

AIR-SEA HEAT FLUX, OCEAN WIND FIELDS, AND OFFSHORE DISPERSAL OF GULLS

J. CHRISTOPHER HANEY¹ AND DAVID S. LEE²

¹Wildlife Technology Program, School of Forest Resources, Pennsylvania State University, College Place, DuBois, Pennsylvania 15801, USA; and

²North Carolina State Museum of Natural Science, P.O. Box 27647, Raleigh, North Carolina 27611, USA

ABSTRACT.—Gull numbers in pelagic habitats off the southeastern United States were weakly associated with seasonal variability in mean wind speeds, but strongly associated with accumulated air-sea heat flux (a surrogate for temperature inversions; i.e. pre-thermal conditions) and wind-speed variance (an energy source for flight, as well as a thermal inducement). Single meteorological variables accounted for as much as 59 to 93% of seasonal changes in gull abundance. Gulls (including nonbreeders) delayed dispersal to oceanic waters until onset of winter meteorological conditions, several months after cessation of breeding. Our findings support Woodcock's convective-soaring hypothesis, which ascribed gull dispersal in winter to boundary-layer dynamics along eastern continental margins. We extend this model by linking gull morphology and flight to energy-efficient reliance on air-sea interactions and spatial patterns in seasonal wind fields. Summer meteorological conditions in much of the western North Atlantic Ocean facilitate coastal foraging by gulls, but act to preclude efficient foraging to and in offshore habitats. The presence or absence of coherence (meteorological consistency) in the aerial environment may have acted to select and maintain divergent life-history strategies in gulls and certain other inshore feeders. Received 26 March 1993, accepted 19 August 1993.

SEABIRDS INHABIT a complex environment composed of terrestrial, marine, and aerial elements (Burger 1989). Meteorological factors in aerial environments are difficult to represent spatially, so they have received less attention than terrestrial or marine variables as forces governing seabird lifestyles (Schneider 1991, Haney and Solow 1992). Nevertheless, maritime weather has profound influences on seabird movement (e.g. Manikowski 1971). In the Kattegat region of the North Sea, Blomqvist and Peterz (1984) analyzed coastal movements of primarily pelagic species in terms of prevailing winds, inertia of wave topography, and efficient flight techniques. Their causal model, which linked progressive, clockwise movements of seabirds to eastward-traveling cyclonic gales, was corroborated by patterns of seabird movement elsewhere in the North Sea (Bourne 1982). Maritime weather may also determine suitability of colonial breeding sites (Kaiser and Forbes 1992). For example, Jouventin and Weimerskirch (1990) noted that, because lengthy foraging trips in Wandering Albatrosses (*Diomedea exulans*) depend on strong and regular winds, populations of these large seabirds have thrived only within certain latitude belts in the Southern Ocean.

Seabirds employ at least three efficient flight techniques, singly or in combination, to extract energy supplied from the ocean's aerial environment (reviewed by Schneider 1991). Dynamic soaring, used by seabirds for both upwind climbs and downwind descents (Pennycuik 1982), is based on vertical gradients in wind velocity caused by wind shear over the sea surface (see theoretical treatments by Cone 1964, Wood 1973). Slope lift (also termed slope soaring or sweeping flight) relies directly on air currents deflected by waves, swells, or other obstructions in the path of the wind (Pennycuik 1982, Wilson 1975). A third technique, convection soaring, is prompted when thermals are created by decreasing air temperature with height such as occurs when cold air overlies warmer ocean water. Of the three flight techniques, convective soaring has been least studied (but see Woodcock 1940b, Pennycuik 1983).

During fall and winter, gulls disperse offshore far from land in the western North Atlantic (e.g. Rowlett 1980, Lee 1993). These movements lag the end of the breeding season by three or more months (Woodcock 1940b:220-221). Woodcock (1940a) proposed that dispersal is delayed because efficient flight techniques depend on seasonal availability of strong con-

vection air currents over the open ocean along the eastern margin of North America. Thermal convection results when cold continental air in the boundary layer is heated and decline of temperature with height (in excess of the adiabatic change) creates vertical instability. Woodcock observed this phenomenon during weather changes lasting several days in the Atlantic Ocean north of Cape Hatteras, North Carolina.

We compared gull movements off the Outer Banks, North Carolina, and South Atlantic Bight (Cape Hatteras to Cape Canaveral, Florida) to seasonality in meteorological regimes. Our purpose was to evaluate whether Woodcock's hypothesis can be extended to longer time scales and to geographically contiguous sectors of the western North Atlantic Ocean. We employed surrogate variables (air-sea heat flux, accumulated heat flux, mean wind speed, wind-speed variance, cross-shelf ocean-temperature differences) to model interactions among wind regimes, air-sea interactions, the convection process, and gull dispersal. We discuss our findings within the context of markedly divergent life-history strategies that distinguish coastal from more pelagic seabird species (Ricklefs 1990).

METHODS

Gull distributions and seasonal abundance.—Gull abundance was estimated with unlimited-distance strip counts during 231 one-day shipboard surveys conducted since 1975 in offshore waters 40 to 60 km east of North Carolina's Outer Banks. Coastal and near-shore waters off North Carolina were not surveyed as consistently as were offshore zones. Abundances of the following gull species recorded offshore were combined and expressed as a mean number per survey per month using data from all survey years (\bar{x} = 19, range 6–47 surveys/month; for additional details, see Lee and Soggi 1989): Laughing Gull (*Larus atricilla*); Little Gull (*L. minutus*; <5 individuals); Bonaparte's Gull (*L. philadelphia*); Ring-billed Gull (*L. delawarensis*); Herring Gull (*L. argentatus*); Lesser Black-backed Gull (*L. fuscus*); Great Black-backed Gull (*L. marinus*); Glaucous Gull (*L. hyperboreus*); Black-legged Kittiwake (*Rissa tridactyla*); and Sabine's Gull (*Xema sabini*; <5 individuals).

In addition to wintering individuals, over 18,900 pairs of Laughing Gulls, and smaller numbers of Great Black-backed Gulls and Herring Gulls, nest along the North Carolina coastline. Nonbreeding populations of these and other species, especially Ring-billed Gulls, also summer commonly along the coast, becoming increasingly abundant by mid-August (Lee unpubl. data).

Surveys in the South Atlantic Bight were based on 2,136 15-min, 300-m strip or band transects (Tasker et al. 1984) conducted all calendar months for 159 days between 1982 and 1985 (see Haney 1986a for details). Numbers of gulls (n = 1,825 total), expressed per count hour for purposes of this study, were stratified according to four survey regions of the continental shelf: inner shelf (0–20 m depth; 0–65 km offshore); mid-shelf (21–40 m; 35–94 km); outer shelf (41–200 m; 75–130 km); and Gulf Stream (200–800 m; > 90 km). Species composition was generally similar to the Outer Banks (with the exception that no Little or Sabine's gulls were recorded); nonbreeding gulls (mostly Laughing Gulls) were common in this region also during summer. An influx of southward-migrating gulls during winter was expected, so a monthly ratio of gull abundance offshore/abundance shelfwide was used as a more robust dependent variable for detecting offshore dispersal. This ratio could not be calculated for the Outer Banks region due to different survey layouts.

Meteorological measurements.—Five variables describing wind, convection, and their consequences in the air-sea boundary layer were derived from available meteorological data. Wind-field information for offshore regions of the southeastern United States was obtained from the National Climate Center, Asheville, North Carolina. Data had been extracted and edited previously by Weisberg and Pietrafesa (1983:figs. 7 and 8). We calculated mean wind velocities (in $\text{m}\cdot\text{s}^{-1}$) by month using multiyear averages, although not from years concurrent with the surveys. Bias due to this practice is unlikely because interannual variation in wind velocity comprises less than 1% of the total energy distribution function (see Weisberg and Pietrafesa 1983:4598). Wind-speed variance (a measure of frequency changes in wind direction and/or strength measured in $[\text{m}\cdot\text{s}^{-1}]^2$) was obtained similarly for each month using multiyear averages from both north- and east-wind vector components ($v-\bar{v}$ and $u-\bar{u}$, respectively; Weisberg and Pietrafesa 1983:4600). Wind energy in the variance field generally exceeds that of the mean in this region. Data from offshore buoys were used because land stations do not accurately characterize wind fields over the ocean (Blanton et al. 1985).

We used climate summaries of Atkinson et al. (1983) for figuring seasonal heat flux between the atmosphere and ocean waters off the southeastern United States. Net heat flux, Q_n , is determined from monthly change in heat content of the inner continental shelf:

$$Q_n = \Delta T \cdot Z \alpha, \quad (1)$$

where ΔT is change in monthly mean temperature ($^{\circ}\text{C}$), Z is mean depth of inner shelf (10 m); and α is heat capacity ($1 \text{ cal}\cdot\text{g}^{-1}$). Negative values for Q_n indicate ocean cooling after passage of continental air masses (cold-air outbreaks) during winter (Fig. 1). Heat flux estimates were converted using:

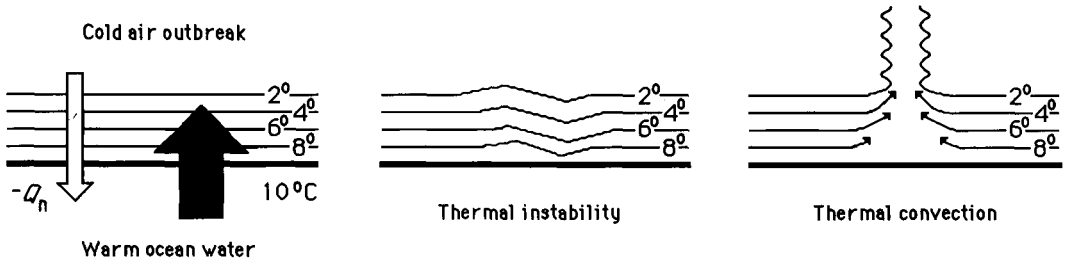


Fig. 1. Mechanism of thermal formation over ocean surface. After cold-air outbreaks associated with continental weather systems during winter (negative values of Q_n ; see text), warmer ocean water heats the boundary-layer air. Resultant superadiabatic conditions create thermodynamic instability. Depending on air-sea ΔT values, thermals can be initiated by gull behavior or triggered by wind (Woodcock 1975). Thermals occur in spatially patchy convection cells that move and propagate along with wind field.

$$1 \text{ kcal} \cdot \text{cm}^{-2} \cdot (30 \text{ days})^{-1} = 16.15 \text{ watts} \cdot \text{m}^{-2}. \quad (2)$$

A single point estimate of heat flux for each month was derived by taking the spatial average over southern (29° and 30°N), middle (31° and 32°N), and northern (33° and 34°N) parts of the South Atlantic Bight after data smoothing had been previously performed by Atkinson et al. (1983:fig. 9a). Monthly values of heat flux were then summed to calculate average accumulated heat flux, ΣQ , for each month.

Heat flux from the ocean to the atmosphere coupled

with horizontal advection results in steep cross-shelf gradients in ocean temperatures (Fig. 2). Monthly differences between near-shore and Gulf Stream temperatures were computed and used as an additional surrogate variable for describing regional seasonality in ocean meteorology. These temperature data were available only for the Outer Banks region off North Carolina.

Data analyses.—Interactions between gull distribution and season were tested with a contingency table with fixed margins (four shelf habitats \times four

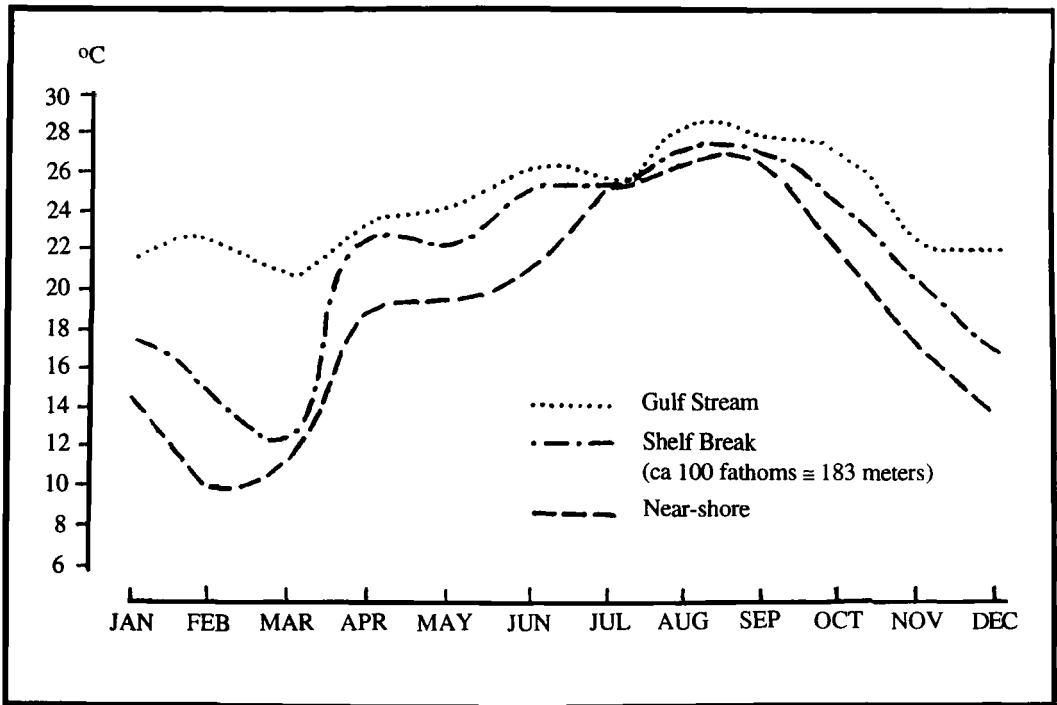


Fig. 2. Monthly changes in sea-surface temperatures for shelf habitats off North Carolina's Outer Banks (after Newton et al. 1971).

seasons). Seasonal categories were designated as follows: spring (March–May), summer (June–August), fall (September–November), and winter (December–February). Prior to the hypothesis test for independence, counts of gulls were weighted by ratios of actual survey effort (Table 1) to equal effort per cell ($1/16 = 0.0625$). All observed cell frequencies were then rescaled to the original sample size ($n = 1,825$). The interaction was tested with the TABLE program in SYSTAT with extended results (Wilkinson 1989). A log-linear model was specified to test for additivity, compute fitted (expected) values, and produce a table of standardized residuals which identified individual cells having the greatest departures from fitted model values.

Indices of gull abundance served as dependent variables. Monthly counts and ratios of gull abundances were transformed prior to regression to stabilize variances from enumerated data (Snedecor and Cochran 1980:287–292). An $\ln(x + 1)$ transformation was applied to the mean number of gulls per survey, and a square-root transformation ($(x + 1)^{0.5}$) applied to the ratio of gull abundance offshore to gull abundance shelfwide. These indices were regressed on meteorological variables with the least-squares MGLH program, including extended output and diagnostics, in SYSTAT (Wilkinson 1989). Diagnostics were used to evaluate the following assumptions: plots of residuals versus predicted values for heteroscedasticity; leverage statistics for detection of outliers and normal distributions in independent (meteorological) variables; and Studentized residuals for detection of outliers in dependent variables (indices of gull abundance). We also used the Cook statistic, which combines leverage and Studentized residuals, to examine any influence of separate observations on estimates of regression coefficients (Velleman and Welsch 1981, Wilkinson 1989:148–149). Performances of individual meteorological predictors were assessed by comparing model estimates of monthly abundances and ratios of gulls offshore to the actual values recorded.

Predictive utility of meteorological variables was evaluated further in multiple-regression models. First, we used a full model with no regressors eliminated and examined computed F -values for significance. For the South Atlantic Bight study area, regressors included mean wind speed (X_1), wind-speed variance (X_2), monthly rates of heat flux (X_3), and accumulated heat flux (X_4). For the Outer Banks study area, all four of these regressors plus the difference in cross-shelf temperatures (X_5) were employed in the full model. To determine whether all regressors were needed for a prediction equation, we used the forward-selection procedure for stepwise linear regression in choosing a potential subset of predictors (Dowdy and Wearden 1991). The meteorological variable most strongly correlated with log or square-root gull abundance was taken as the first independent variable. Residuals were

then correlated with the remaining meteorological variables and the variable with the highest correlation taken as the second predictor, and so on. The procedure was terminated when none of the remaining parameters was significantly correlated with remaining residuals.

RESULTS

Seasonality of wind regimes and heat flux.—Mean wind speeds varied from a monthly low of $0.9 \text{ m}\cdot\text{s}^{-1}$ in November to a high of $3.7 \text{ m}\cdot\text{s}^{-1}$ in January (Table 2). Wind speed showed no consistent seasonal pattern, although late spring and summer wind speeds were somewhat higher on average than wind speeds at other seasons. Wind speeds during fall and early spring were low, with highest wind speeds occurring during midwinter months. In contrast, wind speed variance (a measure of how frequent weather systems and their attendant wind fields change) showed a distinctly seasonal pattern. Lowest variance occurred between May and September ($[33\text{--}47 \text{ m}\cdot\text{s}^{-1}]^2$). Wind-speed variance was highest ($[55\text{--}91 \text{ m}\cdot\text{s}^{-1}]^2$) from late fall through early spring.

Continental shelf waters gain heat from the atmosphere beginning in March and lasting until September. Largest positive rates for heat flux occurred in April, May, and July (48 to $56 \text{ watts}\cdot\text{m}^{-2}$; Table 2). After September, direction for heat flux is reversed (-18 to $-78 \text{ watts}\cdot\text{m}^{-2}$) and cooling of shelf waters continues until February. During this period, thermal instability from ocean heating of the boundary layer occurs during cold-air outbreaks (Fig. 1). Seasonal patterns for accumulated heat flux were similar to mean monthly flux, but lagged that variable by about one month (Table 2). As a consequence of heat flux, temperature differences in inner shelf and Gulf Stream waters were as great as 13.2°C by the end of winter (Fig. 2). Highest cross-shelf temperature differences occur from November through March; lowest temperature differences occur from July through September.

Gull dispersal.—As expected, gulls in the South Atlantic Bight were most abundant regionally (shelf-wide) in mid-winter ($36.7 \text{ birds}\cdot[\text{survey}\cdot\text{h}]^{-1}$), followed by autumn ($26.7 \text{ birds}\cdot[\text{survey}\cdot\text{h}]^{-1}$), spring ($12.4 \text{ birds}\cdot[\text{survey}\cdot\text{h}]^{-1}$), and summer ($6.3 \text{ birds}\cdot[\text{survey}\cdot\text{h}]^{-1}$). Seasonal patterns were similar off the Outer Banks where the mean numbers of gulls per survey in offshore habitats fell below 1 from May through September (Ta-

ble 2). In offshore habitats between October and April, average number per survey ranged from 33 to a high of approximately 1,700.

Distributions of gulls across the continental shelf changed seasonally (Table 1). Habitat occupancy and abundance by gulls displayed significant interactions with season (Pearson $X^2 = 369.009$, $df = 9$, $P < 0.001$). From March through November, 76 to 98% of all gulls occurred in coastal, inner-shelf waters. In offshore waters, gull abundances peaked from December through February when 61 to 97% of individuals recorded shelfwide were observed in these habitats.

Log-linear modeling indicated those combinations of season and habitat occupancy that deviated from expected or fitted values (Table 3). During winter, gulls were more common than expected in the three offshore habitats (more so over the warmest water; i.e. the Gulf Stream), whereas numbers in inner-shelf waters were lower than expected (standardized residuals; Table 3). By spring, numbers in the most distant zone (the Gulf Stream) had declined, although greater-than-expected numbers still persisted in mid-shelf and outer-shelf waters. Numbers in inner-shelf waters during spring were approximately equal to those expected from the fitted model. During summer and autumn, fewer than expected numbers of gulls occurred offshore, and higher than expected numbers occurred over inner-shelf waters.

Meteorological influences on gull abundance.—Log and square-root gull abundances were strongly associated with several meteorological variables measured (Table 4). In the South Atlantic Bight, the proportion of gulls offshore was positively correlated with wind speed and negatively correlated with monthly heat flux (Fig. 3), but not significantly with either variable. Offshore abundance of gulls increased significantly with greater wind speed variance and with larger negative rates of accumulated heat flux (ocean-to-air vs. air-to-ocean). These two variables explained 59 and 41%, respectively, of seasonal change in the square-root ratio of abundance offshore/abundance shelfwide.

Log gull abundance off the Outer Banks was significantly correlated with wind speed variance, accumulated heat flux, and cross-shelf temperature differences (Fig. 4). These three meteorological variables explained 84, 93, and 79%, respectively, of the variation in seasonal abundance. Offshore abundance was negatively

TABLE 1. Interaction of gull distribution and abundance with season in South Atlantic Bight. First value under count is total number recorded; value in parentheses is number recorded per survey hour. First value under percentage is seasonal gull total across habitats; value within parentheses indicates percentage of each habitat's gulls across seasons.

Season	Habitat							
	Inner shelf		Mid-shelf		Outer shelf		Gulf Stream	
	Count	Percent	Count	Percent	Count	Percent	Count	Percent
Jun-Aug	137 (6.2)	98.56 (10.16)	1 (0.1)	0.72 (0.48)	0 (0.0)	0.00 (0.00)	1 (0.0)	0.72 (0.57)
Sep-Nov	547 (24.7)	92.55 (40.58)	41 (1.9)	6.94 (19.81)	2 (0.1)	0.34 (2.13)	1 (0.0)	0.17 (0.57)
Dec-Feb	450 (20.3)	55.21 (33.38)	127 (5.7)	15.58 (61.35)	67 (3.0)	8.22 (71.28)	171 (7.7)	20.98 (97.16)
Mar-May	214 (9.6)	76.43 (15.88)	38 (1.7)	13.57 (18.36)	25 (1.1)	8.93 (26.60)	3 (0.1)	1.07 (1.70)

TABLE 2. Seasonal changes in gull abundance and meteorology off southeastern United States.

Month	Mean wind speed (m·s ⁻¹)	Wind-speed variance (m·s ⁻¹) ²	Mean monthly heat flux (watts·m ⁻²)	Accumulated heat flux (kcal·cm ⁻² ·month ⁻¹)	Inner/outer shelf ΔT (°C) ^a	Gull abundance	
						Outer Banks ^b	South Atlantic Bight ^c
January	3.7	91	-33	-0.6	6.5	420.0 (8)	1.5 (8)
February	3.1	91	-18	-4.2	13.2	1,697.9 (7)	0.7 (122)
March	1.6	70	36	-2.6	9.5	1,295.9 (6)	0.6 (90)
April	1.9	61	48	1.2	4.5	61.9 (22)	0.6 (114)
May	2.8	47	51	4.8	4.5	0.4 (16)	0.1 (478)
June	2.8	38	34	6.8	4.5	0.8 (29)	0.0 (244)
July	2.5	33	56	7.1	1.0	0.1 (33)	0.0 (196)
August	2.3	38	5	7.6	1.8	0.1 (47)	0.1 (224)
September	1.7	41	6	7.8	1.8	0.3 (27)	0.5 (168)
October	1.0	55	-78	2.7	5.3	51.3 (14)	0.1 (307)
November	0.9	72	-67	-0.1	5.5	33.1 (10)	0.1 (83)
December	1.9	86	-41	-2.7	8.0	345.5 (12)	0.5 (102)

^a Variable based on data obtained from ocean waters off North Carolina only.

^b Mean number of gulls counted offshore per survey (number of one-day surveys in parentheses).

^c Ratio of gull abundance offshore to gull abundance shelfwide (number of 15-min, 300-m band transects in parentheses).

and weakly correlated with both monthly heat flux and mean wind speed (Table 4), but neither association was statistically significant.

The full multiple-regression model for the South Atlantic Bight was:

$$Y = -0.214X_1 + 0.052X_2 + 0.006X_3 + 0.159X_4 - 2.496. \quad (3)$$

This model (see also Table 5) explained 79.5% of the seasonal variation in square-root ratio of abundance offshore/abundance shelfwide (adjusted multiple $r^2 = 0.678$, regression sum-of-squares 1.196, mean-square 0.299, $df = 4$, $F = 6.779$, $P = 0.015$). The full model for the Outer Banks was:

$$Y = 0.039X_1 + 0.006X_2 - 0.001X_3 - 0.549X_4 + 0.075X_5 + 3.704. \quad (4)$$

This model explained 93.3% of seasonal variation in log gull abundance offshore (adjusted multiple $r^2 = 0.877$, regression sum-of-squares

86.950, mean-square 17.390, $df = 5$, $F = 16.677$, $P = 0.002$).

Assumptions in regression models.—Diagnostics for the South Atlantic Bight simple linear regression on wind-speed variance indicated an outlier (Studentized residual, $t = 2.254$, $df = 10$, $P < 0.025$) in the dependent variable for September, when the ratio of gulls offshore was higher than predicted for this season (see Fig. 5). This outlier did not, however, significantly influence the estimates for coefficients in the regression equation (Cook's $F = 0.334$, $P > 0.25$). Similarly, outliers (Studentized residual for January, $t = 2.360$, $df = 10$, $P < 0.025$; Studentized residual for September, $t = 2.124$, $df = 10$, $P < 0.05$) were detected among the dependent variables in the linear regression of gulls offshore on accumulated heat flux. These outliers did not affect regression coefficients (for January, Cook's $F = 0.268$, $df = 2$, 10 , $P > 0.25$; for September, Cook's $F = 0.480$, $df = 2$, 10 , $P >$

TABLE 3. Standardized residuals (i.e. [observed - fitted]/fitted^{0.5}) from log-linear model evaluating interaction of season and offshore habitats used by gulls in South Atlantic Bight. Positive values indicate greater-than-expected gull numbers. Values in parentheses are fitted or expected numbers of gulls (cf. observed values; Table 1).

Season	Habitat			
	Inner shelf	Mid-shelf	Outer shelf	Gulf Stream
Jun-Aug	3.39 (102.67)	-3.72 (15.77)	-2.68 (7.16)	-3.39 (13.4)
Sep-Nov	5.29 (436.53)	-3.18 (67.03)	-5.15 (30.44)	-7.42 (57.0)
Dec-Feb	-6.19 (601.98)	3.59 (92.44)	3.86 (41.98)	10.42 (78.6)
Mar-May	0.50 (206.82)	1.11 (31.76)	2.79 (14.42)	-4.62 (27.0)

TABLE 4. Regression models ($Y = a + bX$) used to evaluate seasonal relationships of gull dispersal and meteorology in South Atlantic Bight and off North Carolina's Outer Banks.

Independent variable (X)	Y intercept (a) ± SE ^a	Slope (b)	CI ^b	r ²
South Atlantic Bight^c				
Mean wind speed	0.282 ± 0.134	0.111	-0.189, 0.410	0.064
Wind-speed variance	-0.268 ± 0.003	0.013	0.005, 0.021	0.585**
Monthly heat flux	0.524 ± 0.002	-0.002	-0.007, 0.004	0.050
Accumulated heat flux	0.649 ± 0.020	-0.054	-0.099, -0.009	0.414*
Outer Banks^c				
Mean wind speed	3.223 ± 1.093	0.031	-2.405, 2.467	0.000
Wind-speed variance	-4.177 ± 0.017	0.124	0.086, 0.162	0.840***
Monthly heat flux	3.290 ± 0.018	-0.025	-0.065, 0.015	0.167
Accumulated heat flux	4.764 ± 0.055	-0.636	-0.758, -0.513	0.930***
Inner/outer shelf ΔT	-0.836 ± 0.123	0.752	0.478, 1.025	0.789***

^a Standard error of estimate.

^b 95% confidence interval (lower, upper limit) on slope (b).

^c Significance levels for H₀ that b is 0: *, P ≤ 0.05; **, P ≤ 0.01; ***, P ≤ 0.001; others ns, P > 0.05.

^d Dependent variable (Y) is square root of monthly ratio of gull abundance offshore/abundance shelfwide.

^e Dependent variable (Y) is ln(x + 1) of monthly mean number of gulls offshore per survey.

0.25). No outliers were detected among the independent variables used in the South Atlantic Bight regressions (unpubl. data).

Diagnostics from Outer Banks regressions also revealed outliers. In the simple linear regression on wind-speed variance (Fig. 4, Table 4), the mean number of gulls recorded in March was higher than expected from the model (Studentized residual, $t = 3.194$, $df = 10$, $P < 0.005$; see also Table 2). This outlier did not significantly influence estimates for coefficients in the regression equation, however (Cook's $F = 0.302$, $df = 2$, 10 , $P > 0.25$). In the linear regression on accumulated heat flux, outliers were detected in offshore abundances from both May and November (Studentized residual, $t = -2.104$, $df = 10$, $P < 0.05$; $t = -1.930$, $df = 10$, $P < 0.05$, respectively; see also Fig. 5). Neither outlier affected estimates of the corresponding regression coefficients (for May, Cook's $F = 0.208$, $df = 2$, 10 , $P > 0.25$; for November, Cook's $F = 0.182$, $df = 2$, 10 , $P > 0.25$). In the regression model for cross-shelf temperature differences, outliers were detected in both dependent and independent variables. The Studentized residual from May indicated that the estimate of offshore gull abundance was significantly lower than expected ($t = -1.840$, $df = 10$, $P < 0.05$). In addition, the leverage for the February value of the independent variable was unusually large (0.516 vs. an expected 0.167 to 0.333 for Gaussian data; Wilkinson 1989:149). Neither outlier influenced model estimates of regression coefficients, however (for February, Cook's $F = 1.259$,

$df = 2$, 10 , $P > 0.25$; for May, Cook's $F = 0.137$, $df = 2$, 10 , $P > 0.25$).

When variables in multiple-regression model (Table 5) were evaluated with the forward-selection procedure, results indicated that only a single predictor was needed in both regions. The predictive variable for the South Atlantic Bight was wind-speed variance, which explained 59% of seasonal variability in square-root ratio of gull abundance offshore to abundance shelfwide. The best predictive variable for the Outer Banks was accumulated heat flux which explained 93% of seasonal variability in log gull abundance.

DISCUSSION

Model performance.—The preceding diagnostics indicate that regression models were statistically robust. Single meteorological factors explained approximately 40 to 93% of the variation in seasonal dispersal of gulls offshore. These percentages are quite high for ornithological field studies (cf. Haney and Solow 1992). Remaining variation could have originated from unexamined biological or physical variables (e.g. habitat selection, social flocking, foraging constraints), or from sampling noise arising from measurement of the dependent and independent variables.

Wind-speed variance and accumulated heat flux consistently predicted offshore dispersal in both study areas (cf. Figs. 3 and 4). Gull dispersal off the Outer Banks also was correlated

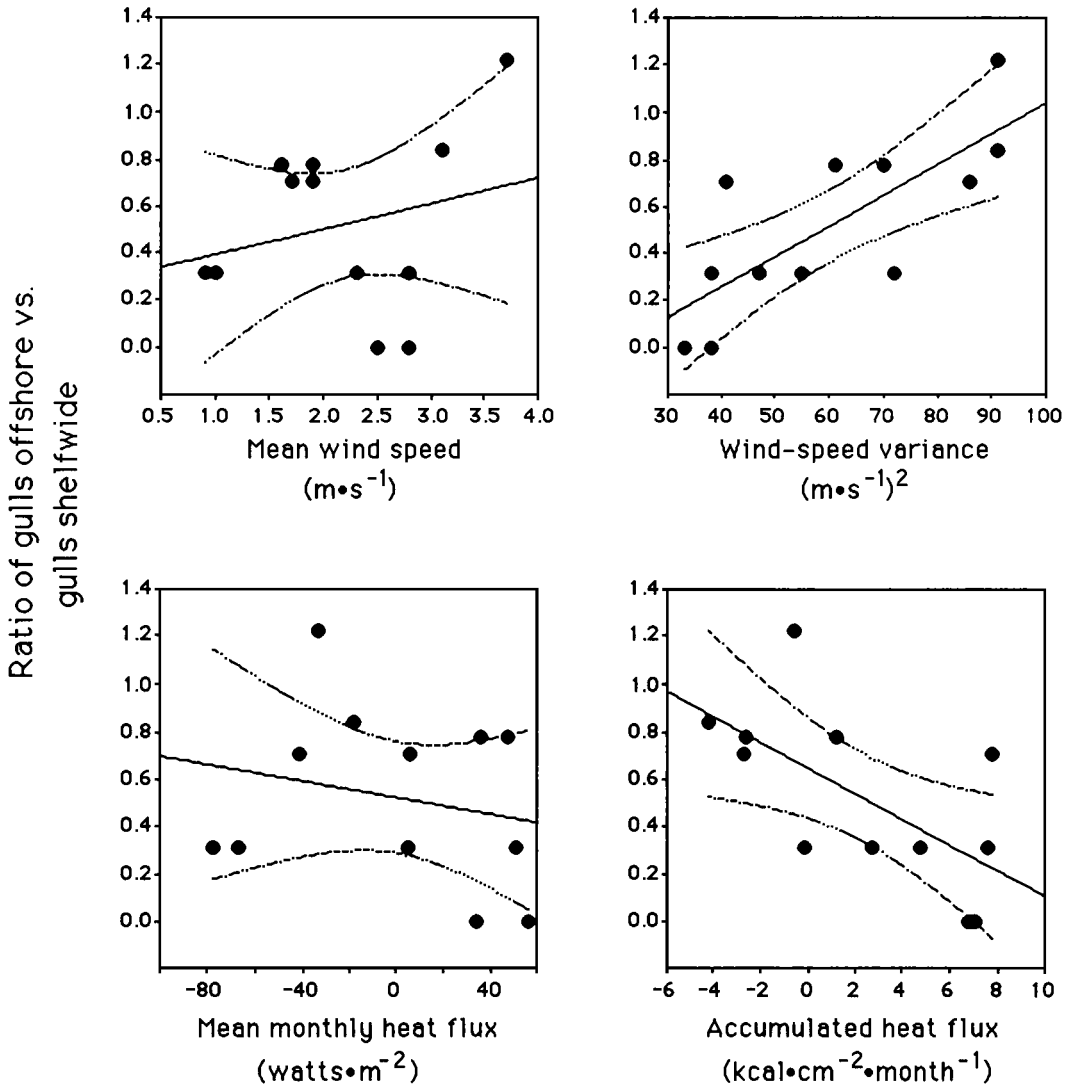


Fig. 3. Ratio of gulls in offshore waters of South Atlantic Bight in relation to monthly variability in winds and air-sea heat exchange. Elliptical 95% confidence bands given for true mean of Y in regressions.

significantly with cross-shelf temperature gradients (Table 4), but its utility as a seasonal predictor is confounded because of colinearity with accumulated heat flux. Ocean temperature gradients result in part from cross-shelf differences in rates of air-sea heat exchange (Atkinson et al. 1983), even though this relationship diminishes in the distant, offshore habitats where effects of cold-air outbreaks are reduced due to continuous replenishment of surface waters by warm southerly currents.

Colinearity among predictor variables prob-

ably accounts for why essentially no additional variation was explained by multiple-regression models (e.g. off the Outer Banks, 93.3% multiple [equation 4] vs. 93.0% best single predictor [Table 4]). Heat flux and wind-speed variance exhibit mathematical interaction at seasonal time scales, but each is a distinct physical phenomenon with the potential to separately influence gull dispersal. Over periods of hours or days, heat flux creates unstable or pre-thermal conditions, but some additional factor, such as change in wind direction or strength (wind-

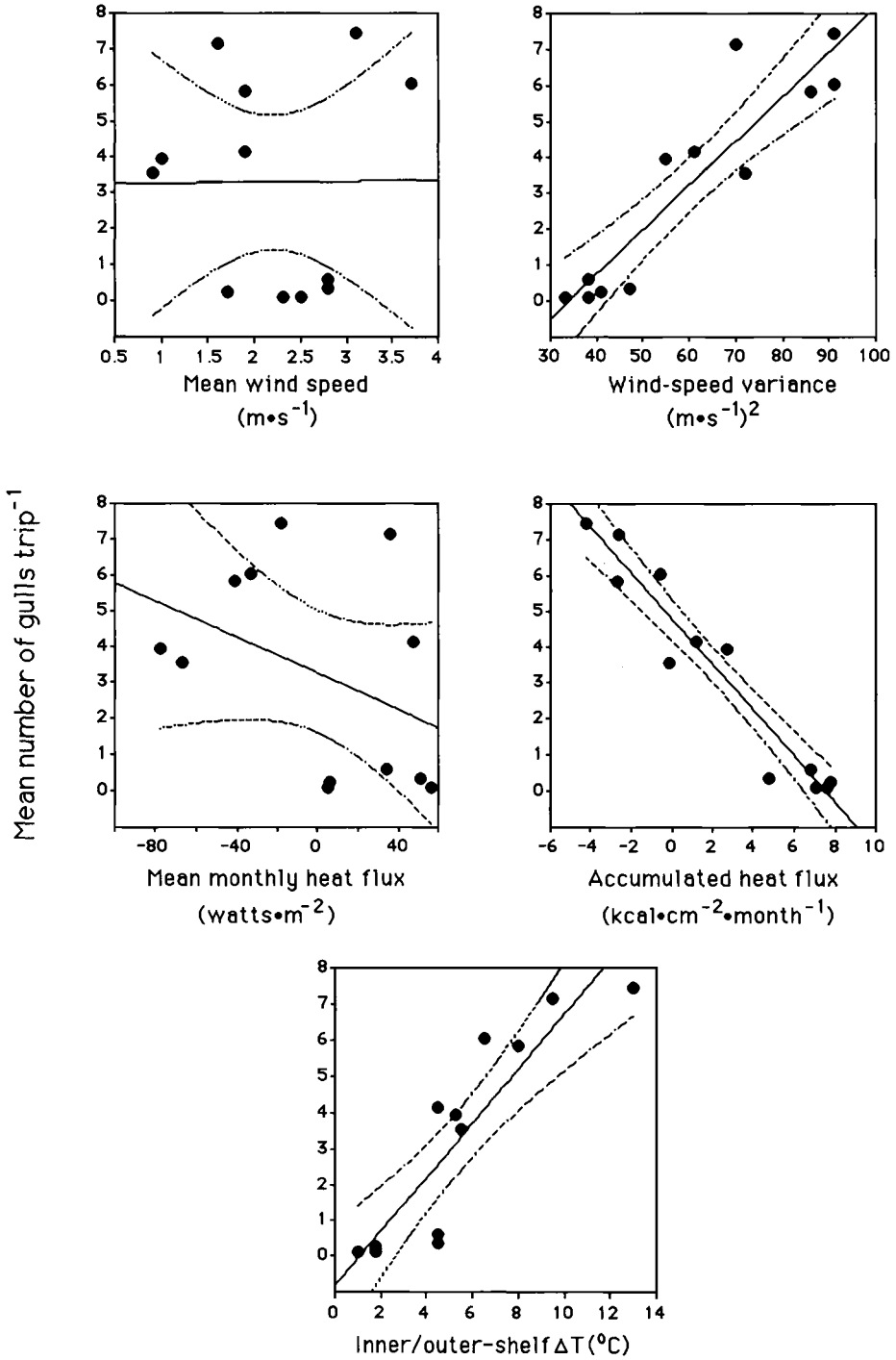


Fig. 4. Gull abundance in offshore waters off North Carolina's Outer Banks in relation to monthly variability in wind and air-sea heat exchange. Elliptical 95% confidence bands given for true mean of Y in regressions.

TABLE 5. Parameters for full-model multiple regressions to evaluate seasonal relationships of gull dispersal and meteorology in South Atlantic Bight and off North Carolina's Outer Banks.

Variable	Parameter coefficient \pm SE ^a	t ^b
South Atlantic Bight^c		
Constant	-2.496 \pm 0.904	-2.759*
Mean wind speed (X ₁)	-0.214 \pm 0.133	-1.606
Wind-speed variance (X ₂)	0.052 \pm 0.016	3.241*
Monthly heat flux (X ₃)	0.006 \pm 0.003	2.304
Accumulated heat flux (X ₄)	0.159 \pm 0.067	2.376*
Outer Banks^d		
Constant	3.704 \pm 6.531	0.567
Mean wind speed (X ₁)	0.039 \pm 0.854	0.046
Wind-speed variance (X ₂)	0.006 \pm 0.097	0.062
Monthly heat flux (X ₃)	-0.001 \pm 0.014	-0.102
Accumulated heat flux (X ₄)	-0.549 \pm 0.543	-1.011
Inner/outer shelf Δ T (X ₅)	0.075 \pm 0.282	0.265

^a Standard error of estimate.

^b ns ($P > 0.05$) unless asterisk included (*, $P \leq 0.05$).

^c Dependent variable (Y) is square root of monthly ratio of gull abundance offshore/abundance shelfwide.

^d Dependent variable (Y) is $\ln(x + 1)$ of monthly mean number of gulls offshore per survey.

speed variance), is required to release the convection cells (see below; also Woodcock 1975). Aside from its influence on convection, greater wind-speed variance provides gulls with an additional energy source for efficient flight. Modeling meteorological effects on gull dispersal with two or more variables may be difficult to justify, however, until further studies can distinguish relative contributions of each predictor.

Alternative influences on gull distribution.—Several considerations strengthen the convective-soaring hypothesis, and weaken alternatives (such as prey movement or accessibility) as explanations for gull dispersal in this region. Through explicit consideration of the seasonal influx of gulls arriving into the study area from the north, the log-linear model distinguishes temporal from habitat effects and demonstrates greater-than-expected numbers occurring offshore during winter. Seasonal change in food availability across the continental shelf is unlikely to account for this dispersal. During winter, gulls continue to have ample food supplies inshore where terrestrial offal, fish kills from

sudden drops in sea temperature in the intertidal zone, and discards from coastal fishing and shrimping fleets augment naturally occurring sources (Haney unpubl. data). In much of the South Atlantic Bight (parts of South Carolina, Georgia, northern Florida), where there are no breeding populations of gulls (Clapp et al. 1983), nonbreeders still do not commute offshore to exploit the zones of very high productivity used by other seabirds (Haney 1986b). However, the most convincing evidence for the convective-soaring hypothesis is the timing of the dispersal itself. After breeding, when all gulls presumably are less tied to nearshore habitats, they delay dispersal to offshore habitats for several months until suitable flight conditions occur (Woodcock 1940b, this study).

Mechanism for winter dispersal.—Physical feedback from the ocean to the atmosphere represents a marked reversal in the direction of air-sea interactions and their influence on seabirds. More commonly, for example, strong winds create a rough foraging "substrate" over which attempt rates, capture rates, or feeding success of marine birds are altered (Dunn 1973, Taylor 1983, Sagar and Sagar 1989). Atmospheric forcing also modifies the structure of the ocean so that foraging by seabirds is enhanced locally (e.g. through formation of seasonally recurrent hydrographic fronts; see Haney and McGillivray 1985). Notably, gulls are capable of "seeding" the air-sea teleconnection themselves through cooperative flight maneuvers. Under calm to light wind conditions (0–1 m s⁻¹) and sea-minus-air temperature differences of 3°–6°C, Woodcock (1975) watched groups of 20 to 100 gulls disturb the surface-boundary layer through vigorous wing actions. Warm and unstable air trapped near the ocean surface was released (Fig. 1), thermals were induced, and gulls then exploited the lift supplied from convective air currents. In other circumstances, natural onset of winds precipitates the thermals, which then propagate along with the wind field in spatially patchy cells (Woodcock 1975).

Cold air from continental weather systems continues to cool shelf waters throughout winter months. Cooling is proportionately greater in shallow inner-shelf waters, however, and offshore water eventually provides a greater heat reservoir (and a more likely site for convection) as the season progresses (Fig. 2). Gull distributions might be expected to shift to this op-

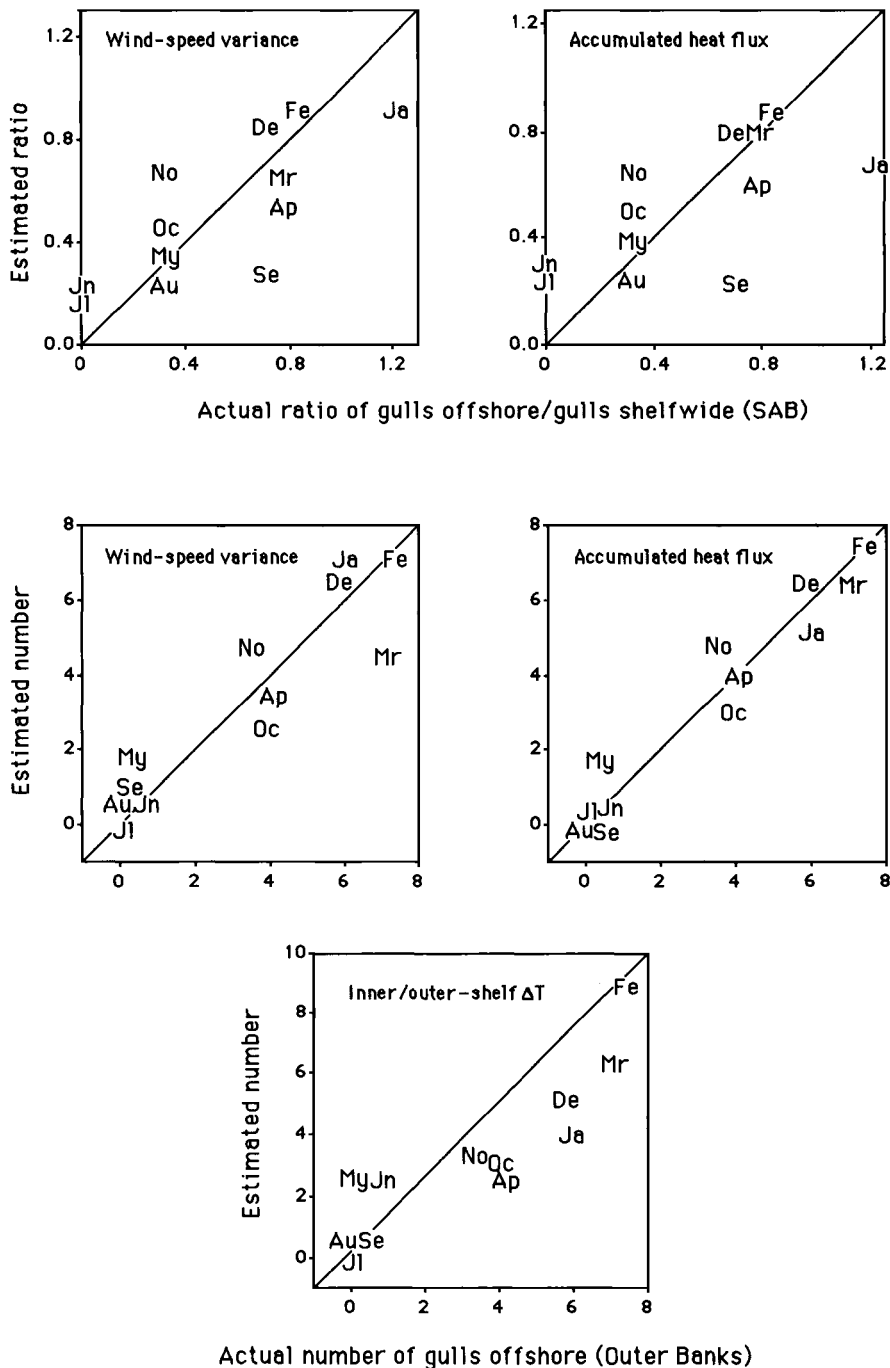


Fig. 5. Scatter plots for meteorological regression models having significantly nonzero slopes (Table 4). Individual months plotted in order to compare estimated offshore abundance vs. actual abundance. Diagonal line designates expected 1:1 relationship.

timal aerial environment by midwinter. Indeed, between December and February, higher than expected numbers of gulls occurred over the western edge of the Gulf Stream (Table 3). During winter, gulls become dominant in the offshore seabird community (see Lee 1987). Bonaparte's (in February) and Herring gulls (in March) represented more than 77 and 57%, respectively, of all seabirds recorded in offshore habitats (Lee 1993). These gulls may have two geographic origins: coastal populations moving laterally offshore; and northern populations migrating southward alongshore, but preferentially aggregating in offshore habitats.

In contrast to winter, during all three years of offshore surveys in the South Atlantic Bight (43 survey days), only two gulls were recorded beyond inner-shelf waters during summer. In 45 days of surveys during summer off North Carolina, fewer than 250 gulls were recorded beyond a distance of 10 km. Air temperatures remain higher than ocean temperatures during this period (Atkinson et al. 1983) and convection is impossible. Gulls, as well as other seabirds, often are "grounded" under such conditions (Woodcock 1940a; see also Jouventin and Weimerskirch 1990). Gulls typically do not appear offshore until late autumn (Figs. 3 and 4, Tables 1–3), a period of vigorous convection and increasing wind-speed variance over the shelf (see Weber and Blanton 1980, Blanton et al. 1985: 19).

Gull reliance on a combination of winds and thermal convection can be linked to their structural adaptations for flight. Wing loadings (in force units of newtons [N]: $\text{kg} \cdot \text{m} \cdot \text{s}^{-2}$) of gulls are comparatively low for seabirds: 32–62 $\text{N} \cdot \text{m}^{-2}$ versus 55–140 $\text{N} \cdot \text{m}^{-2}$ in procellariiforms and 106–132 $\text{N} \cdot \text{m}^{-2}$ in alcids (Pennycuick 1987a). Well adapted for efficient use of slope lift and thermals (Woodcock 1940b, Pennycuick 1987b), gulls may soar up to heights of 620 m (Woodcock 1940a), thereby lengthening the sensible viewing range for detecting distant feeding opportunities (Haney et al. 1992). Gulls closely track wind activity during foraging; Glaucous Gulls switch feeding tactics from terrestrial predation to less risky areal "harrassment" as wind speeds increase (G. Gilchrist 1993, abstract, 20th Annual Meeting of Pacific Seabird Group, Seattle, Washington).

Soaring, or a combination of wind-assisted flight plus soaring, reduces energy expended during both long-term (migratory) and short-

term (foraging) travel. Soaring, however, results in slow travel speeds and less distance traveled per unit time: larids clocked by Pennycuick (1987a:339) flew at 11 to 15 $\text{m} \cdot \text{s}^{-1}$ compared to 13–19 $\text{m} \cdot \text{s}^{-1}$ for procellariiforms, alcids, and cormorants. Low gliding speeds necessary for soaring, and high cruising speeds needed for provisioning young at high rates from distant food sources, require different wing shapes. Structural requirements for both flight methods cannot be maximized simultaneously (Pennycuick 1987b). For incubating or brooding adults, slow flight speeds will place severe constraints on maximum foraging range during the breeding season.

Biogeographic implications.—Very few larids commute to distant pelagic habitats while nesting, and almost no gulls do so. Life-history parameters, often expressed in taxonomic composition, diverge markedly in seabirds that exploit coastal and pelagic habitats. Ricklefs (1990) ascribed "wide gaps" in brood size, chick growth rates, and normalized rates of chick provisioning to different adaptations to corresponding marine environments. Food availability usually is invoked for this dichotomy (e.g. Hunt et al. 1986, Cairns 1992), but such resource patches are notoriously transient and local in the open ocean (Haney et al. 1992).

In contrast, meteorological factors, such as wind fields, have consistent and widespread properties (see Blanton et al. 1985) that could act as selective forces on the evolution of dissimilar lifestyles distinguishing coastal and pelagic seabirds. To illustrate how such selection might operate, we elaborate on energy spectra for winds off the coast of the southeastern United States. Regional wind fields vary on seasonal, synoptic (regionwide weather systems), and diurnal time scales. Wind energy is distributed primarily (58%) in the synoptic band at time scales of 1.5 to 30 days, centered on 4 to 6 days (Weisberg and Pietrafesa 1983). Energy in seasonal and diurnal bands is partitioned in the amount of 5% each. Seasonal and synoptic fluctuations are coherent over the entire region (and probably much of the western North Atlantic Ocean); that is, at least 60% of the fluctuation in wind is geographically consistent over hundreds of kilometers of latitude and longitude. Through behavioral learning and modification, gulls located anywhere within the wind field could rely upon such consistency for directed flight, as has been observed in some seabirds

(Blomqvist and Peterz 1984) and hypothesized for others (Schneider 1991).

Synoptic scale variability is also more spatially coherent during winter than during summer. Regionwide consistency in the wind regime diminishes substantially during the breeding season when coherence in the wind field occurs only in the diurnal, or seabreeze, band (Weisberg and Pietrafesa 1983). Gulls could exploit this energy source for foraging movements, but solely within coastal habitats. Seabreeze winds, oriented perpendicular to the coastline, extend only 20 to 30 km offshore and diminish abruptly at a narrow lateral boundary layer (see Blanton et al. 1985). Oceanic fronts, eddies, and other features provide recurrent foraging sites for other seabird species well beyond this zone (e.g. Haney 1986b, Lee 1993). The absence of thermals and winds during summer, however, likely produces an offshore aerial environment unsuitable for efficient travel by certain inshore species undertaking foraging commutes from coastal roosts or colonies out to these distant pelagic habitats.

In summary, we found substantial support for Woodcock's (1940b) explanation for seasonal offshore dispersal of gulls. Spatial parameters for movement described in our study require atmospheric cooling, convection, and thermal production—meteorological conditions that are expected to occur primarily along western ocean basins having similar westerly wind fields and continental weather systems. Gull dispersal at similar latitudes and coast configurations, such as the western Pacific Ocean off northeastern Asia, are most likely to provide relevant comparisons. We suggest that current geographic distributions, taxonomic composition and life-history traits of coastal and pelagic seabirds evolved and are currently governed in part as a consequence of interactions among colony location, structural adaptations for flight, and suitability of meteorological regimes for efficient foraging.

ACKNOWLEDGMENTS

Field support in the South Atlantic Bight was provided by the University of Georgia, Skidaway Institute of Oceanography, South Carolina Wildlife and Marine Resources Department, the NOAA/National Marine Fisheries Service, Burleigh-Stoddard Fund, Sheldon Fund, and NSF grants OCE81-10707 to L. R. Pomeroy and OCE81-17761 to G.-A. Paffenhöfer. Funds for studies off North Carolina came in part from the

U.S. Fish and Wildlife Service (Contract No. 14-16-0009-84-985), the North Carolina Sea Grant Program (NCSU), the U.S. Army Corps of Engineers (Wilmington, North Carolina District), the Department of the Navy, the Outer Continental Shelf Office, NOAA (North Carolina), and private funds. Data analysis and manuscript preparation were supported by the Wildlife Technology Program, School of Forest Resources, Penn State University, and the North Carolina State Museum of Natural Science. We extend thanks to all of the crews and colleagues who participated in offshore surveys. L. Spear, P. Pyle, and two anonymous reviewers provided valuable comments on earlier drafts of the manuscript.

LITERATURE CITED

- ATKINSON, L. P., T. N. LEE, J. O. BLANTON, AND W. S. CHANDLER. 1983. Climatology of the southeastern United States continental shelf waters. *J. Geophys. Res.* 88:4705-4718.
- BLANTON, J. O., F. B. SCHWING, A. H. WEBER, L. J. PIETRAFESA, AND D. W. HAYES. 1985. Wind stress climatology in the South Atlantic Bight. Pages 10-22 *in* Oceanography of the southeastern U.S. continental shelf (L. P. Atkinson, D. W. Menzel, and K. A. Bush, Eds.). Am. Geophys. Union, Washington, D.C.
- BLOMQVIST, S., AND M. PETERZ. 1984. Cyclones and pelagic seabird movements. *Mar. Ecol. Prog. Ser.* 20:85-92.
- BOURNE, W. R. P. 1982. The manner in which wind drift leads to seabird movements along the east coast of Scotland. *Ibis* 124:81-88.
- BURGER, J. 1989. Seabirds and other marine vertebrates: Competition, predation, and other interactions. Columbia Univ. Press, New York.
- CAIRNS, D. K. 1992. Population regulation of seabird colonies. *Curr. Ornithol.* 9:37-61.
- CLAPP, R. B., D. MORGAN-JACOBS, AND R. C. BANKS. 1983. Marine birds of the southeastern United States and Gulf of Mexico. Part III. Charadriiformes. U.S. Fish and Wildlife Service, Washington, D.C.
- CONE, C. D. 1964. A mathematical analysis of the dynamic soaring flight of the albatross with ecological interpretations. *Virginia Inst. Mar. Sci., Gloucester Pt., Spec. Sci. Rep.* 50:1-108.
- DOWDY, S., AND S. WEARDEN. 1991. Statistics for research. John Wiley and Sons, New York.
- DUNN, E. K. 1973. Changes in the fishing ability of terns associated with windspeed and sea surface conditions. *Nature* 244:520-521.
- HANEY, J. C. 1986a. Pelagic seabird ecology and its relationship to environmental heterogeneity in the South Atlantic Bight. Ph.D. thesis, Univ. Georgia, Athens.
- HANEY, J. C. 1986b. Seabird affinities for Gulf Stream frontal eddies: Responses of mobile marine con-

- sumers to episodic upwelling. *J. Mar. Res.* 44:361-384.
- HANEY, J. C., AND P. A. MCGILLIVARY. 1985. Midshelf fronts in the South Atlantic Bight and their influence on seabird distribution and seasonal abundance. *Biol. Oceanogr.* 3:401-430.
- HANEY, J. C., AND A. R. SOLOW. 1992. Analyzing quantitative relationships between seabirds and marine resource patches. *Curr. Ornithol.* 9:105-162.
- HANEY, J. C., K. M. FRISTRUP, AND D. S. LEE. 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scand.* 23:49-62.
- HUNT, G. L., Z. A. EPPLEY, AND D. C. SCHNEIDER. 1986. Reproductive performance of seabirds: The importance of population and colony size. *Auk* 103:306-317.
- JOUVENTIN, P., AND H. WEIMERSKIRCH. 1990. Satellite tracking of Wandering Albatrosses. *Nature* 343:746-748.
- KAISER, G. W., AND L. S. FORBES. 1992. Climatic and oceanographic influences on island use in four burrow-nesting alcids. *Ornis Scand.* 23:1-6.
- LEE, D. S. 1987. December records of seabirds off North Carolina. *Wilson Bull.* 99:116-121.
- LEE, D. S., AND M. C. SOCCI. 1989. Potential effects of oil spills on seabirds and selected other oceanic vertebrates off the North Carolina coast. *Occas. Pap. North Carolina Biol. Surv.* 1989-1, Raleigh, North Carolina.
- MANIKOWSKI, S. 1971. The influence of meteorological factors on the behavior of seabirds. *Acta Zool. Cracov.* 16:581-668.
- NEWTON, J. G., O. H. PILKEY, AND J. O. BLANTON. 1971. An oceanographic atlas of the Carolina continental margin. Duke Univ. Marine Laboratory, Beaufort, North Carolina.
- PENNYCUICK, C. J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. *Philos. Trans. R. Soc. Lond. Biol. Sci.* 300:75-106.
- PENNYCUICK, C. J. 1983. Thermal soaring compared in three dissimilar tropical bird species, *Fregata magnificens*, *Pelecanus occidentalis*, and *Coragyps atratus*. *J. Exp. Biol.* 102:307-325.
- PENNYCUICK, C. J. 1987a. Flight of auks (Alcidae) and other northern seabirds compared with southern Procellariiformes: Ornithodolite observations. *J. Exp. Biol.* 128:335-347.
- PENNYCUICK, C. J. 1987b. Flight of seabirds. Pages 43-62 in *Seabirds: feeding ecology and role in marine ecosystems* (J. P. Croxall, Ed.). Cambridge Univ. Press, Cambridge.
- RICKLEFS, R. A. 1990. Seabird life histories and the marine environment: Some speculations. *Colon. Waterbirds* 13:1-6.
- ROWLETT, R. A. 1980. Observations of marine birds and mammals in the northern Chesapeake Bight. U.S. Fish Wildl. Serv., Biol. Services Progr. FWS/OBS-80/04.
- SAGAR, P. M., AND J. L. SAGAR. 1989. The effects of wind and sea on the feeding of Antarctic Terns at the Snares Islands, New Zealand. *Notornis* 36:171-182.
- SCHNEIDER, D. C. 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanogr. Mar. Biol. Annu. Rev.* 29:487-521.
- SNEDECOR, G. W., AND W. G. COCHRAN. 1980. *Statistical methods*, 7th ed. Iowa State Univ. Press, Ames.
- TASKER, M. L., P. H. JONES, T. DIXON, AND B. F. BLAKE. 1984. Counting seabirds at sea from ships: A review of methods employed and a suggestion for a standardized approach. *Auk* 101:567-577.
- TAYLOR, I. R. 1983. Effect of wind on the foraging behavior of Common and Sandwich terns. *Ornis Scand.* 14:90-96.
- VELLEMAN, P. F., AND R. E. WELSCH. 1981. Efficient computing of regression diagnostics. *Am. Statistician* 35:234-242.
- WEBER, A. H., AND J. O. BLANTON. 1980. Monthly mean wind fields for the South Atlantic Bight. *J. Phys. Oceanogr.* 10:1256-1263.
- WEISBERG, R. H., AND L. J. PIETRAFESA. 1983. Kinematics and correlation of the surface wind field in the South Atlantic Bight. *J. Geophys. Res.* 88:4593-4610.
- WILKINSON, L. 1989. SYSTAT: The system for statistics. SYSTAT, Inc., Evanston, Illinois.
- WILSON, J. A. 1975. Sweeping flight and soaring by albatrosses. *Nature* 257:307-308.
- WOOD, C. J. 1973. The flight of albatrosses (a computer simulation). *Ibis* 114:244-256.
- WOODCOCK, A. H. 1940a. Convection and soaring over the open sea. *J. Mar. Res.* 3:248-253.
- WOODCOCK, A. H. 1940b. Observations of Herring Gull soaring. *Auk* 57:219-224.
- WOODCOCK, A. H. 1975. Thermals over the sea and gull flight behavior. *Boundary-Layer Meteorol.* 9:63-68.