ALCID PATCHINESS AND FLIGHT DIRECTION NEAR A COLONY IN EASTERN NEWFOUNDLAND

DAVID C. SCHNEIDER, RAYMOND PIEROTTI, AND WILLIAM THRELFALL

Abstract. Topographic features, including shape of the coastline and shape of the bottom, generate spatially predictable flow gradients that can concentrate seabird prey. We hypothesize that bathymetrically induced flow gradients influence the distribution, flight orientation, and patch scale of foraging alcids around colonies. Two potentially important sites were identified from hydrographic charts of the waters around the colony at Witless Bay, in eastern Newfoundland. One site was a bank 70 km southeast of the colony. The second was a strip of high topographic relief running along the western margin of the Avalon Channel, which carries the inshore branch of the Labrador Current southward past the colony. Surveys in 1985 showed that murres (primarily Common Murres, *Uria aalge*) and Atlantic Puffins (*Fratercula arctica*) were present in abundance at the offshore bank. Both species brought fish to the colony from this bank. Surveys also showed that the abundance of murres and puffins was greater along the coastal strip south and north of the colony than at similar distances east of the colony. Surveys in 1987 showed that murres and puffins on the water were aggregated at the scale of the first internal Rossby radius, which is the characteristic scale of flow gradients at water mass boundaries (fronts). Our results suggest that multiple rather than single focus spatial models are required to describe the foraging behavior of colonial alcids.

Key Words: Alcids; habitat selection; oceanography; upwelling; Newfoundland.

Habitat selection by birds has been investigated in many terrestrial environments (Cody 1985); little work has been done in marine environments. Preliminary models of foraging distribution and energetics of marine birds have assumed that rate of encounter with prey is either spatially uniform or unpredictable in oceanic (Diamond 1978) and continental shelf ecosystems (Cody 1973, Furness 1978). A growing body of evidence indicates that, at least in shelf ecosystems, rates of encounter with prey are likely to be predictable in space (Brown 1980a) and time (Schneider et al. 1987). One important source of spatially predictable variability in shelf ecosystems is topography, including shape of the coastline and shape of the bottom. Bathymetric features generate spatially predictable flow gradients in shelf ecosystems (Csanady 1982, Allen et al. 1983), with important effects on the production and local distribution of marine organisms (Holligan 1981, Owen 1981, Richards 1981).

Flow gradients, which are defined as changes in water velocity in horizontal or vertical directions, can concentrate the prey of marine birds in at least four different ways. Convergent flow (downwelling) can increase the patchiness of vertically migrating prey such as myctophids (Olson and Backus 1985) and gelatinous zooplankton (Hamner and Schneider 1986). Divergent flow (upwelling) can bring prey to the sea surface, where it can be captured by non-diving species (Brown 1980a). Coastal upwelling can increase subsurface concentrations of negatively phototactic prey such as euphausiids (Simard et al.

1986). Flow gradients can also maintain temperature gradients to which nekton can respond directly (Laurs et al. 1977, Magnuson et al. 1981, Olla et al. 1985).

Several recent studies indicate that bathymetrically induced flow gradients influence the distribution of alcids around breeding colonies. In the Bering Sea, murres (*Uria* spp.) occurred at greater densities near the shelf break southwest of the Pribilof Islands than at similar distances to the northwest of the Pribilof Islands (Schneider and Hunt 1984). Nearer to the islands Kinder et al. (1983) reported an increase in the number of murres at a shallow sea front associated with a change in bottom slope. In Hudson Bay Cairns and Schneider (this volume) showed that the abundance of Thick-billed Murres (*U. lomvia*) was related to depth gradient as well as to water depth.

If areas of bathymetrically induced flow gradients are important to foraging seabirds, then several predictions can be made about the distribution and behavior of alcids foraging near colonies. First, alcids should be more abundant in areas of high topographic relief than in areas of less relief. Second, alcids should be observed commuting to areas of high topographic relief. Third, patchiness of alcids on the water should be observed at the scale of the first internal Rossby radius, which is the characteristic scale of flow gradients at water mass boundaries (fronts) in the ocean (Gill 1982:207). To test these predictions we measured the distribution and flight orientation of murres and Atlantic Puffins (*Fra-*
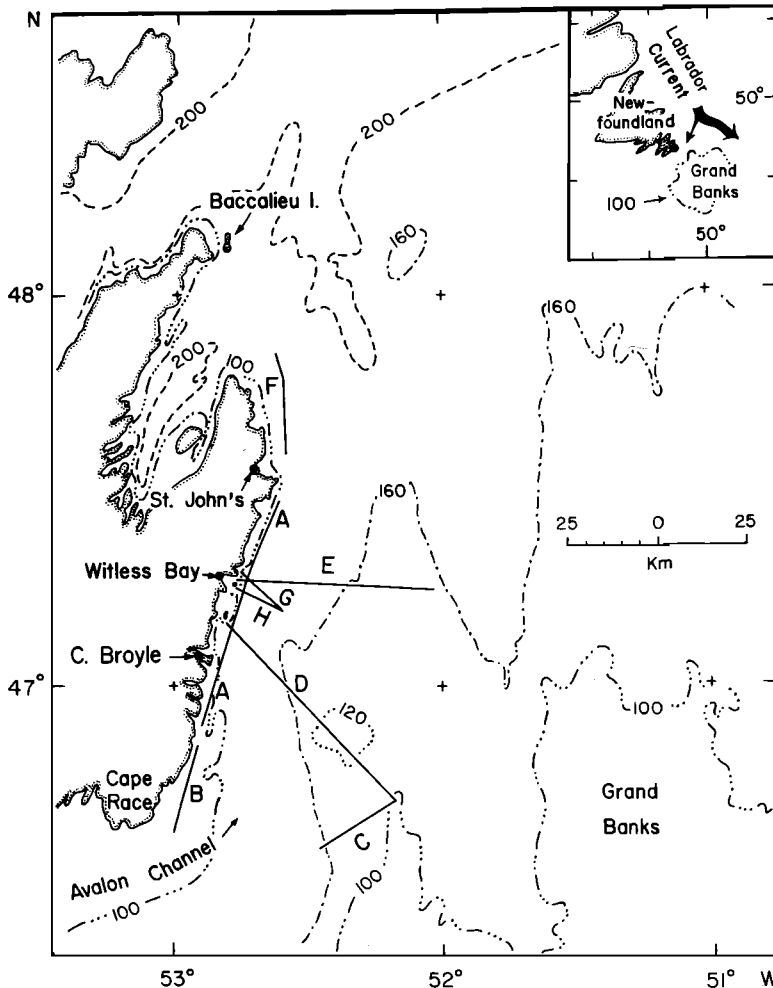
FIGURE 1. Seabird colonies, topographic features, and experimental transects in the Avalon Channel.

tercula arctica) in relation to bathymetric gradients in the Avalon Channel, which carries the inshore branch of the Labrador Current southward past the breeding colony at Witless Bay (Fig. 1).

A variety of standard statistical methods has been used to test hypotheses about the distribution and abundance of marine birds. Confirmatory analyses have been carried out using F-distributions (Abrams and Griffiths 1981, Schneider 1982, Kinder et al. 1983, Briggs et al. 1984), chi-square distributions (Haney 1986), and non-parametric methods based on ranks (Woodby 1984, Schneider and Duffy 1985) or on randomizations (Schneider and Piatt 1986). Counts of marine birds rarely conform to the assumptions underlying parametric methods based on F or chi-square distributions; yet, attempts to identify an appropriate statistical model (Schneider and

Duffy 1985) have been rare. Non-parametric tests based on ranks are relatively insensitive, and can fail to detect a true effect. Diggle (1983) has recommended the use of Monte Carlo randomizations to evaluate Type I error (erroneous rejection of a null hypothesis) in the analysis of spatial data. This non-parametric method makes no assumptions about the error structure of the data, and has greater sensitivity (lower Type II error) than rank-based tests.

PHYSICAL AND BIOLOGICAL SETTING

The study area is strongly influenced by the Labrador Current, which brings cold ($<0°C$) water of relatively low salinity (28–30‰) southward to the Grand Banks. The main branch of the Labrador Current flows around the east side of the Grand Banks, while a secondary branch flows through the Avalon Channel between the Grand

Banks and the Avalon Peninsula (Fig. 1). Stratification of the water column is delayed until June, when a thermocline forms above the cold core of the Labrador Current. Figure 2 shows the typical depth of the upper layer that forms above the cold core of the Labrador Current in the Avalon Channel. Upward deflections of the thermocline, which indicate strong local flow gradients, are associated with shoaling water on the eastern side of the Avalon Channel (Hollibaugh and Booth 1981). A temperature profile along the 47th parallel (Fig. 2) shows an upward doming of isotherms approximately 50 to 100 km east of the Avalon Peninsula; the forces responsible are not known. Upward doming of the thermocline also occurs along the coast of the Avalon Peninsula during the summer (Piatt and Methven 1986). The thermocline can rise to the surface during a single day; rises are associated with southwest winds, which favor upwelling (Schneider and Methven 1988).

Two major alcid colonies occur in the Avalon Channel—one at Witless Bay and one on Baccalieu Island (Fig. 1). Alcids at Witless Bay nest on Great Island, which is located at the western end of transect D (Fig. 1), on PeePee Island, which is just northwest of Grand Island, on Gull Island, which is located at the western end of transect E, and on Green Island, which is located just south of Gull Island. Recent estimates of breeding populations at Witless Bay are listed in Table 1.

Capelin (*Mallotus villosus*) is the predominant prey species in the diet of alcids at these colonies during the nesting period (Brown and Nettleship 1984, Burger and Piatt 1990). Capelin appear along the coast when the water temperature rises to ca. 5°C (Templeman 1948). Near the Witless Bay colony schools concentrate in the warm upper layer (Piatt and Methven 1986). During early July the upper layer varies in thickness from 10 m in a cold year such as 1984 to 30 m in a warm year such as 1987. At the time scale of days,
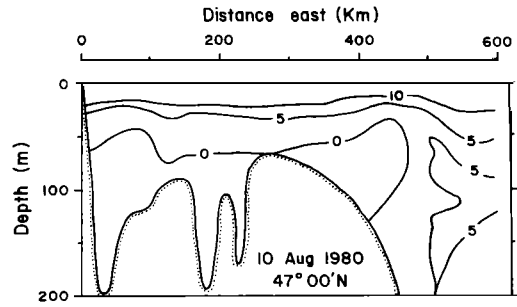

FIGURE 2. Thermal profile across the Avalon Channel and Grand Banks during the summer. Redrawn from Hollibaugh and Booth (1981).

episodic rises of the thermocline concentrate capelin near the sea surface (Piatt and Methven 1986). The horizontal scale of the rise in the thermocline is the first internal Rossby radius, which was calculated as 4.7 km in late July in the Avalon Channel (Appendix I).

METHODS

Nautical charts were used to identify regions of high bathymetric gradient within 100 km of the Witless Bay colonies. Salinity and temperature profiles from Hollibaugh and Booth (1981) and Lively (1983) were used to identify hydrographic gradients associated with bathymetric features. Two areas of bathymetrically-associated hydrographic gradients were identified. The first was an offshore bank 70 km southeast of Witless Bay (Fig. 1), where hydrographic profiles showed upward doming of the thermocline on the western side (Fig. 2). The second area was the coastal strip on the west side of the Channel, where episodic upwelling occurs in response to winds from the southwest.

To test for enhanced abundance and foraging activity along the coast, we ran transects in July of 1985 along the coast (transects A, B, and F, Fig. 1) for comparison with those running away from the coast (transect E and the central third of transect D). To test for enhanced abundance and feeding activity at the offshore bank we compared a transect across the bank (transect D) to a

TABLE 1. APPROXIMATE NUMBER OF BREEDING PAIRS OF SEABIRDS NESTING ON ISLANDS AT WITLESS BAY (FROM CAIRNS ET AL. 1986)

	Gull	Green	Pee Pee	Great
Fulmarus glacialis				20
Oceanodroma leucorhoa	530,000	present		250,000
Larus argentatus	3850	300	75	2700
Larus marinus	113	50	3	80
Rissa tridactyla	10,140	10,000		23,230
Uria aalge	687	74,000		2800
Uria lomvia		600		
Alca torda	60	170		120
Cepphus grylle	present	present	present	present
Fratercula arctica	60,000	17,000	1200	148,000

TABLE 2. Number of Birds Encountered along 6 Transects in the Avalon Channel in 1985. Times are Local (GMT + 3.5 hr)

	A	B	C	D	D	E	F
Date	24 Jul	24 Jul	5 Aug	5 Aug	25 Jul	25 Jul	26 Jul
Start	07:35	15:58	06:39	09:00	05:35	12:35	05:45
Duration (min)	360	120	113	191	345	275	195
Distance (km)	76.28	25.53	46.51	79.90	71.08	56.64	29.85
Area (ha)	763	255			711	566	299
Species							
Fulmarus glacialis	0	3	25	20	28	26	0
Puffinus spp.	1	0	0	0	0	250	0
Puffinus gravis	0	11	20	32	15	32	1
P. griseus	2	6	4	7	17	11	0
P. puffinus	3	0	0	0	1	1	1
Hydrobatidae	0	0	95	45	59	2	0
Sula bassanus	9	4	1	4	2	0	5
Phalaropus fulicarius	7	0	0	0	1	0	0
Sterocorarius spp.	1	0	0	1	0	0	0
Catharacta skua	0	0	0	3	0	0	2
Larus spp.	0	0	1	3	0	0	0
Larus marinus	2	0	0	0	3	2	0
Larus argentatus	48	2	2	0	12	5	85
Rissa tridactyla	174	0	19	12	58	7	23
Alca torda	22	0	2	0	4	0	1
Uria spp.	1404	245	11	32	188	334	171
Fratercula arctica	1457	62	33	138	492	303	27

control transect through a nearby area of low bathymetric gradient (transect E). To test whether murres and puffins on the water aggregate at the scale of the first internal Rossby radius, we first calculated the radius for typical summer conditions in the Avalon Channel, then compared variability at this scale to variability at the scale of the count resolution, which was 300 m in 1985. The analysis was repeated using higher resolution data obtained in 1987 (transects G and H).

Bird abundance and behavior were recorded during 1985 in a 100-m wide strip on one side of a 30-m sailing vessel moving at speeds greater than 9 km/hr. All birds were identified to the lowest possible taxonomic level, usually species. Behavior of each bird was recorded in two categories: on the water or flying. The presence of fish in the bill was noted in flying birds. Flight directions were recorded in 45° sectors.

To determine whether spatial patterns observed in July were repeatable, transect D was re-surveyed in early August. Counts were made from the R/V *Dawson*, using a strip transect out to the horizon. The difference in method does not preclude comparison of spatial patterns in August to those in July because pattern was measured as a dimensionless number, the ratio of two variances. The difference in method does preclude comparison of average abundance in August to average abundance in July.

Temperature measurements were not made during the 1985 surveys, so a theoretical model was used to calculate the approximate scale of the first internal Rossby radius for conditions typical of the Avalon Channel in summer (Appendix I). Variability in abundance at the scale of the calculated Rossby radius (R_2

= 4.7 km) was compared to variability at the scale of minimum resolution, which was the product of temporal resolution (2 minutes) and vessel speed along each transect. Pattern at the scale of $L = R_2$ was measured as:

$$F(L) = [n_L - 1][Var(N_L)][Var(N_0) - Var(N_L)]^{-1},$$

where n_L denotes the number of segments of length L along a transect of total length $T = Ln_L$, $Var(N_L)$ denotes variance among counts within contiguous segments of length L, and $Var(N_0)$ denotes variance among counts within segments of length equal to the minimum spatial resolution. The null hypothesis, no increase in variability at the scale of the first internal Rossby radius, was accepted if the observed F-ratio F(L) was not significant at the 5% level. Significance was evaluated by comparing each observed F-ratio to 500 ratios computed from random permutations of the vector of counts N_0. Randomizations were obtained by assigning a sequential number to each section of a transect, e.g., 258 sections of length 300 m on transect A. Counts were then shuffled by location, using random permutations of the sequence of numbers (GGPER routine, International Mathematics and Statistics Library, Houston, Texas, U.S.A.). Each call to this routine generated a random number that was used as the seed in the next call to the routine. The frequency of identical permutations due to identical seeds was found to be less than 10^{-7}. Type I error was computed as p_M, the proportion of randomized F-ratios exceeding the observed ratio. Aggregation at scale $L = R_2$ was declared significant if p_M was less than the criterion level, 5%. Sokal and Rohlf (1981) describe a similar randomization test.
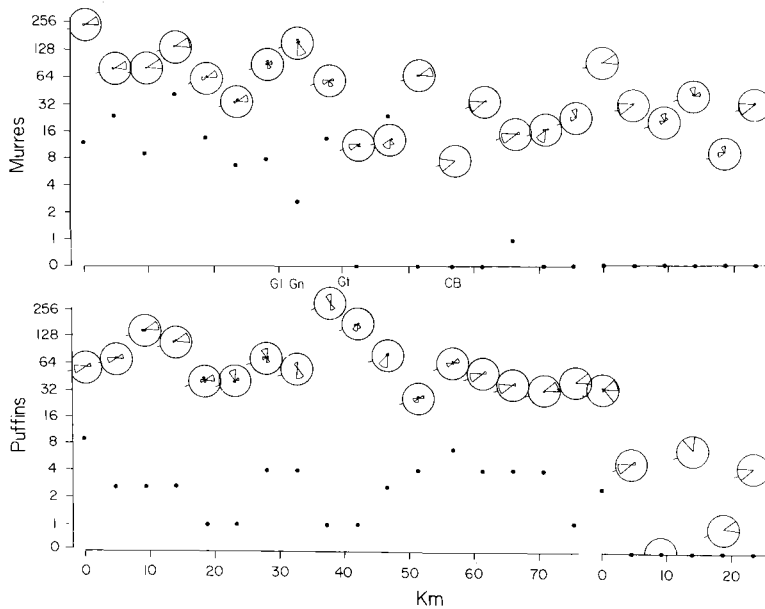
FIGURE 3. Distribution of murres and puffins along transects A (left) and B (right), 24 July 1985. Solid dots indicate density on water in contiguous 4.7 km sections of the transect. Height of circles above the abcissa indicates number of flying birds. Filled areas within each circle indicate percent flying in a given direction. Flight directions are relative to ship direction, which is the same as the abcissa (left to right). North is shown as a tic mark on the circumference of each circle. Gl = Gull Island, at base of transect E. Gn = Green Island. Gt = Great Island, at base of transect D. CB = Cape Broyle.

RESULTS

ABUNDANCE AND FLIGHT ORIENTATION OF MURRES AND PUFFINS

Murres and puffins were the most abundant birds along coastal transects A and B on 24 July 1985 (Table 2). Procellariids (Northern Fulmar *Fulmarus glacialis,* Greater Shearwater *Puffinus gravis,* and storm-petrels) were more abundant along offshore transects than along coastal transects (Table 2).

A more detailed analysis of murre and puffin distribution was obtained by mapping numbers seen per 4.7 km segment of each transect. Murres were abundant on the water along the coast north of the Witless Bay colony on 24 July 1985 (Fig. 3). The number of murres on the water did not decrease with distance out to 30 km north of Gull Island. Murres were less abundant along the coast south of the colony than to the north. Puffins were abundant on the water to the north and south of the colony. The number of puffins on the water did not decrease monotonically with distance from the colony. A sudden decrease along the coast was observed south of Cape Broyle, approximately 40 km from Great Island. Few puffins were observed on the water along the coast

40 km north of Gull Island (Transect F, Table 2).

Similar patterns were observed along the coast on 22 July 1985 while in transit from Cape Race (06:30 local time) to St. John's (15:00 hr). Few alcids were observed on the water from Renews to Cape Broyle (ca. 20 km); many alcids were observed on the water from Cape Broyle to Great Island (ca. 20 km). Many murres and puffins were observed on the water between Gull Island and St. John's (12:00–15:00), the same pattern observed during the morning of 25 July.

Murres and puffins were less abundant on the water along the offshore transects (D and E, Figs. 4–5) than along the coastal transects (A, B, and F, Fig. 3 and Table 2). Few puffins or murres were observed on the water beyond 20 km from the colony (Fig. 5). However, the transect data do not include the large number of murres and puffins observed on the water just before dawn at the southeastern end (beginning) of transect D (George Nichols, pers. comm.).

Flight direction of murres and puffins on coastal transects was generally either toward or away from the colony at ranges of 10 km or more (Fig. 3). Orientation was more variable within 10 km of the colony. Along transect D murres and puf-
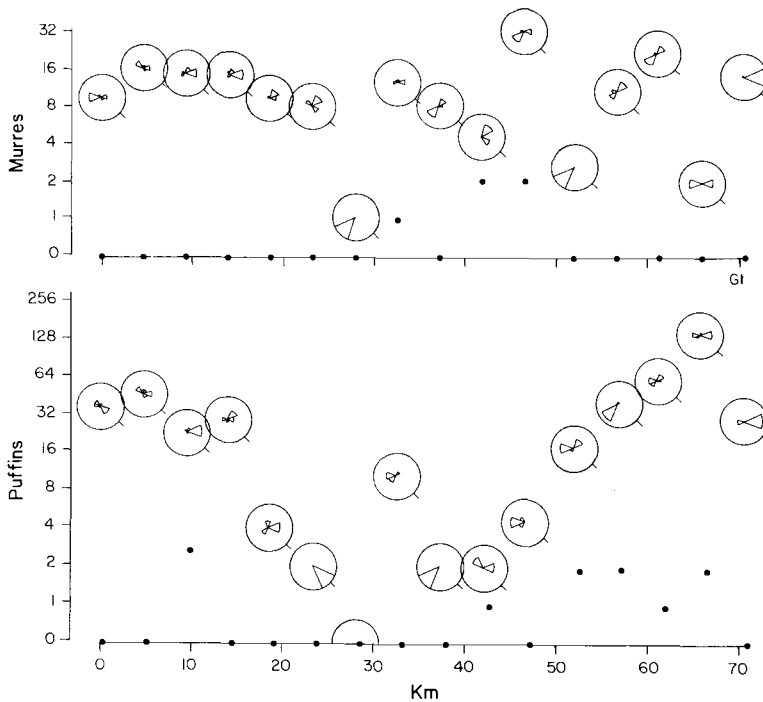
FIGURE 4. Distribution of murres and puffins along transect D, 25 July 1985. Symbols as in Figure 3.

fins were observed flying either toward or away from the colony at ranges of 40 km or more (Fig. 4), while on transect E (Fig. 5) orientation was less consistent. Consistent flight orientation indicates that birds were commuting either along the coast or directly to the offshore bank at the beginning of transect D. Fish of undetermined species were observed in the bills of murres and puffins flying toward the colony along transects A, B, and D.

The repeatability of the results in July was investigated by surveying transect D on the first available occasion, which was in early August. Murres and puffins were associated with the bank during the second traverse (transects C and D, 5 August, Table 2). The pattern of abundance of birds along transect D differed from that observed during the earlier traverse of this transect. Murres (primarily flying birds) were more abundant at the beginning and end of the transect during the second traverse (Fig. 6), compared to similar abundances of flying murres throughout the transect during the first traverse (Fig. 4). Puffins (primarily flying birds) increased near the colony on the second traverse, a pattern that differed from the large number of flying birds observed at the beginning of the transect on the first traverse (Fig. 4). These observations were con-

sistent with our hypotheses. Alcids were more abundant on the water along the coast than in the Avalon Channel. Alcids were found on the water at the change in bathymetry on the eastern side of the Avalon Channel. Alcid flight direction (at distances of 40 km or more from the colony) was generally toward areas of strong bathymetric gradient. However, these patterns were variable. In particular, distribution along transect D varied between the two traverses, and flight orientation within 40 km of the colony was more variable than beyond 40 km. Also, alcids were observed on the water along transect F at distances greater than one internal Rossby radius from the coast.

PATCHINESS OF MURRES AND PUFFINS
ON THE WATER

If flow gradients influence alcid patchiness, then significant spatial variability should be observed at the scale of the first internal Rossby radius, which was calculated at 4.7 km. During 1985 variability of murre counts at this scale was greater than variability at the scale of count resolution, 300 m (Table 3). However, the difference was significant in only one case, transect D. Variability in the abundance of puffins at the scale
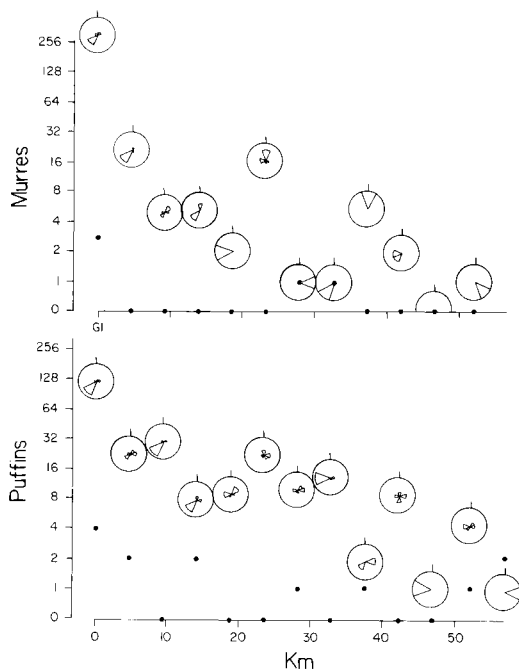
FIGURE 5. Distribution of murres and puffins along transect E, 25 July 1985. Symbols as in Figure 3.

FIGURE 6. Distribution of murres and puffins along transect D, 5 August 1985.

of 4.7 km was not greater than variability at the scale of count resolution, 300 m.

The null hypothesis, no significant aggregation at the scale of the first internal Rossby radius, could be rejected in only 1 of 6 cases (Table 3). Type II error, erroneous acceptance of a null hypothesis, could have resulted from several problems with the 1985 data. The first was the lateness of the counts, which were made after murres had begun to fledge; the resulting low abundances around the colony certainly reduced the sensitivity of the analysis. Second, the scale of upwelling may have deviated from the theoretical value, contributing to a null result. Third, spatial resolution was 300 m, which may have reduced the ability to detect a real difference. Fourth, feeding activity appeared to be greater during the morning, so that counts made later in the day may not have reflected feeding conditions.

These problems were resolved by conducting experimental transects in late June 1987, when murres and puffins were incubating. The Rossby radius was estimated from sea-surface temperatures measured concomitantly with bird counts along two transects (G and H, Fig. 1). Spatial resolution was increased by using a microcomputer to record data to the nearest 5 seconds. Ship speed was 4 m/s, so spatial resolution was 20 m. Counts were made early during the day (07:00 to 09:00).
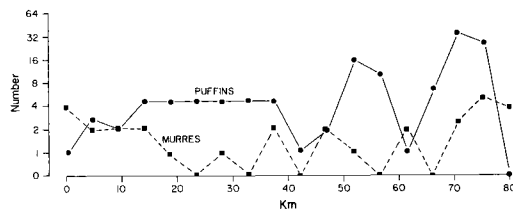
The scale of upwelling (frontal width) was estimated at 5.5 km, using the rate of change in sea surface temperature measured at 1 minute (240 m) intervals along transect G (Fig. 7). Most murres on the water were observed inside the front, i.e., less than 5.5 km from shore. A few were observed in the frontal area, which ran from 5.5 to 11 km offshore. Variability at the scale of 5.5 km was significantly greater than smaller scale variability (Table 4). Puffins on the water were most abundant nearshore or at the front (Fig. 7). Variability at the scale of 5.5 km was significant in 3 out of 3 cases (Table 4). We concluded that significant aggregation did occur at the scale of the Rossby radius.

Temperature and bird distributions along transect H were similar to those along transect G. Murres on the water were more abundant in upwelled water than at the front, whereas puffins were more abundant at the front, defined as the region of strongest horizontal gradient in sea-surface temperature (Fig. 8). Variability in murre abundance at the scale of 5.5 km was significantly greater than smaller scale variability (Table 4). The number of puffins encountered on the water along this transect was too small to permit an adequately sensitive test for aggregation at the scale of 5.5 km.

DISCUSSION

Coarse scale (1–100 km) aggregations of birds were first reported along a 500 km transect across the Bering Sea shelf (Schneider 1982). Extended aggregations have been reported along transects normal to hydrographic features in the California Current (Briggs et al. 1984), the Bering Sea (Kinder et al. 1983), the Benguela Current (Schneider and Duffy 1985), and the Labrador Current (Schneider and Piatt 1986). In the latter study, coarse scale aggregations of alcids near Witless Bay were associated with coarse scale aggregations of schooling fish, primarily capelin. The scale of bird-fish correlation was in the range of 2 to 6 km. Based on these findings, we hypothesized that coarse scale aggregations of marine birds result from concentrating mechanisms

TABLE 3. VARIANCE IN ALCID ABUNDANCE ON WATER IN 1985 AT THE LENGTH SCALE OF COUNT RESOLUTION (0.3 KM) AND AT THE LENGTH SCALE OF THE INTERNAL ROSSBY RADIUS (4.7 KM). N IS TOTAL NUMBER SEEN. TYPE I ERROR ESTIMATES ARE FOR THE NULL HYPOTHESIS THAT $\tilde{N}^2$(0.3 KM) = $\tilde{N}^2$(4.7 KM), WHERE $\tilde{N}^2$(L) DENOTES COUNT VARIANCE AT SCALE L. DEGREES OF FREEDOM SHOWN IN PARENTHESES AFTER EACH VARIANCE. TYPE I ERROR ESTIMATES (p_M) ARE BASED ON 500 MONTE CARLO RUNS. p_F IS TYPE I ERROR ASSUMING AN F-DISTRIBUTION

Transect	Species	N	$\tilde{N}^2$(0.3)	$\tilde{N}^2$(4.7)	F	p_M	p_F
A	Murres	167	6.20 (257)	8.64 (15)	1.43	0.10	0.13
B		0					
D		5	0.029 (237)	0.068 (14)	2.57	0.01	0.002
E		5	0.035 (194)	0.051 (11)	1.46	0.07	0.15
F		0					
A	Puffins	58	0.393 (257)	0.359 (15)	0.91	0.56	0.55
B		3					
D		11	0.061 (237)	0.072 (14)	1.20	0.23	0.28
E		13	0.104 (194)	0.104 (11)	1.00	0.43	0.45
F		1					

at the scale of the first internal (baroclinic) Rossby radius, which is the characteristic scale of flow gradients at water mass boundaries (fronts). Our analysis of murre and puffin abundance supports that prediction.

We did not identify the mechanism responsible for aggregation at this scale in the Avalon Channel. We speculate that along the coastal strip, wind-induced upwelling concentrates capelin, which avoid cold water just before spawning during the summer. Avoidance of a rising thermocline at the coast would tend to concentrate them vertically, whereas wind-induced surfacing of the thermocline, followed by offshore propagation of a cold water front, would tend to concentrate them horizontally. This is consistent with what is known of capelin behavior (Templeman 1948), but needs to be tested.

Upwelling on the coastal (right) side of the Labrador Current is somewhat unexpected, because the effects of the earth's rotation (Coriolis force) will tend to drive this current toward, rather than away from the coast. However, in the zone of prevailing westerly winds (ca. 40°N to 50°N) meteorological forcing would tend to cause upwelling on the coastal (i.e., right) side of the Labrador Current. Calculations (Hay and Kinsella 1985, Schneider and Methven 1988) show that winds prevailing on the Grand Banks are

strong enough to reduce the thickness of the surface layer near a coastal (wall-like) boundary. Measurements in the Avalon Channel in 1984 (Schneider and Methven 1988) show that substantial thinning of the warmer surface layer does occur in response to upwelling favorable (south or southwesterly) winds. We speculate that the energy of the winds, via upwelling, contributes to the productivity of the large alcid colonies found along the coast of eastern Canada between 47°N and 54°N latitude (Brown et al. 1975).

Water depth on the eastern (Grand Banks) side of the Avalon Channel may be too great for simple coastal upwelling, such as that envisioned along the coast strip, to be important. Bathymetric contours diverge considerably in a downstream direction on the eastern side of the Channel, a circumstance that can cause persistent upwelling in a boundary current (Janowitz and Pietrafesa 1982). Temperature and density profiles across the bank (Hollibaugh and Booth 1981) suggest that upwelling does occur on the left side of the inshore branch of the Labrador Current. The observed property gradients, or their affiliated flow gradients, may affect either the density or availability of prey taken by the alcids that were observed feeding on the eastern side of the Avalon Channel. Wynne-Edwards (1935) reported alcids in this area over 50 years earlier.

TABLE 4. VARIANCE IN ALCID ABUNDANCE ON THE WATER IN 1987 AT THE LENGTH SCALE OF COUNT RESOLUTION (20 M) AND AT THE LENGTH SCALE OF THE FIRST INTERNAL ROSSBY RADIUS (5.5 KM). SYMBOLS (N, $\tilde{N}^2$(L), p_F, p_M) AS IN TABLE 3

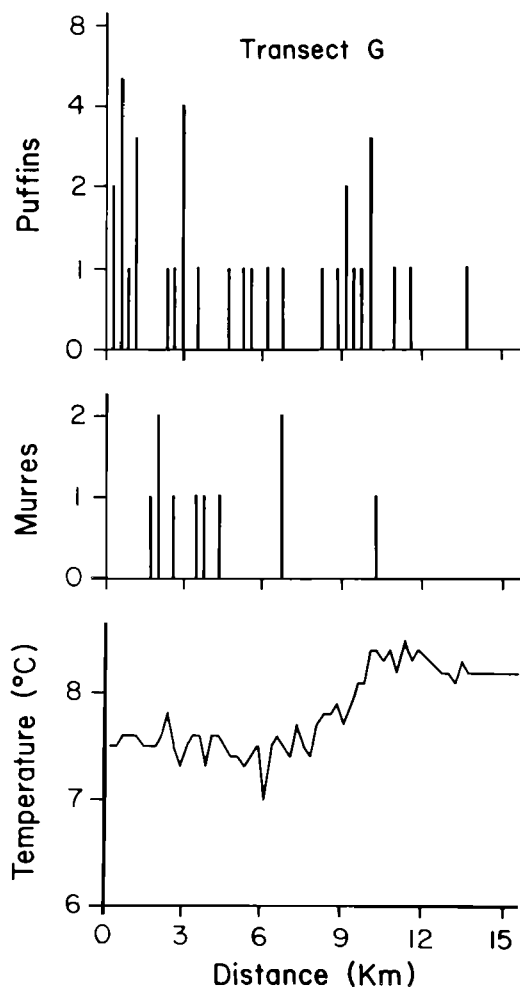| Transect	Species	N	$\tilde{N}^2$(0.02)	$\tilde{N}^2$(5.5)	F	p_M	p_F
G	Murre	10	0.013 (788)	0.038 (2)	3.08	0.02	0.05
	Puffin	35	0.093 (788)	0.295 (2)	3.18	0.05	0.04
H	Murre	65	0.282 (810)	3.64 (2)	13.34	<0.002	0.0001
	Puffin	4	0.0049 (810)				

FIGURE 7. Sea surface temperature and distribution of murres and puffins on the water along transect G, 25 June 1987. Transect runs from coast to deep water.
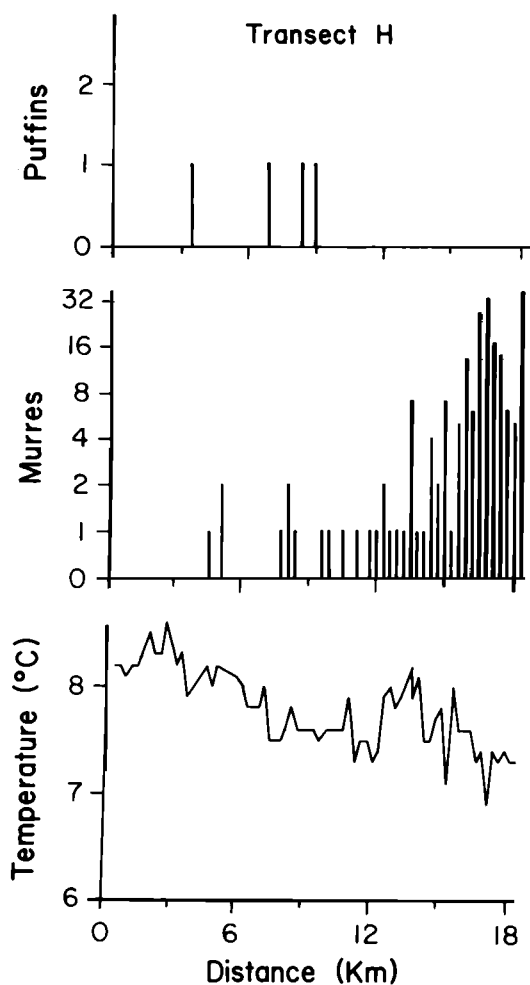
FIGURE 8. Sea surface temperature and distribution of murres and puffins on the water along transect H, 25 June 1987. Transect runs from deep water toward the coast.

The hypothesis that bathymetrically induced flow gradients increase the foraging success of alcids was proposed to explain the distribution of murres away from colonies in the southeastern Bering Sea (Schneider et al. 1986). We suggest that this hypothesis pertains to alcids foraging around colonies because: (1) abundance along radial transects is not uniform in all directions from large colonies (Hunt et al. 1981, Schneider and Hunt 1984, Schneider and Piatt 1986); (2) consistent flight directions have been observed at considerable distances from large colonies of alcids (Brown 1980b, Gaston 1982), and orientation is toward areas of strong hydrographic gradients (Brown 1980b); and (3) areas with high abundance of alcids on the water can be identi-

fied around colonies (Schneider and Hunt 1984, Cairns and Schneider 1990).

Our results, as well as reports on flight directions at other colonies, are consistent with the hypothesis that breeding alcids commute to selected areas. Organized streams of seabirds moving outward from colonies have been reported from the north Pacific (Bédard 1969, Bent 1912, Myres 1962) and the north Atlantic (Kay 1936, Sergeant 1951). In Hudson Bay Brown (1980b) reported that Thick-billed Murres from the large colony at Digges Island flew north of Mansel Island, where temperature and salinity gradients were strong. In 1981 Gaston (1982) found high abundances of murres at the location described by Brown (1980b). Gaston (1982) also reported

high rates of movement to the south of Mansel Island over a period of a month. Farther north, Gaston and Nettleship (1981) reported that Thick-billed Murres leaving a resting area at Prince Leopold Island tended to fly west into Barrow Strait, rather than south into Prince Regent Inlet. These authors found that dense concentrations of murres were confined to coastal transects, but they emphasized that variation in counts was considerable at the time scale of days and months.

Considerable variability in abundance occurs in high usage areas near other colonies. Near the Pribilof Islands Kinder et al. (1983) reported dense concentrations of murres at a front associated with a bathymetric gradient over a 5-day period in August 1977, and again during August 1978. However, the presence of the front explained less than 10% of the total variance in numbers of murres observed on the water. In Hudson Bay Cairns and Schneider (1990) found that variance explained by location was small compared to daily variability. As a result, bathymetric gradients cannot be used to predict the distribution of foraging alcids on any given day.

Our results show that suitable foraging habitat may be much less extensive than the area within a typical foraging radius estimated from time away from a nest (Pearson 1968, Furness 1978). If foraging occurs primarily in restricted areas around colonies then area-specific rates of prey extraction based on foraging radii (e.g., Furness 1978) may underestimate the local impact of seabirds. At Witless Bay, the scale of interaction of alcids with their prey depends on recent upwelling (Schneider 1989) rather than simply on the average foraging radius.

The degree to which large alcids depend on fronts for food cannot be evaluated from our data. The variance in abundance explained by grouping can be calculated as

$$r^2 = [1 + (n_R - 1)(n_0 n_R^{-1} - 1)^{-1}(F)]^{-1}$$

The r^2 values for Tables 3 and 4 are all under 15%, a result that is consistent with previous analysis (e.g., Kinder et al. 1983). Our purpose was not, however, to explain variation in abundance of alcids, but rather to move toward some understanding of habitat selection by marine birds, beginning with an informal or verbal model, viz, that alcids feed on prey aggregated at flow gradients, then testing some simple predictions.

Statistical tests were made at a spatial scale appropriate to the model. This resolves several problems associated with exploratory analyses of spatial variability in marine birds. One problem is that repeating an analysis over a range of spatial scales can, if carried far enough, result in correlation of abundance with another variable.

To take an extreme case the abundance of Atlantic Puffins becomes perfectly correlated with Sargasso weed at the scale of the Atlantic Ocean. Prior specification of scale eliminates Type I errors due to analysis at an inappropriate scale. Another problem is that repeated analyses over a range of scales result in a large number of tests, increasing the number of Type I errors. Reducing the number of tests, by specifying the spatial scale of the analysis, reduces this problem.

In our analysis of alcid abundance we have coupled statistical and graphical presentation of results as closely as possible so as to allow the reader to judge the relation of variables (James and McCulloch 1985) and to judge the "biological significance" (Tacha et al. 1982) of our results. Statistical analyses can close off inspection of the data, because of their powerful summarizing capacity. The analyses in Tables 3 and 4 are based on data displayed in Figures 3 through 8. Figures 3 through 8 were constructed with the idea of opening the original data to inspection by minimizing summary, and by concomitant presentation of variables (e.g., temperature and abundance in Figs. 7 and 8).

Data for this study were collected in the framework of an "observational experiment," (Stommel 1963). This usage is tenable on three counts for the Avalon Channel study: manipulation of a measurement variable relative to an extrinsic hypothesis, local control, and repeatability of results. The extrinsic hypothesis was that alcids aggregate in areas of strong topographic gradient near colonies. The hypothesis arose from work in the Bering Sea, not at the study site. The manipulated variable was transect location and direction. The response variable was number of birds seen per unit effort (transect distance or area scanned). The design consisted of transects run across areas of strong topographic relief. Control transects were run in nearby areas of weak topographic relief. Repeatability was assessed by re-surveying one of the 1987 transects as soon as practical, ten days after the first traverse. Repeatability was also assessed by performing the experiment with a slightly different protocol in 1987. One can argue that lack of intervention to change a variable weakens an experiment by reducing the chances of controlling for correlated effects. However, one can also argue that in any field situation, intervention will create correlated effects. In the absence of any logical grounds for preference, the strength of the experiment would then rest more on the use of comprehensive controls than on whether the experiment was manipulative or observational.

Uncontrolled variables limit interpretation of the results from the Avalon Channel. The experiments were carried out during limited peri-

ods in 1985 and 1987, so longer term variability, at the scale of weeks, seasons, or years, was not controlled. The experiment was carried out in a limited area in the Avalon Channel, so larger scale variability, at horizontal scales greater than one transect length from the colony, was not controlled.

Given these limitations, what can we conclude? First we can be sure that flow gradients were associated with topographic gradients in the Avalon Channel. This conclusion rests on our knowledge of fluids in motion, rather than on results from the Avalon Channel. Second, we can be sure that alcids were associated with topograhic gradients, and therefore with flow gradients, on the two occasions when transects were run. We cannot conclude that this will occur at other times or locations, nor can we conclude that flow gradients caused seabird aggregations, through the mechanism of change in prey abundance or availability due to flow gradients. However, the concept that flow gradients determine seabird distribution was derived from work in the Bering Sea (Ford et al. 1982). It has now been verified for murres in Hudson Bay (Cairns and Schneider 1990), and so it provides a reasonable working hypothesis at other colonies. The mechanisms that link alcids to flow gradients remain to be determined.

ACKNOWLEDGMENTS

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APPENDIX I.

The Rossby radius of deformation is a length scale that is of fundamental importance in atmosphere-ocean dynamics (Gill 1982). It is the horizontal scale at which rotation effects become as important as inertial effects. The first internal (baroclinic) Rossby radius is the characteristic scale of boundary phenomena such as fronts and eddies. The Rossby radius (R_n) is calculated as:

$$R_n = c_n f^{-1}, \qquad (1)$$

where n is mode number, c_n is the phase speed (m s^{-1}) of the nth mode perturbation, and f is the Coriolis parameter (s^{-1}). The Coriolis parameter depends on latitude and has a value of 1.07×10^{-4} s^{-1} at 47°N.

An equation from Csanady (1982, Eq. 3.96) was used to calculate the phase speed of the first baroclinic mode in a two layer stratified fluid along a straight coast:

$$c_2 = (agh_t h_b/(h_t + h_b))^{1/2}. \qquad (2)$$

Parameter values for the Avalon Channel are density anomaly (a = 0.001), gravitational acceleration (g = 9.8 m s^{-2}), Coriolis frequency at 47°N (f = 1.07×10^{-4} s^{-1}), upper layer (h_t = 30 m), and lower layer (h_b = 160 m). Using these values, c_2 is 0.50 m s^{-1}, and R_2 is 4.7 km.