

Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem

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ABSTRACT: The distribution of piscivorous seabirds relative to schooling fish was investigated by repeated censusing of 2 intersecting transects in the Avalon Channel, which carries the Labrador Current southward along the east coast of Newfoundland. Murres (primarily common murres *Uria aalge*), Atlantic puffins *Fratercula arctica*, and schooling fish (primarily capelin *Mallotus villosus*) were highly aggregated at spatial scales ranging from 0.25 to 15 km. Patchiness of murres, puffins and schooling fish was scale-dependent, as indicated by significantly higher variance-to-mean ratios at large measurement distances than at the minimum distance, 0.25 km. Patch scale of puffins ranged from 2.5 to 15 km, of murres from 3 to 8.75 km, and of schooling fish from 1.25 to 15 km. Patch scale of birds and schooling fish was similar in 6 out of 9 comparisons. Correlation between seabirds and schooling birds was significant at the minimum measurement distance in 6 out of 12 comparisons. Correlation was scale-dependent, as indicated by significantly higher coefficients at large measurement distances than at the minimum distance. Tracking scale, as indicated by the maximum significant correlation between birds and schooling fish, ranged from 2 to 6 km. Our analysis showed that extended aggregations of seabirds are associated with extended aggregations of schooling fish and that correlation of these marine carnivores with their prey is scale-dependent.

INTRODUCTION

Marine birds form aggregations that range from a few metres to tens of kilometres in lateral extent. Aggregations ranging from 5 to 50 km in chord length have been reported in the Bering Sea (Schneider 1982, Kinder et al. 1983, Woodby 1984), the California Current (Briggs et al. 1984), and the Benguela Current (Schneider & Duffy 1985). The existence of these aggregations suggests that seabirds may be correlated with prey at a similar scale, but this has not been tested directly.

We investigated the distribution of murres (primarily the common murre *Uria aalge*) and Atlantic puffins *Fratercula arctica* relative to schooling fish at Witless Bay, the site of a major seabird colony in the northwest Atlantic. This colony consists of 3 closely spaced islands on the western side of the Avalon Channel, a relatively deep (>150 m) nearshore trough that funnels the inshore arm of the Labrador Current southward along the east coast of Newfoundland. Capelin spawn along this coast from late June into mid-July (Templeman 1948), and during this period they are the most

abundant schooling fish nearshore. Capelin are the most important prey in the diets of murres and puffins at Witless Bay (Mahoney 1979, Brown & Nettleship 1984, J. Piatt unpubl. data).

We investigated variability in the abundance of birds and schooling fish by making repeated surveys of 2 transects at Witless Bay during the summer of 1984. Our objectives were to determine (1) whether variability in the abundance of birds and schooling fish was scale dependent; (2) whether birds and fish were locally correlated; and (3) whether correlation was scale-dependent.

METHODS

Surveys were made along an offshore transect running eastward from Green Island into the Avalon Channel and along a coastal transect running parallel to the coastline from Bay Bulls to Cape Broyle (Fig. 1). The offshore transect was surveyed 4 times and the coastal transect was surveyed 3 times during the summer of 1984.

Bird counts were made from a 12 m fishing vessel

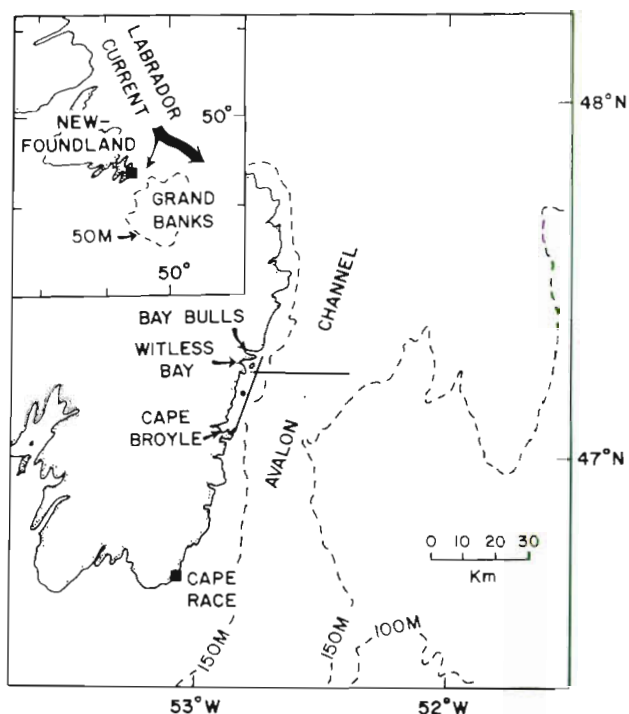


Fig. 1. Location of transects in Northwest Atlantic

equipped with a depth sounder for acoustic recording of schooling fish. The depth sounder (Kelvin-Hughes Mark 2, 42 kHz) was mounted on the bottom of the vessel, approximately 1 m below the water line. Cone angle was 33° and effective recording depth ranged from 2 m below the surface down to the ocean floor. Murres and puffins on the water were counted in a semicircular zone from the vessel forward. The area of the observation zone was 0.79 ha, with a radius of 50 m. Counts were recorded to the nearest second and grouped into 1 min intervals for comparison with echograms from the depth sounder.

The echogram from each acoustic survey was divided horizontally into 1 min intervals and vertically into 10 m depth intervals. The most important criteria were school shape and definition at the boundary. Schooling fish were identified according to the criteria of Forbes & Nakken (1972). The registration intensity of schooling fish within each 1 min (250 m) by 10 m block was scored visually on a scale of 0 to 9. This score was squared to make it proportional to fish abundance (Forbes & Nakken 1972), and then summed by depth categories to obtain an index of relative abundance during each minute of survey. The dynamic range of the echograms was low and most of the registrations were black or nearly so. The squaring of registration scores had little effect on the index of relative abundance, which was primarily a function of school size rather than density.

Spatial variability in the abundance of murres, puffins, and schooling fish was measured by computing a variance-to-mean ratio, I' , for measurement distances ranging from 0.25 to $T/2$ km, where T was the total number of kilometres per transect.

$$I'(F) = s^2(F) \bar{x}^{-1}(F) \quad (1)$$

where F = measurement distance (km cycle⁻¹);

$$\bar{x}(F) = n^{-1} \sum_{i=1}^n \sum_{j=1}^F x_{ij};$$

$$s^2(F) = (n-1)^{-1} (\sum_{i=1}^n [\sum_{j=1}^F x_{ij}]^2 - n \bar{x}(F)^2);$$

x_i = bird count or fish score at the minimum measurement distance, 0.25 km;

n = sampling frequency (cycles transect⁻¹).

Computations were restricted to values of F corresponding to integral values of n within each survey. Strength of association of birds with schooling fish was measured by computing the Pearson product moment correlation coefficient, r , as a function of measurement distance. Correlations were computed for the same measurement distances as $I'(F)$.

The seabird data could not be described by standard statistical models such as the normal and negative binomial distributions, so randomization tests were used to evaluate statistical significance. The first null hypothesis, scale-independent variability, $H_0: I'(0.25) = I'(F)$, was rejected in favor of the alternative hypothesis, $H_A: I'(0.25) < I'(F)$, if an observed value of $I'(F)$ exceeded 95 out of 100 values of $I'(F)$ obtained by randomizing the 1 min counts, x_i . A Fortran subroutine (GGPER) from the International Mathematics and Statistics Library (IMSL 1982) was used to obtain random permutations of the location index (i), and these were used to reassign each 1 min (0.25 km) count to a new location along the transect. Patch scale was defined as the measurement distance corresponding to the maximum value of $I'(F)$ that was significantly greater than $I'(0.25)$.

Correlation of puffins and murres with fish at the smallest measurement distance was tested for significance by comparing the observed value of $r(0.25)$ to 100 values obtained by randomizing 1 min (0.25 km) bird counts with respect to location. Fish abundance was not randomized in this analysis. The second null hypothesis, $H_0: r(0.25) = 0$, was rejected if an observed value of $r(0.25)$ was greater than 95 out of 100 values of $r(0.25)$ from randomized data.

The third null hypothesis, scale-independent correlation, $H_0: r(0.25) = r(F)$, was rejected in favor of the alternative hypothesis, $H_A: r(0.25) < r(F)$ if an observed value of $r(F)$ was greater than 95 out of 100 values obtained from randomized data. Tracking scale was defined as the measurement distance correspond-

Table 1. Abundance of murres, puffins, and schooling fish along offshore and coastal transects in the Avalon Channel in 1984. Bird counts are number seen on the water within 50 m of either side of the vessel. Relative abundance of fish based on visually graded echograms. Ship speed = 250 m min⁻¹. Censusing rate = 2.5 ha min⁻¹. Local time (NST) = Universal time - 2.5 h

Date	Start (NST)	Length (km)	Murres	Puffins	Schooling fish
Offshore transect					
30 May	0834	30	249	145	9
6 Jun	0835	25	12	1	99
16 Jul	0753	30	41	8	38
14 Aug	0735	30	0	52	13
Coastal transect					
14 Jun	0707	15	48	121	35
8 Jul	1016	30	746	233	286
18 Jul	0750	17.5	226	265	159

ing to the maximum value of r (F) that was significantly greater than r (0.25).

Type I error, erroneous rejection of a null hypothesis, was estimated by Monte Carlo methods (Schneider 1966). Values of I' (F) and r (F) were obtained from 100 randomizations of a single set of data, and these were tested for significance. The expected number of Type I errors was 5 in 100 trials.

RESULTS

Abundance of murres, puffins, and schooling fish

The number of murres and puffins recorded along the 2 transects varied from survey to survey (Table 1). The highest fish abundances were recorded along the coastal transect during the spawning season in July (Table 1). The highest murre and puffin abundances were also recorded along the coastal transect in July.

Distribution of murres, puffins, and fish along the offshore transect (Table 2) was a function of distance from land. Murres and puffins were more abundant nearshore than offshore during all 4 offshore surveys. Fish were more abundant nearshore than offshore during 3 of the 4 surveys (Table 3).

Type I error for randomization tests

Fig. 2 compares the observed values of I' (F) to values of I' (F) obtained from 5 randomizations of the data from the 30 May survey. We expected values of I' (F) from randomized data to be scale independent, i.e. I' (F) = I' (0.25). Inspection of Fig. 2 shows that randomized values of I' (F) fluctuated around the expected value, I' (0.25), while observed values of I' (F) tended to exceed the expected value. Randomized values of I' (F) in puffins did appear to be biased toward low values at large measurement distances, possibly because of bias

introduced by small sample sizes (Reed 1983). None of the low values of I' (F) in the randomized puffin data were significant, which indicated that Monte Carlo tests were not sensitive to bias at large measurement distances. The expected number of Type I errors in the 5 randomizations in Fig. 3 was 10.5 (5 % of 210 tests); the observed number was 6.

Type I error rate for each of the 3 null hypotheses was estimated from 100 randomizations of the 30 May data. Type I error rate for randomization tests was close to the expected rate of 5 % (Table 4). Type I error for randomization tests of the first null hypothesis, scale-independent variability, averaged 4.1 % in murres, 5.6 % in puffins, and 3.4 % in fish. Type I error for the

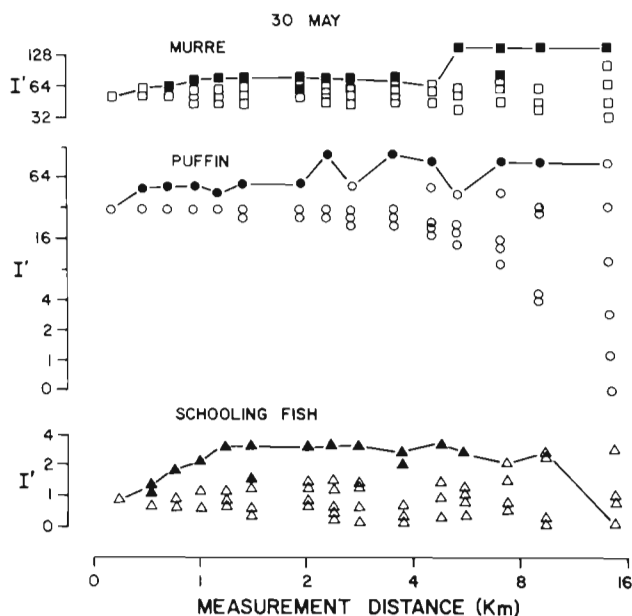


Fig. 2. Variance-to-mean ratios, I' , for observed data (connected by lines) and randomized data (not connected by lines) on murres, puffins, and schooling fish during first survey of offshore transect, on 30 May. Statistical significance indicated by solid symbols ($p < 0.05$) and open symbols ($p > 0.05$)

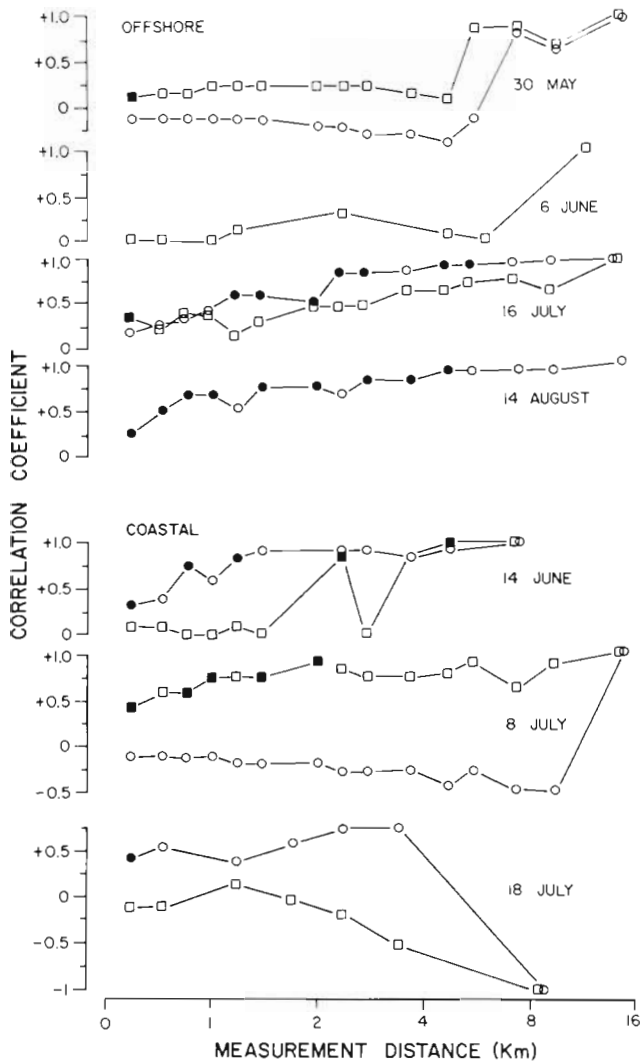


Fig. 3. Correlation of murre (squares) and puffins (circles) with schooling fish, as a function of measurement distance along coastal and offshore transects. Statistical significance as in Fig. 3

second null hypothesis, no correlation at a scale of 0.25 km, averaged 3.5 % (Table 4). Type I error for the third null hypothesis, scale independent correlation, was 4.8 % (upper tail) and 5.1 % (lower tail) in murre. For puffins, Type I error was 6.4 % in the upper tail and 4.3 % in the lower tail. Type I error was no greater at large measurement distances than at smaller distances (Table 4), so we concluded that randomization tests were not biased at small sample sizes, which correspond to large measurement distances.

Spatial variation and correlation as a function of measurement distance

Variability in murre, puffin, and schooling fish during the first survey of the offshore transect was

significantly higher at large measurement distances than at the minimum measurement distance, 0.25 km (Fig. 2). Significant increase in variance-to-mean ratios occurred in fish in 3 of 4 surveys of the offshore transect, and in 2 of 3 surveys of the coastal transect (Table 5). Scale-dependent increase in variability occurred in murre during 2 of 3 surveys of the offshore transect, and during 2 of 3 surveys of the coastal transect. Scale-dependent increase in variability of puffin occurred during all 6 of the surveys where puffins were present in any number.

Patch scale, based on the maximum significant variance-to-mean ratio, varied from survey to survey. Patch scale ranged from 2.5 to 15 km in puffin, from 3 to 8.75 km in murre, and from 1.25 to 15 km in schooling fish (Table 5). We expected the patch scale of puffin and murre to be similar to the patch scale of fish within surveys. Patch scale of puffin was similar to patch scale of schooling fish (within a factor of 2) during 2 of 3 offshore surveys, and during 2 of 3 coastal surveys (Table 5). Patch scale of murre was similar to patch scale of schooling fish during 2 out of 3 coastal surveys. Patch scale of birds and schooling fish differed by a factor of 2 or more in 3 of the 9 cases where comparison was possible (Table 5).

Significant correlation of murre with schooling fish, at the minimum measurement distance of 0.25 km, was observed during 2 of 3 offshore surveys, and during 1 of 3 coastal surveys (Table 6). Significant correlation of puffin with fish, at the same scale, was observed during 1 of 3 offshore surveys, and during 2 of 3 coastal surveys. The highest correlations at this scale were observed along the coastal transect.

Correlation of murre and puffin with fish was scale-dependent, as indicated by significant increases in correlation with increase in measurement distance along both offshore and coastal transects (Fig. 3). Scale-dependent correlation of murre with fish was observed during 2 of the 3 coastal surveys, but was not observed during offshore surveys. Scale-dependent correlation of puffin with fish was observed during 1 of the 3 coastal surveys, and during 2 of 3 offshore surveys. Larger scale (>1 km) correlation in the absence of finer scale correlation was observed in puffin during the 16 July survey of the offshore transect. Larger scale correlation accompanied by finer scale correlation of puffin with fish was observed during a subsequent survey of this transect. Finer scale correlation in the absence of larger scale correlation was observed in puffin during the first survey of the long-shore transect.

Tracking scale, based on the maximum significant correlation coefficient, ranged from 2.0 to 6 km (Table 6). Tracking scale and patch scale of birds were similar (within a factor of 2) during the third offshore survey

Table 4. Type I error for randomization tests of scale-dependent variability, based on 100 randomizations of data from the first offshore survey, 30 May 1984. Values are number of Type I errors (erroneous rejection of null hypothesis in favor of the alternative hypothesis at $p = 0.05$) in 100 trials. nt: no test. % is error per 100 trials

Measurement distance (km)	$H_A: I'(0.25) < I'(F)$			$H_A: r(0.25) > 0$		$H_A: r(0.25) < 0$		%
	Murre	Puffin	Fish	Murre	Puffin	Murre	Puffin	
0.25				11	3	0	0	3.5
				$H_A: r(0.25) < r(F)$		$H_A: r(0.25) > r(F)$		
	Murre	Puffin	Fish	Murre	Puffin	Murre	Puffin	
0.50	2	4	1	2	11	3	1	3.4
0.75	7	9	1	6	11	3	7	6.3
1.0	4	9	3	7	9	4	3	5.6
1.25	3	5	2	4	7	8	1	4.3
1.5	6	7	6	2	6	6	9	6.0
2.0	1	5	3	6	5	4	6	4.3
2.5	2	5	4	7	6	8	2	2.4
3.0	3	6	3	5	5	6	6	4.9
3.75	5	7	4	3	4	6	7	5.1
5.0	5	8	2	4	1	8	3	4.4
6.0	8	6	8	5	5	8	6	6.6
7.5	6	2	5	2	9	5	7	5.1
10.0	3	2	3	3	8	2	2	3.3
15.0	3	4	3	nt	nt	nt	nt	2.5
Total	58	79	48	67	90	71	60	
%	4.1	5.6	3.4	4.8	6.4	5.1	4.3	4.8

and the first coastal survey (Tables 5 & 6). Tracking scale and patch scale of birds differed by more than a factor of 2 during the fourth offshore survey and the second coastal survey.

Table 5. Maximum variance-to-mean ratio, $I'(F)$, of murres, puffins, and schooling fish along strip survey. * indicates $I'(F)$ significantly greater than $I'(0.25)$ at $p = 0.05$. Patch scale is corresponding measurement distance (km), if $I'(F)$ significant

Date		$I'(F)$		Patch scale (km)
Offshore transect				
30 May	Puffin	106.9	*	2.5
	Fish	3.0	*	1.25
	Murre	155.8	*	6.0
6 Jun	Fish	2.8		
	Murre	2.0		
16 Jul	Puffin	2.7	*	6.0
	Fish	27.0	*	15.0
14 Aug	Murre	6.3	*	3.0
	Puffin	24.9	*	15.0
14 Jun	Fish	13.0	*	15.0
	Coastal transect			
	Puffin	111.3	*	3.0
8 Jul	Fish	7.9	*	5.0
	Murre	40.5	*	3.75
	Puffin	282.8	*	6.0
18 Jul	Fish	252.2	*	6.0
	Murre	295.9	*	6.0
	Puffin	197.0	*	2.5
18 Jul	Fish	39.6	*	
	Murre	119.1	*	8.75

DISCUSSION

Repeated survey of 2 intersecting transects near the Witless Bay seabird colony showed that extended aggregations of murres and puffins were associated with extended aggregations of schooling fish. Patch scale of birds and fish was similar (within a factor of 2)

Table 6. Correlation of murres and puffins with schooling fish along offshore and coastal transects. $r(0.25)$ is Pearson product-moment correlation coefficient for 0.25 km (1 min) counts. * indicates $H_A: r(0.25) > 0$ accepted at $p = 0.05$. $r(F)$ is maximum significant correlation coefficient, $H_A: r(0.25) < r(F)$ accepted at $p = 0.05$. Tracking scale is corresponding measurement distance (km)

Date		$r(0.25)$	$r(F)$	Tracking scale (km)
Offshore transect				
30 May	Puffin	0.04		
	Murre	0.10	*	
6 Jun	Murre	0.008		
16 Jul	Puffin	0.14	0.93	6.0
	Murre	0.30	*	
14 Aug	Puffin	0.28	0.88	5.0
Coastal transect				
14 Jun	Puffin	0.35	0.89	2.5
	Murre	0.07	1.0	5.0
8 Jul	Puffin	-0.05		
	Murre	0.44	0.90	2.0
18 Jul	Puffin	0.42	*	
	Murre	-0.05		

in 6 out of 9 cases where comparison was possible. Murres and puffins tracked prey at scales on the order of 2 to 6 km. Our transects were too short to detect tracking at scales larger than 6 km.

Extended aggregations of murres and puffins were not simply reflections of extended aggregations of schooling fish. In 3 of 9 comparisons patch scale of birds and schooling fish differed by more than 2-fold. Also, the observed tracking scale, 2 to 6 km, was generally less than the observed patch scale of predators. This can result from any of several mechanisms, including preferential foraging within extended aggregations of prey, or inability of birds to track rapidly moving prey over distances greater than several km. The interactions of seabirds with their prey needs to be investigated at a scale of tens of kilometres. Foraging interactions at this scale may differ from those reported at smaller scales (Hoffman et al. 1981).

We found that the correlation between birds and schooling fish was stronger over distances of a km or more than over lesser distances in 5 out of 12 cases. Scale-dependent correlation with prey has been reported for zooplankton (Mackas & Boyd 1979, Star & Mullin 1981) and has been hypothesized for marine birds (Hunt & Schneider in press). Reduced correlation at a scale of hundreds of meters can result from any of several mechanisms, including local avoidance of diving birds by schooling fish, differences in the locomotory capacities of diving birds and schooling fish, and sit-and-wait predation by diving birds within extended aggregations. Capelin were the only abundant schooling fish at Witless Bay during the study, and the reported swimming behaviour of capelin in spawning condition could have reduced finer scale correlation. Offshore feeding schools of capelin descend rapidly out of the surface layer after dawn (Pitt 1958), but capelin in spawning condition occur either as rapidly swimming schools in the surface layer (Atkinson & Carscadden 1979) or as dense relatively stationary masses near beaches (Sleggs 1933) or within a few metres of subtidal spawning beds (Baake & Bjorke 1973, Saetre & Gjosaeter 1975). Alcids, especially murres, may forage on subtidal spawning aggregations, but this appears to be more important during the early morning (Piatt & Nettleship 1985), than later in the morning, when transects were surveyed. During the day, rapid lateral movements of capelin schools in the nearshore surface layer may have reduced local tracking by alcids.

Three different techniques have been used to investigate spatial correlation and cross-correlation of marine organisms: spectral analysis (Platt & Denman 1975), auto-correlation analysis (Jumars et al. 1977), and variance-distance curves (Cox & Isham 1980) scaled to a Poisson process (Angel & Angel 1967,

Schneider & Duffy 1985). The procedures used are different, but all 3 produce estimates of covariance functions, whose use has been described by Matern (1960). The equivalence between the first 2 methods (via a Fourier transform) has been noted in the marine literature (Mackas 1984). The equivalence of the first and third methods was noted by Ripley (1978), who showed that constructing a variance-distance curve according to the method of Grieg-Smith (1964) is equivalent to constructing a periodogram using square waves, rather than the trigonometric functions used for standard spectral analyses.

Field data often do not meet the assumptions underlying a given method and this raises questions of reliability (Type I error) and sensitivity (Type II error). Our analysis of Type I error showed that randomization tests on scaled variance-distance curves were robust to bias at large measurement distances (Fig. 3, Table 4). Randomization tests on scaled covariance-distance curves constructed from bird and fish data were also reliable (Table 4). Randomization tests have been found to be reliable for methods based on auto-correlation analysis (Sokal 1979) and presumably would prove to be reliable for spectral analysis of non-normal data.

The sensitivity (Type II error) of the 3 methods has not been compared. Sokal (1979) found that randomization tests on spatial correlograms were most sensitive when correlation is linear. An informal sensitivity analysis based on simulations (Schneider & Duffy 1985) showed that variance-distance curves can detect at least 2 types of spatial structure, exponential attenuation with distance from a central point (as in birds), and regular spacing within a patch having a discrete border (as in schooling fish).

Randomization tests require far more computer time than standard parametric or non-parametric analyses, so we investigated Type I error of Spearman rank correlation tests for increase in variability (I' [F]) with increase in scale (F). The Type I error, for the 100 trials in Table 4, was 51 % for murres, 43 % for puffins, and 49 % for schooling fish. Type I error for the third hypothesis, change in bird-fish association with change in scale, was 40 % for puffins and 49 % for murres, using the same 100 trials. This was far higher than the expected error rate, 5 %, so we concluded that non-parametric methods were not a reliable way to test for scale-dependence in our data.

The correlation between alcids and schooling fish at Witless Bay was scale-dependent and highly variable from survey to survey along the same transect. This has implications for the design and analysis of transect studies of mobile marine organisms. Correlation was intermittent and this means that repeated surveys may be necessary to detect interaction between mobile pre-

dators and prey. Correlation was scale-dependent and this means that short transects, or long transects with coarse resolution, may fail to detect significant correlation between seabirds and their prey. Similarly, analysis at a single measurement period (e.g. a 10 min count) may fail to detect large or smaller scale association. Recent studies on murres (Woodby 1984) and terns (Safina & Burger 1985) have reported no significant association between seabirds and nekton. Correlation was tested at a single scale in these studies, ca 3 km in murres and ca 0.5 km in terns. Association at a different scale may have gone undetected in both studies. A more complete discussion of scale-dependence and its implications for the collection and analysis of transect data can be found in Denman & Mackas (1978).

The interaction of mobile populations of predators with their prey depends on the form of the aggregative response to prey abundance (Murdoch & Oaten 1975), but little is known about the aggregative response of marine vertebrates to their prey. We found that the strength of association between seabirds and schooling fish varied with spatial scale. This means that spatial scale needs to be considered in the analysis of the strength and form of aggregative response to prey by highly mobile predators such as birds.

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