Studies in Avian Biology No. 14:52–60, 1990.

HOT SPOTS IN COLD WATER: FEEDING HABITAT SELECTION BY THICK-BILLED MURRES

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Abstract. We used repeated transects to examine the relationship between habitat variability and the feeding distribution of Thick-billed Murres (*Uria lomvia*) near the Nuvuk Islands, northeastern Hudson Bay. Murres preferred waters between 40 and 120 m in depth, and were rarely sighted in shallow water. Abundance was correlated with degree of bottom relief, and the strength of correlation increased with the frame size at which abundance was measured. Murre abundance varied with phase in the tidal cycle, but did not consistently reach expected peaks at the midpoints of ebb and flood tides. Murre distributions were highly aggregated in space and time, and were positively correlated with densities of shoaling prey. Our data suggest that Thick-billed Murre feeding distributions are influenced by coarse-scale (1–100 km) flow gradients, and that birds track preferred feeding conditions at the scale of several kilometers.

Key Words: Thick-billed Murres; habitat selection; scale of aggregation.

Habitat selection has been investigated in a wide variety of avian species (Cody 1985), yet little is known about the spatial scale of habitat selection in birds (Wiens 1985, 1986). In marine birds, selection of feeding habitat is thought to be influenced by oceanographic processes which act at several spatial scales (Hunt and Schneider 1987). During the breeding season habitat selection is additionally constrained by the maximum foraging radius. Aggregation of feeding seabirds has been demonstrated at scales smaller than the foraging range (Schneider and Duffy 1985), and has been related to coarse-scale (1–100 km) variation in prey abundance (Schneider and Piatt 1986) or variation in physical processes that can alter prey abundance around colonies (Kinder et al. 1983). The spatial predictability of physical processes in coastal waters (Csanady 1982) suggests that seabirds may select feeding habitat relative to coarse-scale physical features that concentrate prey at food-rich "hot spots." The consistency over time of coarse scale habitat selection during the breeding season has not been investigated.

We examined habitat selection by Thick-billed Murres (*Uria lomvia*) within the foraging range of a major colony at the boundary of Hudson Bay and Hudson Strait. Adult murre diet in this area includes both crustaceans and small fish (Gaston and Noble 1985). Because of strong currents in the area, distribution of crustacean prey is likely to be influenced by drift as well as by active swimming. Fish taken by murres may feed on the same crustaceans consumed by murres (e.g., Arctic cod *Boreogadus saida*, Bradstreet and Cross 1982), so fish prey is likely to concentrate in areas of high crustacean density. Based on these considerations and on knowledge of the physical environment (Beals 1968; Griffiths et al. 1981; Prinsenberg 1986a, b), we constructed a set of hypotheses about habitat selection in Thick-billed Murres in relation to physical processes likely to concentrate prey organisms.

Our hypotheses were:

1. Abundance of murres on the water should be consistently higher in relatively shallow areas that have bottom relief, because flow gradients generated by tidal oscillations of water over uneven topography can enhance prey supply to foraging birds (Brown 1980).
2. Murre abundances in the central part of the study area will be greater during ebb tide than flood tide, because the prevailing counter-clockwise circulation in Hudson Bay (Barber 1968) will result in greater advection of nekton from the south during ebb tides than from the north during flood tides.
3. Murre abundance will be greatest during mid-tide, when effects of tide velocities on prey abundance and availability are maximal. Potentially important mechanisms include (i) production of fronts by friction against the sea floor, and (ii) generation of convergent and divergent flow above and in the wake of obstacles to tidal flow. Little relation between murre abundance and tidal stage was expected in the eastern part of the study area, because the deep water there reduces the importance of both mechanisms as concentrators of nekton.
4. The mobility of nektonic prey will produce fine-scale (< 1 km) decoupling of the distribution of murres and their prey.

Since present understanding does not permit clear predictions as to the scales at which physical processes influencing prey supplies might operate, we examined murre distributions on a range of scales from 50 m to about 5 km.

STUDY AREA AND METHODS

OCEANOGRAPHY

This study was conducted in waters near the Nuvuk Islands, N.W.T. (Fig. 1). Bathymetry of the northern

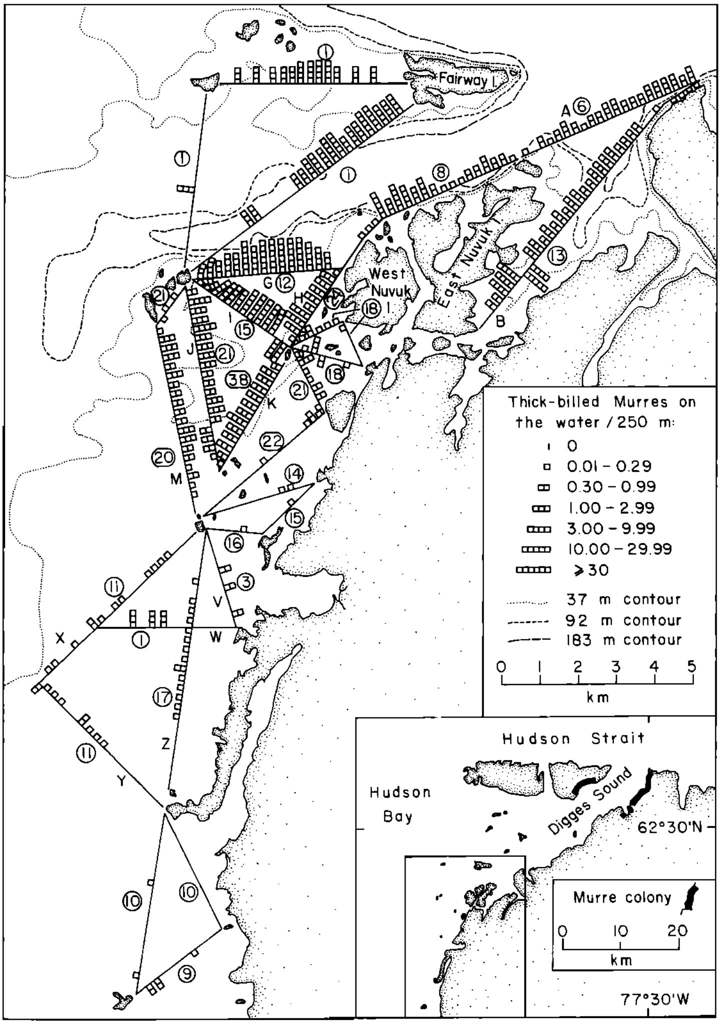

FIGURE 1. Study area, with inset-map showing its position relative to the Thick-billed Murre colonies at Digges Sound. Straight lines are transect routes. Histograms indicate mean sighting frequency per 250 m on a logarithmic scale. Circled numbers indicate how many times each transect was run.

part of the study area is dominated by a deep trench that extends west from Digges Sound and terminates off West Nuvuk Island. This trench, which attains maximum depths of 400 m, has several south-branching arms with depths greater than 50 m. In contrast, the southern part of the study area is a shallow platform with little relief and is generally less than 30 m deep.

Circulation in Hudson Bay-Hudson Strait is generally counter-clockwise (Canadian Hydrographic Service 1983). A west-trending current on the north side of Hudson Strait brings water into Hudson Bay, where it moves counter-clockwise around the bay before exiting via the south side of Hudson Strait. Overall water movement in the study area is northeastward, but flow is strongly influenced by the tidal cycle. The m_2 (principal lunar) tidal current varies from northeast at 60 $cm \cdot sec^{-1}$ to southwest at 60 $cm \cdot sec^{-1}$ (Prinsenberg 1986b:232).

The biota of the study area was described by Gaston et al. (1985) and Morrison and Gaston (1986). The large Thick-billed Murre colonies at Digges Sound, containing some 300,000 pairs, dominate the region's avifauna (Gaston et al. 1985). These birds forage over a large area in western Hudson Strait and northeastern Hudson Bay, apparently feeding up to 160 km from their colonies (Gaston and Smith 1984). Several hundred pairs of Black Guillemots (*Cepphus grylle*) and gulls (*Larus* spp.) also breed in the area.

SURVEY METHODS

The distribution of Thick-billed Murres on the water was recorded from an inflatable boat, which was run

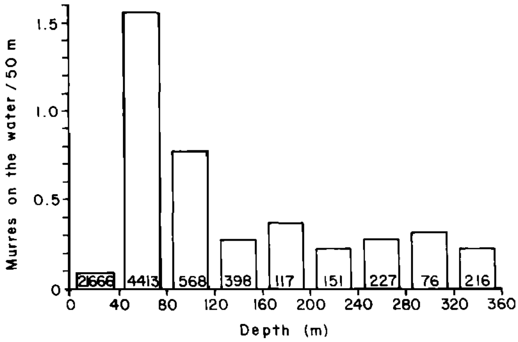

FIGURE 2. Number of murres on the water per 50-m transect segment in relation to water depth. Number of transect segments run in each depth category is given at the base of each column.

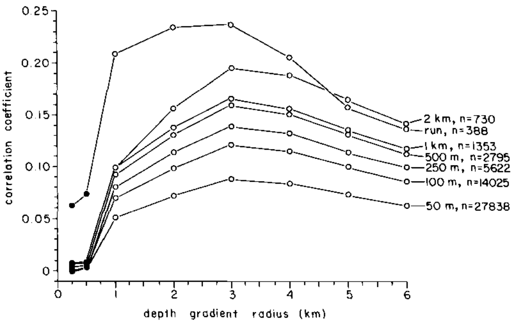

FIGURE 3. Pearson correlation coefficients between murres sighted per segment and depth gradient of that segment. Solid circles are non-significant (P > 0.05); open circles are significant (P < 0.05). Frame sizes and number of segments run are given at the right of the figure.

at constant throttle along fixed routes (Fig. 1). Murres seen within 125 m on both sides of the boat were noted on a tape recorder, together with the exact sighting time. Surveys were conducted from 22 June to 6 August 1982 and from 21 June to 27 August 1983. Distance of transect routes from the Digges Sound murre colonies ranged from 16 to 48 km. Details of survey operations are given by Cairns (1987). To obtain detailed depth profiles and information on the distribution of potential seabird prey, all routes were surveyed at least once with a continuous-trace echosounder. Density of potential prey recorded on the sounder trace was evaluated on a four-point scale, with 0 indicating no trace and 3 a high-density trace.

Times of bird sightings were converted into distance along the transect by assuming constant boat speed between the known start and end points of the transect. The basic units of analysis were 50 m segments of the transect, for which number of murres on the water and water depth were recorded. We also integrated sighting data into larger "frames" of 100, 250, 500, 1000, and 2000 m by summing sightings within adjacent 50 m segments. Depth for larger frames was the mean of the depths of the 50 m segments that composed them. The largest frame was the "run," which was the full length of each transect. We truncated data at the end of transects for frames between 250 and 2000 m if the last segment was less than one half the frame size; otherwise sightings in the last segment were multiplied by frame length and divided by segment length to correct for their shorter length.

We used depth gradients as an index of bottom relief. These were calculated for each transect segment by subtracting minimum from maximum water depths within circles of 250, 500, 1000, 2000, 3000, 4000, 5000, and 6000 m radius, centered on the midpoint of the segment.

STATISTICAL ANALYSIS

Statistical relations between murre abundance and physical parameters were calculated with the SAS package of programs. The criterion for statistical significance was 5% for all tests. Frequency of Type I error for parametric significance tests was checked by Monte Carlo randomization trials, in which murre counts were assigned to random locations along a transect (see Schneider and Piatt 1986). Twenty-nine of 800 (3.6%) correlations in our Monte Carlo runs showed significance levels greater than 5% according to standard tables, indicating an acceptable estimate of Type I error by parametric methods. Similarly, we tested ANOVA significance levels by randomly reassigning murre sighting frequencies. Six of 100 runs were significant at 5%. This indicates that parametric ANOVA procedures gave acceptable estimates of Type I error.

RESULTS

MURRE DISTRIBUTION IN RELATION TO DEPTH AND DEPTH GRADIENT

We recorded 9680 murres on the water in 1391.9 km of transect, for an overall sighting frequency of 1.74 birds per 250 m. Murre distribution was distinctly heterogeneous, and sighting frequencies differed among areas by several orders of magnitude (Fig. 1). The most favored area was west of West Nuvuk Island, where mean sighting frequencies were generally higher than 10 murres per 250 m. Murres occurred in moderate abundance north and east of the Nuvuk Islands, but were rare in the southern part of the study area.

Murre distribution was closely related to depth (Fig. 2). Water less than 40 m deep was infrequently visited by murres, which accounts for the scarcity of murres in the shallow waters of the southern part of the study area and the nearshore shallows southwest of West Nuvuk Island. Waters between 40 and 120 m deep were most frequently visited. This depth range is typical of the heavily used area west of West Nuvuk Island. Abundance was moderate in waters deeper than 120 m to the north and to the east of the Nuvuk Islands. Sighting frequencies varied little with depth in waters deeper than 120 m.

To examine the relation between murre density and bottom relief, we calculated correlation coefficients between sighting frequencies for each transect segment and the depth gradient for that segment. Correlations were low and non-significant for gradient radii of 250 and 500 m, but rose sharply with larger gradient radii, and peaked at gradients with radii of 3 km (Fig. 3). Correlations diminished with gradient radii larger than 4 km. Correlations increased with increasing size of measurement frame, and were highest when frame size was the run.

Since depth gradients were generally greater in deep water (Fig. 1), we used ANOVAs to test whether murre abundance was related to depth gradient regardless of depth. At small and medium frame sizes (≤500 m) depth gradient produced significant improvement in the ANOVA model over that given by depth alone (Table 1). At large frame sizes (particularly 2000 m) depth gradient gave little or no model improvement over depth alone. This suggests that depth gradient, acting independently of depth, may be an important determinant of murre sighting frequencies at small and medium scales.

MURRE DISTRIBUTION IN RELATION TO TIDE

We plotted frequencies of murre sightings on the water against stage of the tidal cycle for the areas west and east of the Nuvuk Islands. Distributions were similar for all frame sizes; Figure 4 plots data for frame size of 250 m. Birds were more abundant west of the Nuvuk Islands during ebb tide than during flood tide. Tidal response was tested with one-way ANOVAs, which compared mean number of birds sighted on the water per 250 m among tide periods grouped as two-hour blocks. Sighting frequencies differed among tidal stages west of the Nuvuk Islands ($F = 14.8$; $df = 6,2049$; $P = 0.0001$), although tidal stage explained only a very small part of the sighting variability ($R^2 = 0.042$). Sighting frequencies did not differ significantly with tidal stage east of the Nuvuk Islands ($F = 1.28$; $df = 6,606$; $P = 0.26$; $R^2 = 0.013$).

MURRE DISTRIBUTION IN RELATION TO PREY SHOALS

Correlations between murre sighting frequencies and density indices of prey shoals were calculated for 65.15 km of transect. Correlations were positive and generally highly significant (Table 2). Prey density was negatively correlated with depth gradient at small depth gradient radii and small frame sizes, and positively correlated at larger gradient radii and small frame sizes (Table 2).

TABLE 1. F-VALUES OF TYPE I ANOVAS RELATING FREQUENCY OF MURRES SIGHTED ON THE WATER (DEPENDENT VARIABLE) TO DEPTH AND DEPTH GRADIENT (SOURCE VARIABLES). THIS PROCEDURE FIRST DETERMINES VARIANCE DUE TO DEPTH AND THEN CALCULATES THE INCREMENTAL IMPROVEMENT IN VARIANCE DUE TO INCLUSION OF GRADIENT. DEPTH IS IN 20 M CATEGORIES

Depth gradient radius (m)	Frame size (m)											
	50		100		250		500		1000		2000	
	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient	Depth	Depth gradient
250	34.2***	21.8***	37.8***	20.8***	18.1***	12.3**	15.0***	9.2**	7.4***	0.5	6.9***	1.7
500	34.2***	25.2***	37.8***	24.4***	18.1***	13.8**	15.1***	11.1**	7.4***	1.2	6.9***	2.5
1000	34.2***	1.8	37.7***	1.0	18.1***	1.0	15.0***	0.0	7.4***	4.2*	6.9***	0.2
2000	34.2***	19.3***	37.8***	15.1***	18.1***	9.4**	15.0***	3.8*	7.4***	6.9*	6.9***	2.0
3000	34.3***	39.0***	37.8***	34.2***	18.2***	21.4***	15.1***	14.4**	7.5***	10.7**	7.0***	5.6*
4000	34.2***	20.5***	37.8***	17.9***	18.1***	11.1**	15.0***	6.9*	7.4***	4.3*	6.9***	2.1
5000	34.2***	9.1**	37.8***	8.4**	18.1***	5.6*	15.0***	3.7	7.4***	2.3	6.9***	0.8
6000	34.2***	3.4	37.7***	3.4	18.1***	2.6	15.0***	1.6	7.4***	0.9	6.9***	0.3

* $P \le 0.05$; ** $P \le 0.005$; *** $P \le 0.0001$.

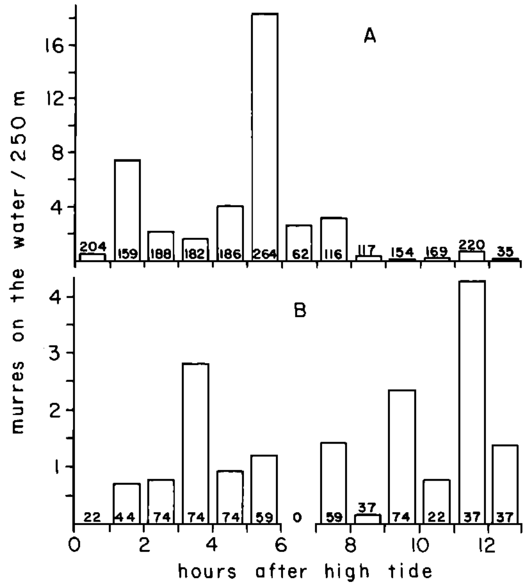

FIGURE 4. Number of murres on the water per 250 m segment in relation to time since high tide. Number of transect segments run in each tide category is given at the base of the columns. (A) shows results for an area of high murre density west of West Nuvuk Island (Routes G, H, I, J, K, and M), and (B) shows data for a medium density area to the east of East Nuvuk Island (Routes A and B). Note differing ordinal scales.

PATTERNS OF AGGREGATION

Murre distributions on the water were aggregated in space and time. For example, mean sighting frequencies along routes G, H, and I were up to two orders of magnitude higher than along routes V through Z (Fig. 1). We used a two-way ANOVA to test whether usage was significantly higher on some routes than on others and whether variation in abundance among routes could be explained by date. Counts from routes G, H, and I, which had the largest sample sizes, were used. Frame size was 500 m and only segments within the preferred depths of 40–120 m were included. Variation among routes was significant (F = 3.39, P = 0.006), but was exceeded in strength by variation among dates (F = 9.95, P = 0.0001). Variation among routes was independent of date (F = 1.21; df = 11,115; P = 0.30).

Variance/mean ratios, which increase with degree of clumping, are used to indicate aggregation intensity of murre sightings in two areas (Fig. 5). The pooled data in this figure reflect the combined effects of temporal and spatial variation, since variance/mean ratios were calculated from different segments and different days. The variance/mean ratio measured over two years in the high density area of Routes G, H, and I increased with frame size, and reached 751 when frame size equaled the run. Aggregation was much weaker in the low density area of Routes V–Z.

In the high density area of Routes G, H, and I, variance/mean ratios were much lower when measured within individual days than over seasons. Figure 5 gives typical examples of variance/mean ratios for two individual days in this area. Maximum ratios were 4.3 and 43.7. Variance/mean ratios on Routes V–Z were lower than those on Routes G, H, and I, probably because of the low numbers of birds sighted. Temporal variation, as expressed by variance/mean ratios of summed daily counts in the G–H–I and V–Z areas, were 7.9 and 0.94 for the two areas, respectively.

TABLE 2. PEARSON CORRELATIONS OF PREY DENSITY, AS INDICATED BY ECHO STRENGTH, WITH FREQUENCY OF MURRES ON THE WATER AND WITH DEPTH GRADIENT

	Frame size (m)					
	50	100	250	500	1000	2000
Frequency of murres on the water	0.35***	0.47***	0.48***	0.49***	0.21	0.54***
Depth gradient						
Depth gradient radius (m)						
250	−0.14***	−0.15**	−0.16*	−0.14	−0.16	−0.15
500	−0.11***	−0.11**	−0.13*	−0.12	−0.15	−0.14
1000	0.04	0.04	0.00	0.02	−0.13	−0.12
2000	0.12***	0.12**	0.09	0.10	−0.09	−0.07
3000	0.12***	0.12**	0.08	0.08	−0.11	−0.11
4000	0.15***	0.15***	0.12*	0.11	−0.03	−0.12
5000	0.07*	0.06	0.04	0.03	−0.08	−0.16
6000	0.07*	0.06	0.04	0.03	−0.03	−0.11

* $P \leq 0.05$; ** $P \leq 0.005$; *** $P \leq 0.0001$.

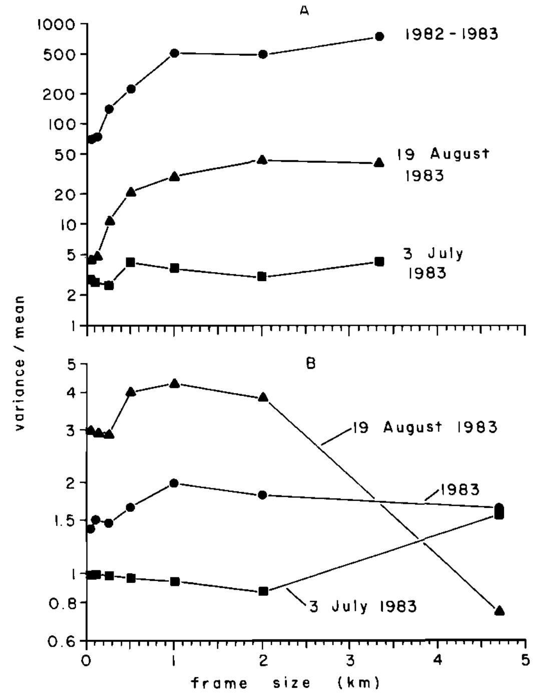

FIGURE 5. Aggregation of murres on the water, as indicated by the variance/mean ratio of birds per segment. Results are given for the pooled data set and for two individual days for an area of high murre density (Routes G, H, and I; panel A) and a low density area (Routes V, W, X, Y, and Z; panel B). The largest frame size in each panel is the run. The ordinal scale is logarithmic.

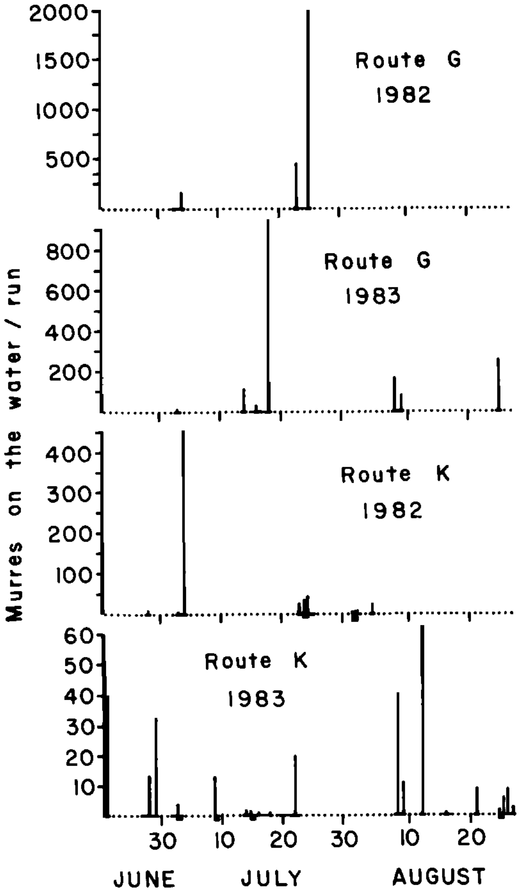

FIGURE 6. Temporal variation in number of murres sighted per run for Routes G and K. Horizontal bars on the abscissa indicate days on which transects were run. Double and triple bars indicate two and three runs on that day, respectively. Note differing ordinal scales.

Figure 6 shows temporal variation in bird numbers in the absence of spatial effects. Sighting frequencies often changed dramatically between survey dates, and variation sometimes exceeded two orders of magnitude. For example, on Route G, nine murres were counted on 17 July 1983, but on the following day 982 murres were recorded.

DISCUSSION

Qualitative predictions of the habitat requirements of marine birds can be derived from considerations of locomotory efficiency, body size, and fasting endurance. Non-diving species require vertically predictable concentrations of prey at the scale of a meter or less near the sea surface. Pursuit-diving species require vertically predictable prey within their diving range, which depends on body size (Piatt and Nettleship 1985). Diving ranges are typically 10 to 100 m. Species with flapping flight move in air at high energetic cost (Flint and Nagy 1984, Birt-Friesen et al. 1989), and hence may depend on small-scale, lateral-prey predictability to avoid extensive searching flight. Constraints on these species are modified by body size, which allows large divers to swim or fly for longer periods without food than small ones (Goudie and Ankney 1986).

Based on this qualitative model, murres require vertically predictable prey concentrations at the scale of tens of meters, and laterally predictable prey at a scale determined by fasting endurance and by the speed and cost of flight. During the breeding season the lateral range is on the order of 100–200 km (Gaston and Nettleship 1981). Lateral predictability in the ocean at this scale is typically low except in shallow (<200 m) water, where bottom topography produces spatially predictable habitat variation at the sea floor, as well as generating spatially predictable flow gradients near the sea surface (Csanady 1982). Within the constraints of locomotory efficiency and starvation resistance determined by body size, murre-sized pursuit-divers must forage either at the sea floor or in relatively shallow water columns in order to find laterally predictable prey concentrations at spatial scales on the order of hundreds of kilometers or less.

Our prediction that murres would aggregate in relatively shallow water with high topographic relief, which generates laterally predictable flow gradients that can increase the concentration or supply of nektonic prey, was confirmed: density was significantly greater in areas of strong topographic gradient than in areas of weak topographic gradient.

Previous characterizations of seabird habitat have emphasized depth (Wynne-Edwards 1935, Ashmole 1971) rather than depth gradient (but see Porter and Sealy 1981). Near the Nuvuk Islands, murre densities were strongly associated with depth, with maximum densities occurring in waters of 40 to 80 m. Within depth categories, murre abundance depended on depth gradient at small and medium scales. Preferential foraging in areas of high bottom relief has been previously found in Barrow Strait, where, in the absence of ice, murres tend to forage along the coastline instead of in the strait itself (Gaston and Nettleship 1981).

Murre abundance varied significantly with tidal stage, and murres were observed more often during ebb than flood tides west of the Nuvuk Islands, as expected. However, the predicted maxima in murre abundance at mid-tide (3 and 9 hours after high tide) was not observed. Instead, maximum counts occurred there just after high water and just before low water. Our prediction that murre abundance would peak at mid-tide was based on the assumption that maximum tidal velocity occurs at this time. Tidal phenomena in northern Hudson Bay are strong and complex (Canadian Hydrographic Service 1983, Prinsenberg 1986a), and present data are inadequate to confirm this assumption or to specify other explanations for the observed relation between bird abundance and tide cycle.

Murre distribution was correlated with acoustic estimates of the relative abundance of nekton. Correlation did not increase with increasing frame size, in contrast with the findings of Schneider and Piatt (1986) for Common Murres (*U. aalge*) and Atlantic Puffins (*Fratercula arctica*). Murre sighting frequencies were more strongly correlated with echo strength of prey schools than they were with depth gradient (Table 2, Fig. 3). Prey densities as shown by echo strength were inconsistently related to depth gradient, indicating that areas of strong bathymetric relief do not always harbor prey. The wide fluctuation of murre abundance, even in areas with high mean density (Fig. 6), may reflect strong temporal variation of prey concentration in these areas.

Spatial variation in the abundance of Thick-billed Murres was scale-dependent. Variability increased from fine (<1 km) to coarse (>1 km) measurement intervals, as has been reported in other seabird species (Schneider and Duffy 1985) including alcids (Briggs 1986, Schneider and Piatt 1986). We attribute this to coarse scale flow gradients, which appear to be a major source of coarse scale patchiness in the abundance of nekton (Olson and Backus 1985, Simard et al. 1986). Griffiths et al. (1981) predicted that local intensification of tides results in tidal fronts in the general vicinity of the Nuvuk Islands, but the scale of their analysis does not permit prediction of suitable habitat at the scale of murre censusing.

Previous transect studies around colonies have demonstrated coarse scale variability within the foraging range, but transects have not been traversed frequently enough to determine the consistency of aggregation. Repeated transects around the Nuvuk Islands showed that the abundance of murres on the water was localized, and that spatial variability was independent of temporal variability.

Coarse-scale habitat selection has important implications for the analysis and interpretation of interactions between seabirds and their prey. If spatial variation in consumption exceeds spatial variation in prey supply within the foraging range of a seabird colony, then the impact of seabird predators on local prey will be greater than that predicted from larger-scale calculations, which are typically based on a maximum or average foraging radius (Furness 1978, 1982). Calculations of prey removal at the scale of the average or maximum foraging radius may underestimate local impact on prey, even though such calculations may overestimate impact on fish stocks at a larger scale (Bourne 1983).

Models of local impact of seabirds on prey stocks around colonies must also consider the effects of larger scale lateral advection, which can act to renew local prey supplies. Assuming a foraging range of 160 km, typical advection rates can offset prey mortality estimated from respiratory requirements (Appendix 1). The importance of advective import is likely greatest in colonies that depend heavily on planktonic crustaceans for food, as fish are typically able to control their position in the water. In the Nuvuk area, Thick-billed Murres prey on both fish and crustaceans (Gaston and Noble 1985). The simple advective model shown in Appendix 1 also assumes that advectively-delivered food supplies are not previously depleted by predation from other seabird colonies. This assumption is valid for murres breeding at Digges Sound, because coastlines along eastern Hudson Bay (the advective source) lack suitable breeding habitat for murres. In some seabird communities advection may prove to be more important than production in determining impact of birds on food supplies at the scale of habitat selection, which our study suggests is on the order of 1–10 km.

Our results support earlier conclusions that breeding Thick-billed Murres favor specific "hot spots" (Bradstreet 1979). However, the strong short-term variability in bird abundance (Fig. 6) suggests that murres do not forage solely by prior knowledge of favored sites. Information exchange among foragers (Ward and Zahavi 1973, Gaston and Nettleship 1981) may also aid murres in choosing sites that are rich in food at a particular time.

ACKNOWLEDGMENTS

We thank J. A. F. Macfarlane, W. E. C. Wake, and V. L. Birt for sharing the rigors of Arctic field work. Citizens of Ivujivik, Quebec and staff of its Nursing Station gave invaluable logistic support. We are particularly indebted to Adami Mangiok, Johanne Coulombe, and Marc-André Dubé for many services rendered. The Ikaluit office of the Department of Indian and Northern Affairs and the Canadian Coast Guard furnished communication and transport services. A. J. Gaston provided the opportunity for field work, and supported it throughout. A. J. Gaston, M. B. Fenton and J. M. Green gave advice and information. We thank B. deYoung, D. C. Duffy, A. J. Gaston, D. Heinemann, W. A. Montevecchi, and two anonymous reviewers for critical comments. This study received funding from the Canadian Wildlife Service and the Canadian Department of Supply and Services. This is contribution no. 166 from the Newfoundland Institute for Cold Ocean Science.

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APPENDIX I.

IMPACT OF CENTRAL PLACE FORAGERS ON PASSIVELY TRANSPORTED PREY

Consider a seabird colony located on a straight coastline. Birds forage in a semi-circle of radius r (km) around the colony. Advective (current-induced) import (i) is defined as the mass of prey (m) arriving per day within foraging radius r (km) of a colony $\left(\frac{\Delta m}{\Delta t} = g\cdot day^{-1}\right)$ divided by the mass (M = g) within the foraging radius.

$$i = \frac{1}{M}\cdot\frac{\Delta m}{\Delta t}, \qquad (1)$$

$$\frac{\Delta m}{\Delta t} = Bvr, \qquad (2)$$

where B = prey density ($g\cdot km^{-2}$), v = net advection ($km\cdot day^{-1}$), M = BA, where A is area within the foraging radius (km^2).

Then:

$$i = \frac{Bvr}{BA} \qquad (3)$$

and hence

$$i = \frac{2v}{\pi r}. \qquad (4)$$

Avian consumption, in dimensionally equivalent units, is:

$$a = \frac{F}{T_b} \qquad (5)$$

where F = proportion of prey lost $\left(\frac{\Delta m}{M}\right)$ during the breeding season. T_b is length of the breeding season (days).

Advective import equals consumption when:

$$a = i, \qquad (6a)$$

$$\frac{F}{T_b} = \frac{2v}{\pi r} \qquad (6b)$$

$$v = \frac{\pi r F}{2T_b} \qquad (6c)$$

If T_b = 55 days and r = 160 km, and using Furness' (1982) value of F = 30%, then v = 1.37 $km\cdot day^{-1}$ = 0.016 $m\cdot s^{-1}$. The reported advective rate in the vicinity of the Nuvuk Islands is 0.07 $m\cdot s^{-1}$ (Prinsenberg 1986b), which suggests that advective import could supply food needs even if F is much lower than 30%.