectris diomedea* and *Puffinus gravis*) migrating through the study area. Seasonal variation in seabird abundances on the OSh/USl domain was significantly lower than elsewhere on the continental shelf (Haney and McGillivary, 1985b).

Seabirds were more patchily-distributed during months of frequent and extensive eddy-related upwelling (Fig. 8D). Seabirds were more evenly-distributed within the OSh/USl from June through September when near-surface upwelling was virtually absent within this domain.

Some seabird taxa exhibited declines in seasonal abundance corresponding to upwelling seasonality (Fig. 9). Storm-petrels (Hydrobatidae) show widespread affinities for and dependence on regions of small- and large-scale upwelling (Gould, 1971; Stallcup, 1976; Haney, 1985b). *Oceanites oceanicus,* the most abundant species in the study area, nests in the Southern Hemisphere during austral summer and migrates into North Atlantic waters after breeding is terminated. This species is widespread and abundant in the North Atlantic from April to October (Clapp *et al.,* 1982; Powers, 1983). Two rarer species, *Oceanodroma castro* from the eastern Atlantic and
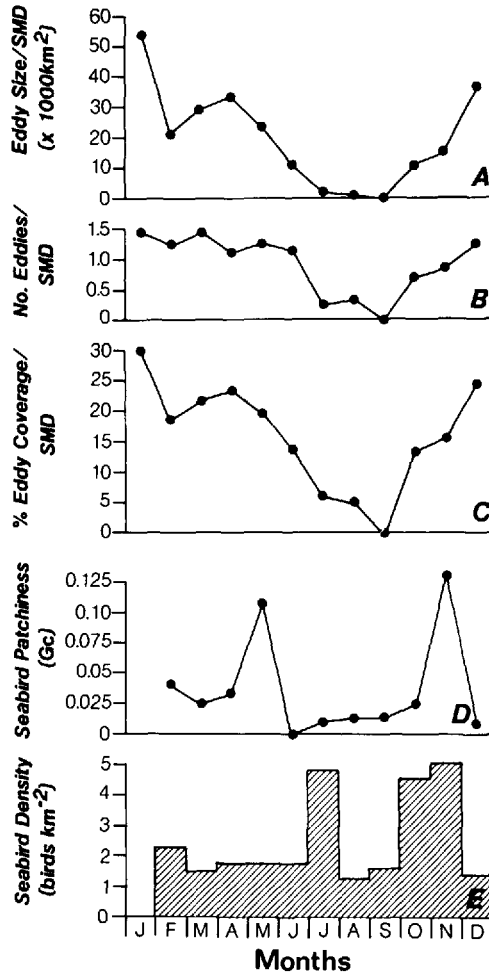
Figure 8. Monthly upwelling indices based on eddy size, frequency, and percent coverage (A–C), and their relation to monthly seabird patchiness (D) and abundance (E) in the South Atlantic Bight. Eddy indices are expressed per satellite map day (SMD). Percent eddy coverage (C) refers to relative coverage of the 200 m isobath. Eddy indices and seabird data originated from the outer continental shelf and upper slope (40–400 m isobaths) between 29 and 33N latitude. G_c = Eq. (2).

Oceanodroma leucorhoa breeding in the northern Atlantic, also occur in the South Atlantic Bight between April and October. From April to June, storm-petrel abundances increased, primarily from the phenological influx of migrant birds (Fig. 9). Storm-petrel abundances subsequently declined, however, as surface-manifested upwelling decreased in frequency and in areal coverage during summer and early fall.
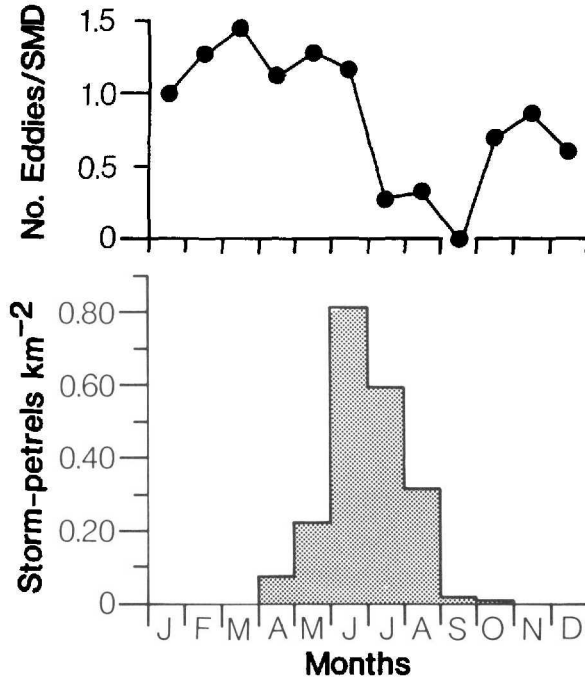
Figure 9. Relationship of monthly storm-petrel abundance to monthly frequency of Gulf Stream frontal eddies. Storm-petrel abundance is based on pooled data for three species (*Oceanites oceanicus, Oceanodroma castro,* and *Oceanodroma leucorhoa*) from the period 1982–1985 on the South Atlantic Bight outer shelf and upper slope.

4. Discussion

a. Seabird attraction to Gulf Stream frontal eddies. Seabirds were consistently attracted to water masses with the greatest biological potential, i.e., upwelled versus resident shelf and Gulf Stream water, and cold-core versus warm filament water (Tables 3 and 4). Upwelling velocities of 8.5 m d^{-1} at eddies (Lee and Atkinson, 1983) support phytoplankton patches with dimensions similar or identical to the cold core (Yoder *et al.,* 1981b). These localized regions of high phytoplankton biomass lie immediately adjacent to oligotrophic Gulf Stream and resident shelf water, where chlorophyll levels are 10^{-1} to 10^{-2} the concentrations in the eddy cold-core.

The association of seabirds with small-scale and episodic physical features is somewhat unexpected considering seabird positions in marine food webs, and the time scales (2 to 14 days) of Gulf Stream frontal eddies. Seabirds feed at trophic positions at least one and usually two or three steps from primary producers, yet were attracted to eddies only a few days old (Table 2). Some seabird species, e.g. storm-petrels (*Oceanites* and *Oceanodroma*) may feed directly on first-order consumers. Copepods and some other zooplankton, however, take at least three weeks to respond to Gulf

Table 7. Relative proportions of zooplankton- and nekton-feeding seabirds at seven Gulf Stream frontal eddies.

				Eddy			
	83-5	83-6B	83-7	83-10	84-5	84-5*	84-8
Numbers							
Zooplankton-feeders	8	26	6	0.5	56	15	31
Nekton-feeders	92	74	94	99.5	44	85	69
Biomass							
Zooplankton-feeders	1	2.5	0.5	0	8	4	4.5
Nekton-feeders	99	97.5	99.5	100	92	96	95.5

*Eddy 84-5 was sampled on two different dates (Table 2).

Stream-induced upwelling events (Paffenhöfer, 1980; Paffenhöfer *et al.*, 1984). Deibel (1985) found that gelatinous doliolids (*Dolioletta gegenbauri*) are adapted to respond quickly (days) to the "event" time scales of eddies, and suggested that doliolids trap phytoplankton biomass, thereby "smoothing" the energy pulses of aperiodic phytoplankton blooms. Recent studies have shown that seabirds feed more extensively than previously thought on gelatinous zooplankton, overlooked before because of rapid tissue breakdown in avian stomachs (Harrison, 1984; Lee, 1984).

Even with the possibility of rapidly-proliferating, gelatinous zooplankton as a trophic pathway for hydrobatids, the associations of other, nekton-feeding species with eddies remain to be explained. Many species recorded at eddies (Table 5) feed on fish, squid or large carnivorous zooplankton. Except for eddy 84-5 on 9 May 1984 (Table 2) the majority of eddy-associated seabirds were of nekton-feeding species (Table 7). One possible mechanism for seabird attraction to eddies is that highly mobile seabird prey (fish and squid) are recruited directly to the feature from elsewhere, and concentrate at eddies either to feed, or because the physical processes at eddies limit dispersal. Fish may be aggregated at fronts (see Fig. 3) because of convergent flow (Olson and Backus, 1985). Fish may also alter their distribution to maintain a preferred body temperature in heterothermal environments (Neill and Magnuson, 1974). Both benthic and pelagic fishes respond to Gulf Stream frontal movements and upwelling (Magnuson *et al.*, 1981; Atkinson and Targett, 1983). If seabirds feed on prey aggregated by physical factors at eddies, these "shortcuts" in trophic pathways may explain seabird affinities for rapidly-propagating upwelling events. This type of trophic pathway does not, however, require transfer of eddy-related phytoplankton biomass.

Higher primary production associated with eddy-forced upwelling may support fish species feeding directly on phytoplankton (Yoder *et al.*, 1981a,b). The South Atlantic

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Bight shelf break is one of the major spawning grounds of Atlantic menhaden (*Brevoortia tyrannus*) (Nelson *et al.*, 1977; Nicholson, 1978) and bluefish (*Pomatomus saltatrix*) (Kendall and Walford, 1979). Adults and larvae can feed directly on the chain-forming diatoms (*Skeletonema costatum, Asterionella japonica,* and *Rhizosolenia fragilissima*) common in upwelled water (Yoder, 1985). A shorter food chain could also partially explain why nekton-feeding seabirds aggregate at short time-scale features like Gulf Stream frontal eddies.

The between-eddy variation in seabird abundance and biomass (Fig. 6) may be due to eddy-specific variability in food web development. Yoder *et al.* (1983) found that the phytoplankton response to three eddy/upwelling events was dependent, at least in part, on the physical dynamics of water motion. Primary production was highest following repeated, sequential upwelling events that propagated along the Gulf Stream front in rapid succession. The relative percentage of primary production below and within the surface mixed layer also varied. The strong relationship between seabird food requirements per unit area and eddy size (Fig. 7) suggest that this trophic group is indirectly linked with the physical dynamics of eddy-related upwelling.

The affinities of apex marine consumers like seabirds for eddies is likely to be influenced by both past and current physical conditions which affect(ed) biological interactions at primary and intermediate trophic levels. The degradation of Gulf Stream frontal eddies apparently occurs as a shear-induced dissipation process rather than a collapse of isopycnal surfaces (Lee and Atkinson, 1983). Upwelled nutrients would remain on the outer shelf, and thus be available for continued phytoplankton uptake, albeit "downstream" from the initial location of eddy propagation. One prediction from this is that near-surface production appears as chlorophyll bands in the Gulf Stream front (Yoder *et al.,* 1981b), with phytoplankton biomass increasing latitudinally from south to north along the front, possibly accompanied by greater biomasses of higher trophic groups as well. Seabird data analyzed by 30' latitude blocks indicate that this trophic group increases in abundance from south to north along the South Atlantic Bight outer shelf and upper slope (Haney, unpubl. data).

b. Upwelling seasonality and seabirds. Gulf Stream frontal meanders vary seasonally, with less-prominent weekly time scales apparent during summer (Brooks and Bane, 1983). Eddies result from unstable frontal meanders (Pietrafesa and Janowitz, 1980). The outer shelf (41–200 m) becomes increasingly stratified during summer (Atkinson *et al.,* 1983), and eddy-related upwelling is largely below the mixed layer during this season (Atkinson *et al.,* 1984; Yoder, 1985). Intrusion-type upwelling (Fig. 2) is of less potential importance to surface-foraging seabirds. In spite of high near-bottom primary and secondary productivity in the middle shelf caused by summer intrusions (Paffenhöfer *et al.,* 1984; Yoder, 1985), summer seabird densities in the middle shelf were 10^{-1} or less the densities on the outer shelf (Haney and McGillivary, 1985b).

The summer decline in frequency of near-surface upwelling may be a factor in the

local decreases in storm-petrel abundance between June and October (Fig. 9). A large percentage of storm-petrel variation in abundance can be attributed directly to near-surface upwelling (Haney, 1985b). Storm-petrels migrate further north to the Georges and Grand Banks where vertical mixing and upwelling continue all summer (Brown *et al.*, 1975; Powers, 1983). When eddy-based foraging is no longer productive, the nekton-feeding seabirds may switch to foraging on prey concentrated or localized by other factors. Many of these seabird species accompany and feed with schools of large predatory fish (e.g. jacks: Carangidae; mackeral and tuna: Scombridae) during summer and early fall (Ashmole and Ashmole, 1967; Jehl, 1974; Haney, unpubl. data). The more patchy distribution of seabirds from late fall through early summer within the OSh/USl domain (Fig. 8d) may be because eddies exert relatively more influence on local, within-domain patterns of seabird distribution during these seasons.

c. Implications for outer shelf food web dynamics. Results indicate that energy flux additional to or beyond the producer level occurs at Gulf Stream frontal eddies. All near-surface production may not be exclusively downwelled off the shelf if seabirds are feeding on prey attracted to eddy-related phytoplankton biomass. The northward-advection hypothesis better accounts for the association of seabirds with near-surface upwelling events. The mobility of seabirds allows them to respond rapidly to near-surface features with high prey biomasses. The relative ease with which seabirds are sampled, and the degree of spatial resolution in that sampling, should provide valuable future insights into quantitative and qualitative trophic interactions at transient mesoscale features in marine environments.

Physical inputs and biological consequences on the outer southeastern United States continental shelf are distinct from other regions. Gulf Stream frontal eddies differ significantly from the larger eddies (cold-core rings) found north of Cape Hatteras, North Carolina. Gulf Stream frontal eddies do not detach from the stream, do not entrain resident slope water, and do not persist for as long as the larger ring features (cf. references in: Lee and Atkinson, 1983; Wiebe *et al.*, 1976). The causes and sources of higher primary production at Gulf Stream frontal eddies also differ from production associated with other shelf break frontal systems. Phytoplankton blooms at shelf break fronts may occur in response to high levels of irradiance within a nutrient-rich surface layer, a consequence of an elevated pycnocline near the front decreasing the mixing depth of the surface phytoplankton population (Pingree *et al.*, 1978; Fournier, 1978; Iverson *et al.*, 1979). Eddy-related production at the Gulf Stream front is caused by upwelling (Lee *et al.*, 1981), since both resident shelf and Gulf Stream mixed-layer water have very low concentration of nutrients (Haines, 1974; Dunston and Atkinson, 1976; Bishop *et al.*, 1980). Models of energy and nutrient flux to higher trophic groups on the outer southeastern U.S. continental shelf should address the episodic nature of upwelling in this region.

The structure, dynamics, and trophic pathways of the pelagic food web at eddies are still little-understood. Mean rates of primary production on the outer southeastern U.S. continental shelf are lower than wind-driven upwelling systems, yet similar to rates for spring blooms in temperate and subarctic waters (Yoder *et al.,* 1985). Does the episodic nature of blooms affect higher trophic groups other than seabirds, and are trophic pathways shorter? Is the food web of a highly-episodic system fundamentally different from other shelf systems? Do species and populations of marine organisms within this system have special adaptations to aperiodicity? Studies of seabird diets may provide some direction for future research, but time-series sampling of zooplankton and fish are also needed. Measurements of between-eddy variation in physical dynamics and corresponding food web development will allow an evolving view of physical/biological interactions on the outer southeastern U.S. continental shelf.

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