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Scale-dependent correlations between the abundance of Brünnich's guillemots and their prey

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Summary

1. The foraging ecology of Brünnich's guillemots *Uria lomvia* was studied during the breeding season in south-eastern Svalbard. In the region of Storfjorden there are two large breeding colonies comprising a total of about 540 000 individuals. These birds forage in the western part of Storfjorden and further to the south. Their main prey are polar cod *Boreogadus saida*, pelagic amphipods *Parathemisto* spp. and euphausiids *Thysanoessa inermis*.

2. A ship-based transect survey was used to record bird abundance and the acoustically determined biomass of presumed prey. The five transects were divided into 33 segments, each 8–11 km in length. The resolution of the survey was 150 m, and analyses of correlations between predators and prey were performed at length scales from 150 m to 9 km. We differentiated acoustic signals into aggregated and dispersed categories according to the estimated horizontal distribution of presumed prey.

3. Foraging guillemots were consistently more strongly correlated with the aggregated prey than with dispersed prey over scales ranging from 150 m to 9 km. Correlations were weak at small scales (150 m – 1 km) and increased and stabilized at scales of 2–3 km. The spatial scale at which we obtained a shift from weak to strong correlations between guillemots and their prey was similar to the scale at which the spatial variances in both guillemot and prey abundance were high.

4. Guillemots showed low correlations with prey at low prey densities. Similarly, correlations between guillemots and prey were low at low bird densities. The data support the hypothesis that the birds associate with prey patches with densities above a certain threshold, and that 'regional' prey abundances affect local use of patches.

5. The numerical aggregative response curves between guillemot and prey density were classified as being neither hyperbolic (type II) or sigmoidal (type III) within the range of prey densities observed in this study. The aggregative response curves were sensitive to spatial scales, which suggest that studies of response curves should be conducted at a range of spatial scales.

Key-words: aggregative response, Brünnich's guillemots, foraging ecology, scale dependence, *Uria lomvia*.

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Introduction

Spatial variability in the abundance of foraging animals and the spatial interactions between predators

and prey are fundamental themes in ecology. Studies exploring predator–prey interaction have been mainly limited to a single spatial scale, i.e. the scale of a single individual or that of the population (Horne & Schneider 1994). In recent years, the need for selection of appropriate spatial or temporal scales has been acknowledged in the study of a number of different ecological interactions, including density dependence (Ray & Hastings 1996) and social organization (Coul-

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son *et al.* 1997). Investigations require the use of a multiscale approach if predator selection of foraging habitat is to be identified (Schneider & Duffy 1985; Schneider & Piatt 1986; Hunt, Harrison & Cooney 1990; Russell *et al.* 1992; Schneider 1993, 1994). The importance of selecting the appropriate spatial scales is illustrated by the observation that the sign of association between predators and prey may change from positive to negative when the scale of observation decreases (Fairweather, Underwood & Moran 1984; Smith 1978; Schmitt 1982, 1985; Fairweather 1988; Rose & Leggett 1990).

The spatial associations between predators and prey may be considered as a special case of habitat selection in which prey aggregations are patches within a larger matrix. If the distribution and abundance of prey can be assessed by the predator, the spatial distribution of a predator would be expected to follow the dispersion of the prey at fine spatial scales as predicted by the ideal free distribution model (Fretwell & Lucas 1970; Morris 1987). Alternatively, if the prey cannot be assessed by the predator because of perceptual constraints, or if habitat selection is not related to resource exploitation, the distribution of predators may or may not be associated with that of their prey.

In predator-prey systems, the numerical response curve between predator aggregation and prey density is most often described as being nonlinear (Holling 1959, 1965; Hassell & May 1974). This response curve may be hyperbolic (type II) or sigmoidal (type III), the latter being the most common for higher vertebrates (Goss-Custard 1970, 1977; Hassell & May 1974; Piatt & Methven 1992). Following Hassell & May (1974) the sigmoidal aggregative response curve may be interpreted as follows: In areas with low prey density, predators do not find it worthwhile to search for prey, and thus the densities of predators will be low. In areas with increased prey density, the predators can obtain their prey more easily, and successful predators may attract more predators and this reinforces their aggregation. However, at a certain level of prey density, satiation in predator density is reached, and the response curve levels off.

Seabirds are predators which are patchily distributed while foraging at sea. The patchiness of marine birds and other predators at scales < 5 km has been partially explained by patchiness in the distribution of their prey and by the birds' selection of foraging habitats where prey could be most profitably acquired (Hunt & Harrison 1990; Hunt *et al.* 1990; Hunt, Heinemann & Everson 1992). At coarser scales, seabird distributions can to a large extent be explained by hydrographic structure, even though the underlying cause of their distributions most likely is determined by prey availability (Shuntov 1974; Pocklington 1979; Brown 1980; Hunt *et al.* 1981; Griffiths, Siegfried & Abrams 1982; Hunt & Schneider 1987; Veit 1988).

Recent improvements in acoustic techniques for

measuring marine fish and plankton densities have allowed students to investigate the strength of associations between the abundance of foraging seabirds and their prey at multiple spatial scales. There is considerable variation in the strength of correlation between seabird and prey abundance reported by various authors (see review by Hunt 1990; Hunt *et al.* 1992). Typically, most investigations have reported weak correlations at fine scales (< 5 km), and most studies have shown increasingly stronger correlations at larger scales.

Previous studies of distributions of marine avian predators with respect to their prey have employed techniques that integrated prey biomass over transect segments varying in length from 0.1 km to 10 km. Mehlum *et al.* (1996) analysed the spatial correlation between Brünnich's guillemots *Uria lomvia* L. and their presumed prey at the scale of ≈ 10 km in the vicinity of two large high arctic breeding colonies in southern Spitsbergen. They differentiated two classes of signals in their hydroacoustic data – aggregated and dispersed. They interpreted aggregated targets to reflect schools of fish or dense aggregations of large zooplankters, whereas dispersed targets were reflected from scattered organisms. By classifying echo types, Mehlum *et al.* (1996) were able to show that whereas correlations between seabirds and all prey combined were similar to the values found in studies reviewed by Hunt *et al.* (1992), correlations between guillemots and aggregated prey were among the strongest recorded for any study of seabirds.

This study focuses on associations between Brünnich's guillemots and different classes of acoustically detected prey at a range of spatial scales from 150 m to 9 km. We reasoned that if guillemots were strongly associated with aggregated prey at relatively large spatial scales, similarly strong correlations should be found at smaller scales down to the scale at which the predators no longer differentiate between subsections of an aggregation (Kotliar & Wiens 1990). This minimum scale should be set by a combination of the density structure of an aggregation as well as by the spacing between schools within the aggregation. We also investigate the shape of the aggregative response curve for Brünnich's guillemots and their prey at multiple spatial scales.

STUDY AREA

Storfjorden is a shallow fjord with depths < 180 m located in the south-eastern part of Svalbard (Fig. 1a). The most prominent bathymetric feature of the fjord is a north-south orientated submarine ridge located in the western part of the fjord. The study area is usually completely ice-covered during winter. No sea ice was present during our study in this portion of Storfjorden.

Two large and several smaller breeding colonies of Brünnich's guillemots are located on the western coast

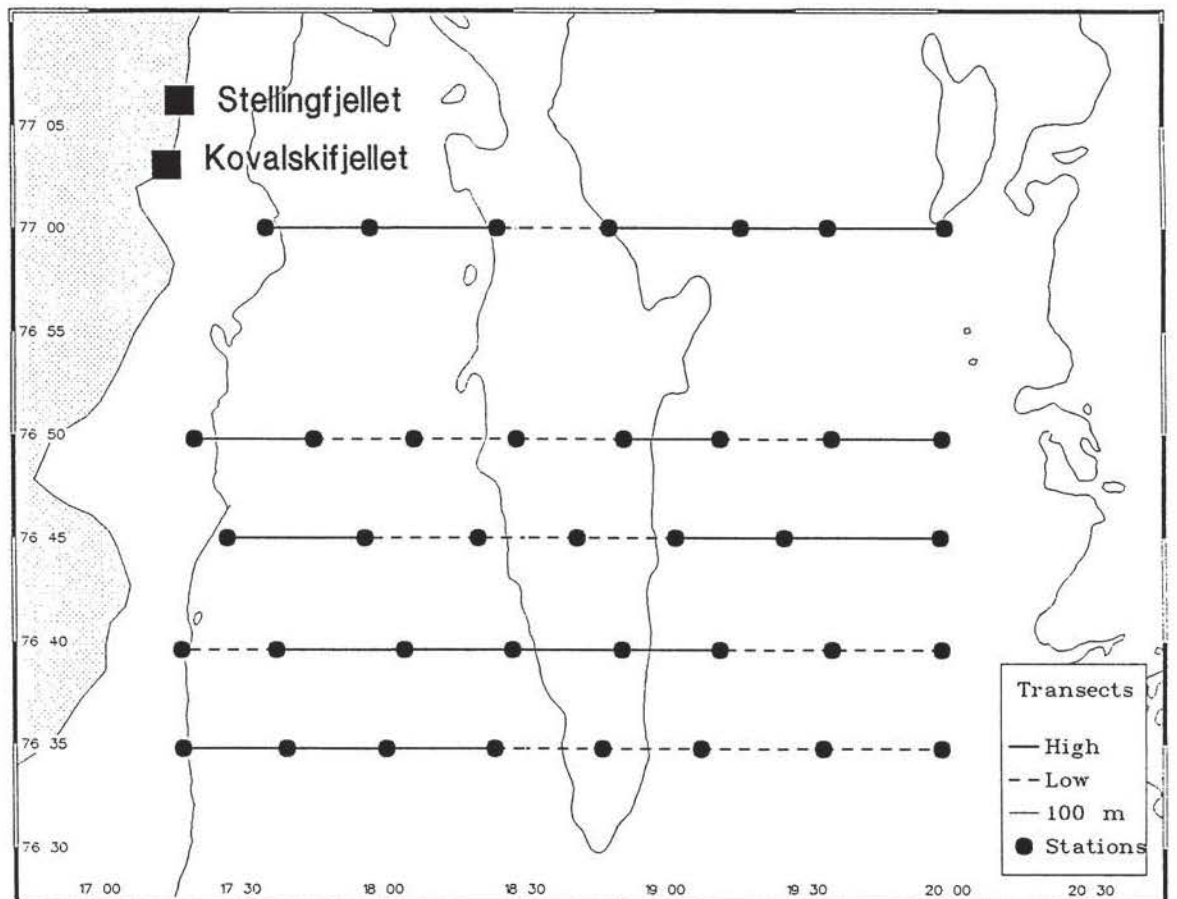
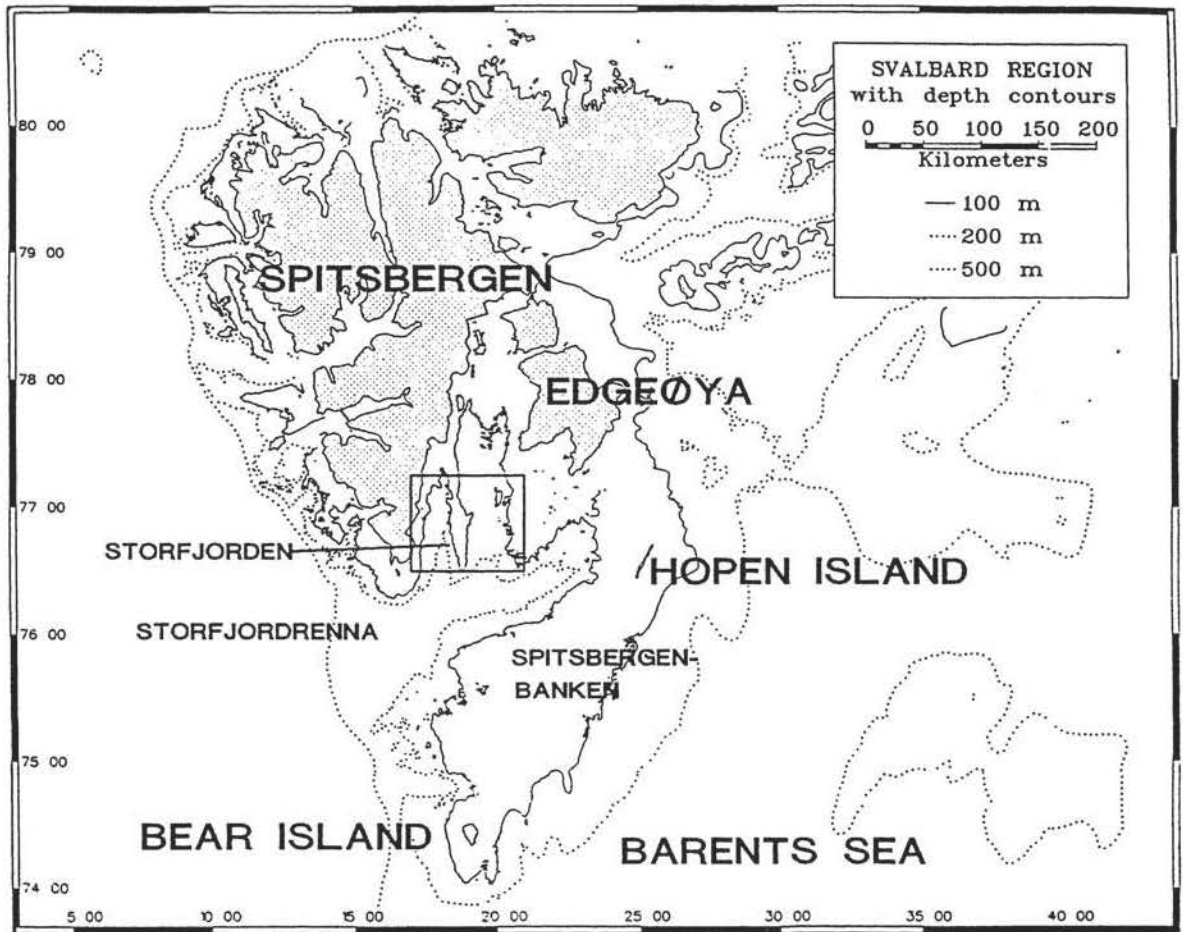


Fig. 1. (a) Svalbard archipelago and the northern Barents Sea. The study area in Storfjorden is indicated by a box. The 100, 200 and 500 m depth contours are given. (b) The five east–west seabird transects and sampling stations included in the study, which were located to the south of the two main breeding colonies in Storfjorden. Each transect is separated in high (\geq the median) and low ($<$ the median) guillemot density segments. The 100 m bathymetry contours are shown.

of Storfjorden (Mehlum *et al.* 1996). The populations of the two large colonies, Stellingfjellet (77°06' N, 17°20' E) and Kovalskifjellet (77°03' N, 17°17' E), have been recently estimated at about 450 000 and 90 000 individuals, respectively (Mehlum & Bakken 1994). Birds from these colonies forage in Storfjorden and in waters further south in Storfjordrenna. In Storfjorden, most guillemots forage in relatively deep waters in the western part, coincident with a weak subsurface front between warm Atlantic water and cold Arctic water (Mehlum *et al.* 1996).

Methods

SURVEY DESIGN

A ship-based transect study was conducted in an area where Brünnich's guillemots from the two large breeding colonies of Stellingfjellet and Kovalskifjellet forage (Mehlum *et al.* 1996). The Brünnich's guillemot was the only abundant avian consumer of larger zooplankton and fish in southern Storfjorden at the time of the study. To study relationships between guillemot abundances and prey distribution, we selected five latitudinal transects (59–68 km in length) that ranged eastward from shallow waters near the eastern coast of Spitsbergen to 20° 00' E, at latitudes of 76° 35', 76° 40', 76° 45', 76° 50', and 77° 00' N (Fig. 1b). All transects were surveyed once during the period 21–24 July 1992. The ship travelled at a speed of 5.0–5.5 knots and traversed \approx 150 m per minute. The transects were divided into segments, each 8–11 km in length, corresponding to the distance between oceanographic sampling stations (Fig. 1b). For the analyses in this paper, data were not aggregated across oceanographic stations.

BIRDS

The abundance of Brünnich's guillemots observed sitting on the sea surface was recorded from the bridge of the research vessel *Lance* by standardized strip transect methods as described by Tasker *et al.* (1984). Bird observations were made continuously between stops at each station along transects. A 300 m transect width was used and all birds observed within the transect were entered directly into a field computer. The lowest spatial resolution of bird abundance along transects was set at 1 minute (or 150 m).

ACOUSTICS

Details of the methods used for bioacoustical recordings are described by Mehlum *et al.* (1996). We used a single beam/single frequency echo sounder (LAZ 4700 ELAC) operating at 30 kHz, and recorded echoes on a ping by ping basis. The transducer with a beam angle of 16° was mounted inside a V-fin body towed at a depth of 2–3.5 m. Because we did not know

the target strength of the organisms detected by the echo sounder, echo signals are represented as Volts². Estimates of biomass are not essential in this study because we are interested in relative differences in acoustically detected biomass between different parts of transects. During most of the transects, the sea was calm (0–1 Beaufort scale), and unwanted noise and excess attenuation of acoustical signals from bubbles was low.

Post-processing of echo signals included filtering out the ship's echo sounder signals, echo type recognition, and integration of echo intensity at 1-min (150-m) intervals along the transects. The sampling window for the quantitative analysis was in the interval from 10 to 50 m depth. The acoustic signals were classified into two groups: dense concentrations of targets (echo type A – aggregated) and dispersed targets (echo type D – dispersed). A simple algorithm for discriminating between the two different type of echoes was developed based on the dimension and the strength of the echoes. The methods used for removing echoes from the ship's depth sounder are described by Mehlum *et al.* (1996). The algorithm for discriminating between the two types of targets is presented in Appendix 1.

ANALYSES

We analysed correlations between guillemot abundance and acoustic biomass along transects at scales ranging from 150 m to 9 km. When calculating correlations within each transect segment (8–11 km), the largest spatial scale (bin size) used was 2.0 km. For analyses using a bin size of 2 km, the number of bins per transect segment varied between 3 and 5. For analyses using bin sizes smaller than 2 km, the number of bins per correlation statistic increased with decreasing bin size. When combining data from all segments, the sample sizes permitted analyses at scales up to 9 km (sample sizes ranged from 12 for 9 km segments to 1780 for 150 m segments).

Statistical analyses of guillemot and acoustical data were performed using STATISTICA vs. 5.0 (Statsoft, Inc. 1995), assuming 2nd order stationarity (i.e. expected value and variance constant for any subset of a time series) in guillemot and prey abundance within each 8–11 km transect segment. Because the Pearson correlation method is not robust to 'outliers' or asymmetry in data sets, we preferred to use non-parametric Spearman rank correlations. However, as most previous studies correlating seabird and prey abundances have used the Pearson method, we also present results using this method for comparative purposes in our initial analyses. If the two methods yielded similar results in the initial analyses, we selected the Pearson method for the subsequent analyses. We used autocorrelation analysis to investigate serial dependency in the abundance of guillemots within transect segments.

On transect segments with low bird densities we expected to obtain no or only weak positive correlations between the abundance of guillemots and their prey because there would be too few birds to provide proportional coverage of all prey patches available. We therefore selected transect segments with guillemot abundance \geq the median for further analyses of correlations between bird and prey abundance. To investigate the ability of the predator to track prey patches, we calculated cross-correlations between guillemot and the aggregated type prey at the smallest scale possible (150 m).

To characterize the horizontal dimension of prey patches, we used two different methods. In the first method, we determined the upper 25%, the median, and the lower 25% values of the distribution of acoustic return in all 150 m bins ($n = 1780$) surveyed during the five transects. These values were selected as thresholds for acoustic values above which we would classify the return as belonging to a prey patch. We then estimated the length of a patch (chord length) in a transect segment as the distance between contiguous bins with acoustic values above the threshold. Similarly, we estimated the interpatch distance as the distance between contiguous bins below the acoustic threshold.

The second method for characterizing prey patch dimensions was based on wavelet analysis (Bradshaw & Spies 1992). We also used wavelet analysis for describing patch dimensions of foraging guillemots. This method is useful for analysing nonstationary or nonsinusoidal multifrequency data (Bradshaw & Spies 1992; Bradshaw & McIntosh 1994). It can detect aggregative patterns in time series (or along transects) at different scales which may be overlooked by methods such as the Fourier spectral analysis.

We used the WaveLab 0.7 Toolbox (Stanford University freeware) under MATLAB (MathWorks, Inc.) for calculating the wavelet transform at different spatial scales of aggregated prey and guillemot densities, respectively, in each transect segment. The selected analysing wavelet was 'Sombrero', which is similar to the 'Mexican Hat' wavelet described by Daubechies (1988). The wavelet variance was applied for detecting the spatial scales which dominated the spatial patterns in the data. This function is given for a specific scale as the average of the squares of the wavelet coefficients at every point along the transect at this scale (Bradshaw & Spies 1992). Large wavelet variance at a scale identifies this scale as important for describing the spatial pattern along the transect.

Results

NUMBERS AND DISTRIBUTION OF BRÜNNICH'S GUILLEMOTS

The average number of Brünnich's guillemots observed per minute in the 33 transect segments was

0.60 ± 0.76 (SD) (or 0.18 ± 0.23 individuals per km^2), and median guillemot abundance was 0.31 birds per min (or 0.11 birds per km^2). The locations where guillemot abundance was \geq the median (= high) is shown in Fig. 1b. Of the 18 transect segments in which guillemot densities were \geq the median, only two segments showed significant ($P < 0.05$) autocorrelation at a lag of 1 for the lowest bin size (1 min or 150 m), but none of these autocorrelations was above 0.5. This indicated that the serial dependency of guillemot observations at a bin size of 150 m was negligible.

SCALE-DEPENDENT CORRELATION BETWEEN BIRD AND PREY ABUNDANCE

The strength of correlation between Brünnich's guillemots and the acoustically determined biomass of presumed prey varied with bin size and whether prey were aggregated or dispersed. Using data from all 33 transect segments, we found that correlations between birds and acoustically detected biomass were weak at the smallest bin sizes, but increased, and then more or less stabilized, at bin sizes between 2 and 9 km (Fig. 2). Correlations between guillemots and acoustically detected biomass were consistently stronger for aggregated biomass than for diffuse biomass, regardless of bin size (Fig. 2). The Pearson correlation coefficient for guillemots and aggregated biomass stabilized at about $r = 0.70$ for bin sizes ≥ 3 km. The differences in guillemot responses to biomass aggregation were most striking when Pearson correlation's were used, especially for bin sizes of 3–9 km.

DIFFERENCES IN BIRD-PREY CORRELATIONS AMONG TRANSECT SEGMENTS

Correlations between guillemots and acoustically detected biomass were sensitive to the total density of prey (Fig. 3) and the average density of foraging guillemots within each transect segment (Fig. 4). For bin sizes between 0.3 and 2.0 km, scatter in the distribution of Pearson correlation coefficients for individual transect segments in relation to summed (averaged) acoustic return increased markedly once echo return values fell below about 100 V^2 (Fig. 3). Above this value, correlation coefficients increased gradually with increasing acoustic biomass, and the correlations were consistently strong at relatively high acoustic biomass. Similarly, in transect segments where the average guillemot density was below about 0.2–0.3 birds km^{-2} , there was a wide scatter in Pearson correlation coefficients between guillemots and acoustic return; the three data points above these values showed strong correlations ($r > 0.80$) over a range of bin sizes from 0.3 km to 2.0 km (Fig. 4).

We found differences between transect segments in the strength of the correlations between guillemot and echo returns. When calculating correlations between guillemots and aggregated biomass for each of the 33

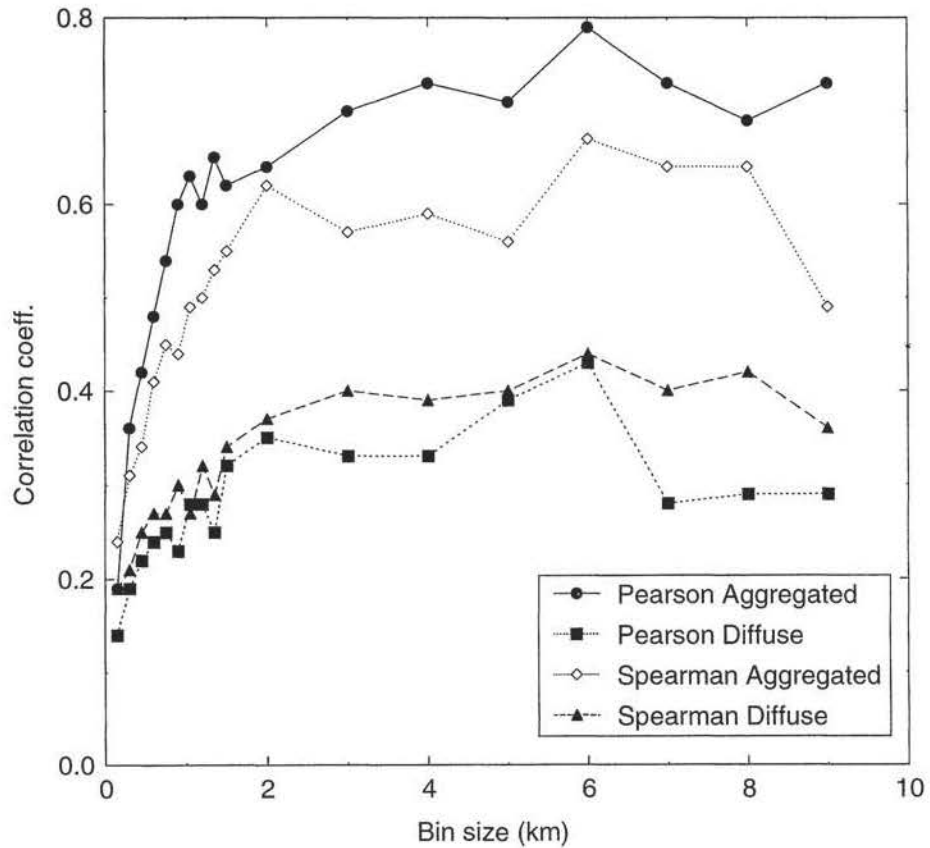


Fig. 2. Correlations between prey and guillemot abundance at bin sizes 0.15–9 km. Correlation coefficients (Spearman and Pearson) are given for both echo types representing aggregated and dispersed prey.

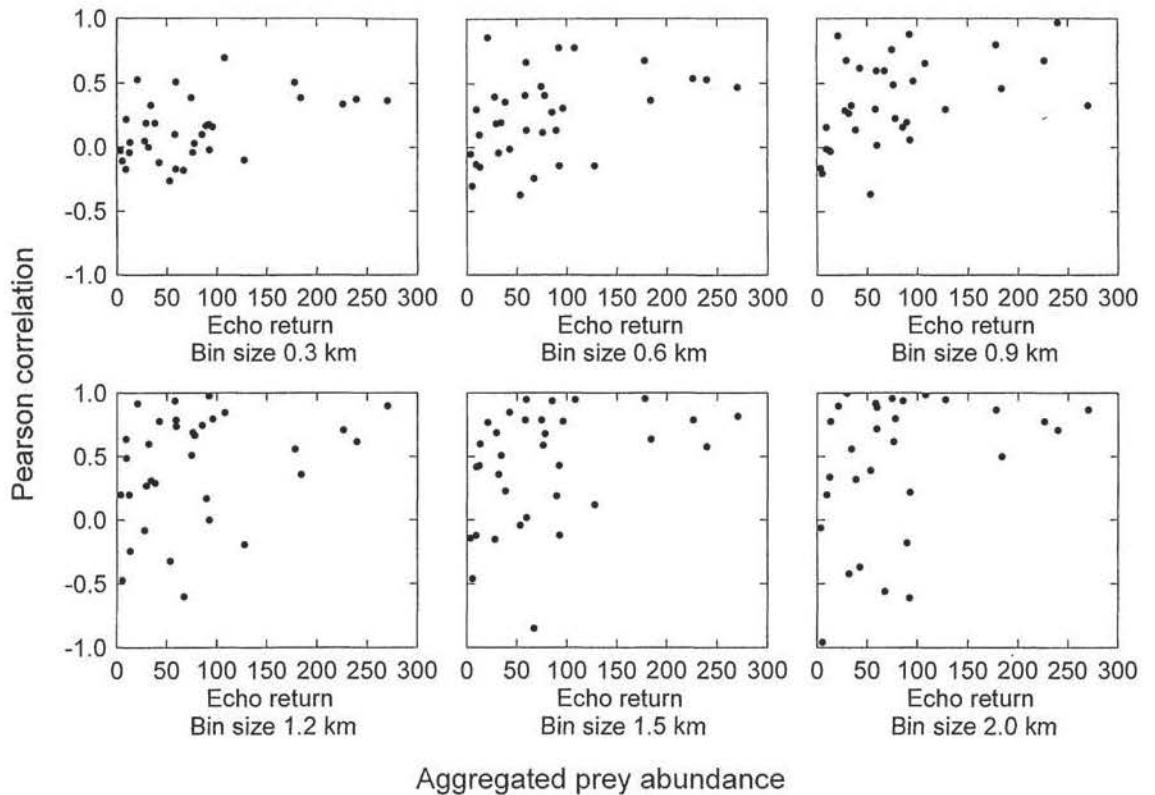


Fig. 3. Correlations between guillemot and aggregated prey at bin sizes 0.3–2.0 km within single transect segments as a function of the average echo return (in Volt²) for the same segments.

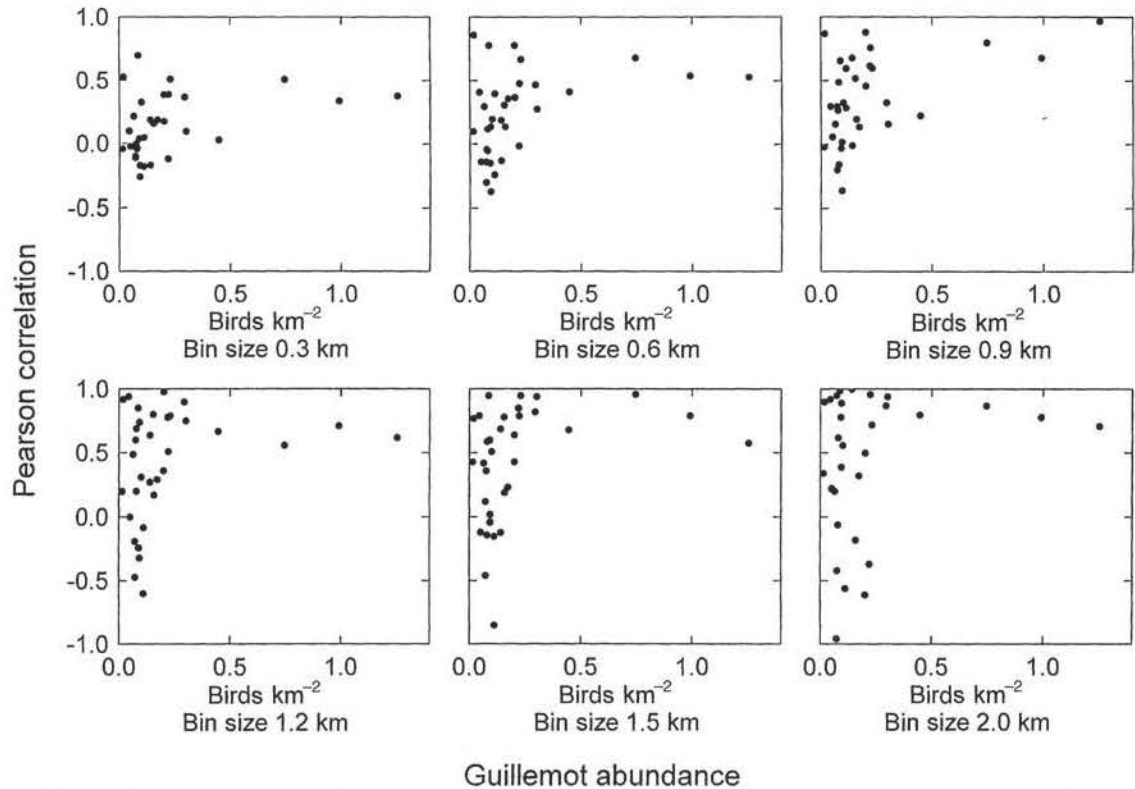


Fig. 4. Correlations between guillemot and aggregated prey at bin sizes 0.3–2.0 km within single transect segments as a function of the average density of guillemots for the same segments.

transect segments separately, we found that strong correlations (here defined as $r \geq 0.6$) were infrequent at bin sizes below 600 m, but were encountered in between 30% and 48% of correlations computed using larger bin sizes (Table 1). When we used the 18 transect segments in which bird densities were \geq the median for all segments, strong correlations were obtained in 33–61% of segments when bin sizes were ≥ 600 m.

It is possible that our analyses underestimated the actual strength of the correlations reported above because of imperfect match between predator and prey aggregations. We performed cross-correlation analyses at a bin size of 150 m for transect segments with guillemot densities \geq the median value. We found that the aggregations of guillemots were offset from prey aggregations in all 18 cases where significant

cross-correlations were encountered at lags ≤ 1.5 km (Fig. 5). In 12 segments, the strongest correlations were obtained between -3 and $+2$ lags, equivalent to the prey being lagged 450 m behind and 300 m in front of the birds along the transects, respectively. Examination of the spatial distribution of these lags with respect to the side of prey patches nearest the guillemot breeding colonies showed no tendency of the guillemots to use preferentially either side of prey patches (Mann–Whitney U -test, $U = 126.0$, $P > 0.05$).

AGGREGATIVE RESPONSE OF BRÜNNICH'S GUILLEMOT TO PREY DENSITY

The aggregative response of Brünnich's guillemots showed no consistent pattern for low bin sizes (< 1 km), but at larger bin sizes (1–4 km) we generally

Table 1. Number of 8–11 km long transect segments with Pearson correlation coefficient between guillemots and acoustic returns ≥ 0.6 at different bin sizes

Bin size (min) (km)	1 0.15	2 0.30	3 0.45	4 0.60	5 0.75	6 0.90	7 1.05	8 1.20	9 1.35	10 1.50
All segments ($n = 33$)		1	2	5	10	11	11	16	14	16
Segments with \geq median bird density ($n = 18$)		1	1	3	7	9	6	11	8	11

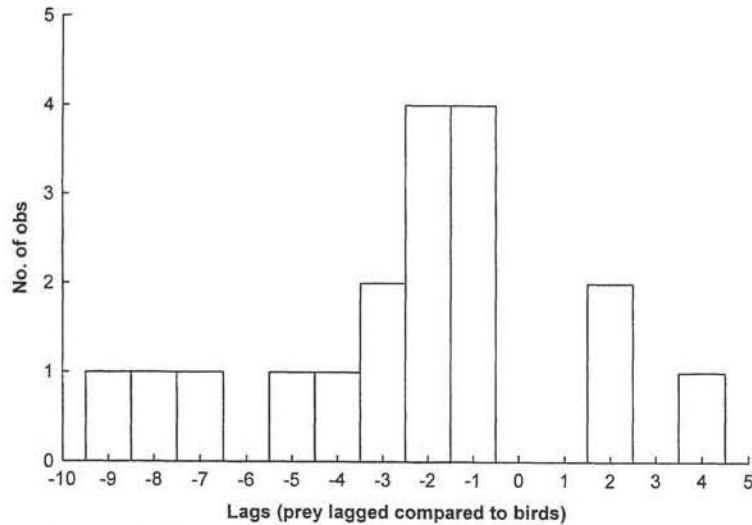


Fig. 5. Cross-correlations between guillemot and aggregated prey densities for 18 transect segments. Positive values on the x -axis represent cases where prey is lagged behind the guillemots along the transects.

obtained a positive response in bird density with increase in prey abundance (Fig. 6). There was a wide scatter in the data, but in general the data followed a concave curve and neither a hyperbolic (type II) nor a sigmoidal (type III) curve. The number of high prey density data points was too low to let us draw a conclusion about the shape of the upper part of the curve.

PATCH SIZE CHARACTERISTICS

The average sizes of prey patches depended on the arbitrary threshold levels of echo return set to define

a patch. If we included only prey densities in the upper 25% of echo values from all 150 m bins, mean patch chord length was estimated to be 372 m and the mean interpatch distance was 992 m (Table 2). In contrast, if the threshold for detection of a patch was set to include all echo return values above the bottom 25%, then the average length of a patch chord was 1107 m and the average distance between patches was 399 m.

The wavelet analysis of acoustic biomass in the 33 transect segments showed the highest wavelet variance at small spatial scales (150–300 m), indicating that these scales dominated the spatial structure of our transect data. The curves representing wavelet vari-

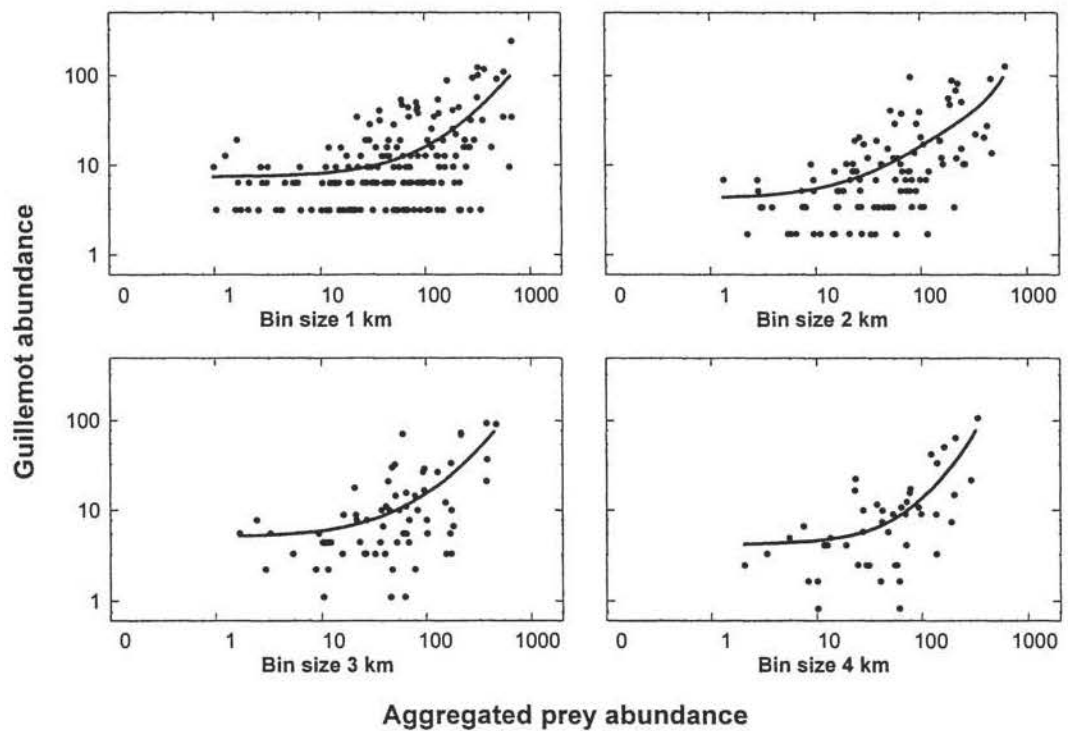


Fig. 6. Aggregative response of Brünnich's guillemots (in birds km^{-2}) to prey abundance (in Volt^2) at bin sizes 1–4 km. The data are represented in log–log scale with all zero values omitted.

Table 2. Chord lengths measured within patches and distances between patches (in m) of aggregated biomass along the transects. A patch is defined as containing one or more bins with echo return above a predetermined threshold: (a) above the upper 25%, (b) above the median, or (c) above the lower 25% of all 150-m bin echo values

Level	Mean	Median	SD	N
Patch chord length				
Upper 25%	372	150	473	181
Median	566	150	1005	237
Lower 25%	1107	450	1848	181
Inter-patch distance				
Upper 25%	992	450	1508	200
Median	563	300	886	236
Lower 25%	399	150	583	158

ance as a function of spatial scale for acoustic biomass showed quite large individual variations but were of three major types (Fig. 7):

1. in seven cases (21%), variance generally decreased with increasing scale;

2. 18 cases (55%) were similar to type 1 but with a second peak in variance at intermediate scales; and
3. eight cases (24%) were similar to type 1 at small and intermediate scales, but showed increasing variance at larger scales. The high percentage of type 2 curves indicates that the acoustic biomass showed spatial structure at intermediate as well as small scales. The peak in variance at intermediate scale in the type 2 curves (mean \pm SD = 1220 m \pm 570 m, median = 1100 m, range = 600 m – 2.7 km) was in the range of values obtained in our estimates of the distance between peaks of prey patches. This distance averaged 1363, 1129 and 1506 m (calculated from Table 2), when patches were defined by echo returns above the upper 25%, above the median, and above the lower 25% of all the 150 m bin echo values, respectively.

Wavelet analysis of guillemots in the 18 transect segments with guillemot abundances \geq the median value showed patterns similar to those found in the wavelet analysis of the acoustic biomass. For all segments, the highest wavelet variance was obtained at the lowest spatial scale (150–300 m). Four segments (22%) showed type 1 curves, 11 segments (61%), exhibited type 2 curves, and three segments (17%) type 3

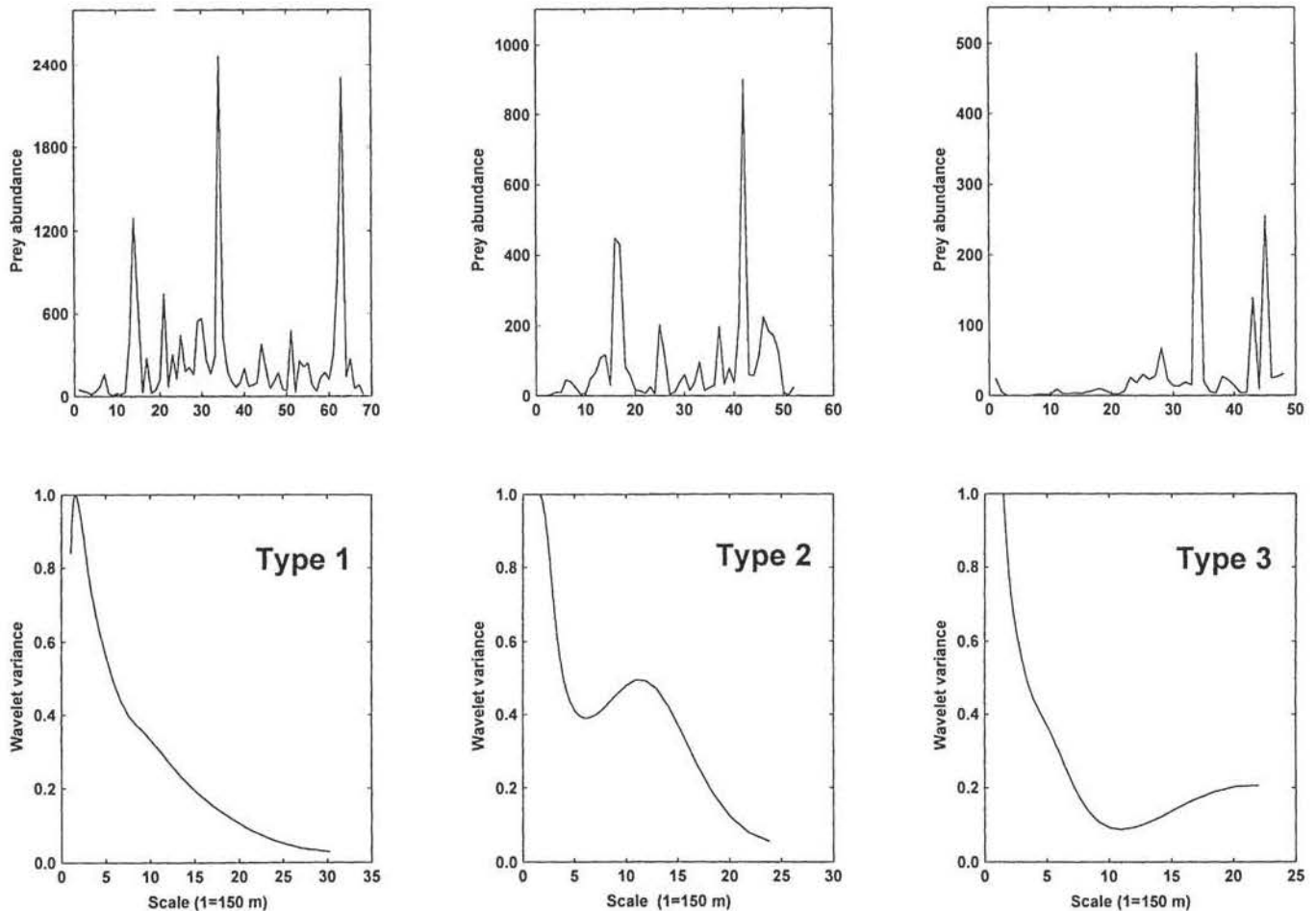


Fig. 7. Aggregated prey abundance (in Volt²) and scale-dependent wavelet variance along three transect segments showing the three typical wavelet variance curves. For comparative purposes the wavelet variances are standardized on the scale 0–1.

curves. The predominance of transect segments with type 2 curves of wavelet variance with peaks at scales 600 m to 2.3 km (mean \pm SD = 1420 m \pm 590 m, median = 1350 m, range = 600 m – 2.3 km) was interpreted as an indication of a spatial structure of the guillemot distribution. The scale of the intermediate peak in predator wavelet variance in type 2 curves was similar to the scale at which there was a corresponding peak in wavelet variance for acoustic biomass, as well as the distance between the centres of neighbouring prey patches (Table 2).

Discussion

Diet analyses of Brünnich's guillemots collected during the study period showed that crustaceans and fish were the main prey items (Mehlum *et al.* 1996). The crustaceans consisted mainly of two species of pelagic amphipods, *Parathemisto abyssorum* and *P. libellula*, and the euphausiid *Thysanoessa inermis*. Of fishes, polar cod *Boreogadus saida* occurred most frequently, whereas capelin *Mallotus villosus* was encountered less frequently. These prey species are the most abundant pelagic fish and large zooplankton species in the northern Barents Sea region (Sakshaug *et al.* 1994). Although we had no information on the composition of the biomass from which we obtained echoes, we interpreted the class of aggregated targets as being from schools of fish or dense aggregations of large zooplankters such as *Parathemisto* spp. and *Thysanoessa inermis*.

Our results show that spatial correlations between aggregated determined biomass and Brünnich's guillemot densities along ship transects were weak at small bin sizes and increased strongly at bin sizes between 150 m and 1 km, reaching a plateau at a bin size of 2–3 km. Thus, the transition region between low and high spatial association of guillemots and their prey occurred at scales where the spatial variance in prey biomass was high (Fig. 7). Our wavelet analysis showed that the spatial variance of both guillemot distribution and presumed prey biomass showed a peak at these scales. Similarly, Logerwell *et al.* (1998) found peaks in spatial variance around 3 km and greater for Brünnich's guillemots and at 2 km and greater for prey in a study in the Bering Sea using spectral analysis. They found little spatial variance at smaller scales.

The increase in correlation strength with increasing bin size is in agreement with those of most other workers (see review by Hunt *et al.* 1992), and may be the result of reduction of the variance from aggregating data. However, the finding that correlation values reached a plateau at a bin size of 2–3 km is new, and suggests that at least a portion of the change in correlation strength with bin size reflects the scale at which guillemots in this study were related to prey distributions. Our transects were too short to docu-

ment the strength of association between guillemots and their prey at scales larger than 9 km.

Our correlation analyses showed that there was a low spatial association between guillemots and their prey at the smallest scales (< 1 km), and our cross-correlation analysis showed that the guillemots did not perfectly track the patches of prey at the smallest scales. We interpret these results as indicating that the guillemots were indifferent (Kotliar & Wiens 1990) to patches at these scales. Thus, in the terminology of Kotliar & Wiens (1990) we argue that the first-order patchiness, or grain, of prey patches as perceived by the guillemots occurred at scales close to 1 km. Alternatively, the lack of association between foraging seabirds and their prey at small spatial scales might be explained by the patches being too ephemeral for the birds to track (Hunt & Schneider 1987), or that there was a spatial shift or drift that resulted in a displacement of the predators subsequent to foraging on their prey (Veit, Silverman & Everson 1993).

In this study, we split the echo signals into aggregated and dispersed biomass, respectively. Correlations between guillemots and aggregated prey biomass were much stronger than with diffuse biomass. Also, the correlations between guillemots and aggregated prey were stronger compared to most previous studies, where no differentiation between aggregated and diffuse biomass had been made (Hunt *et al.* 1992). This result agrees with previous studies which have indicated that correlations between aggregated prey, such as schooling fish (capelin) or surface swarming zooplankton (McClatchie, Hutchinson & Nordin 1969), and birds are stronger, and often at smaller bin sizes (Schneider & Piatt 1986; Erikstad, Moum & Vader 1990) than correlations with prey that form diffuse patches (Hunt *et al.* 1990, 1992). In a recent study of association between guillemot *Uria* spp. density and acoustic biomass of capelin schools, Skarsfjord (1995) reported stronger correlation coefficients at scales of 15–41 km than those reported for Brünnich's guillemots and aggregated prey in the present study (scales 2–9 km). As stated by Mehlum *et al.* (1996), our results suggest that in future studies it will be important to separate diffuse biomass from aggregated biomass. This will require a ping by ping recording of data for post processing of the acoustic returns, something that has also been lacking in most previous studies which have integrated primary echo returns over hundreds to thousands of meters.

Our results show that the strength of the spatial association between the guillemots and the presumed prey biomass is sensitive both to prey abundance, as did Veit *et al.* (1993), and predator abundance. Strong correlations between guillemots and prey were only found when mean guillemot densities within transect segments were above a threshold of 0.2–0.3 birds km⁻². At lower bird densities there may have been too few birds to provide a match between the abundances of birds and their prey.

When prey is scarce, a high quality, but isolated, patch has a lower probability of being used by a predator than an intermediate quality patch in close proximity to a high quality patch (Milne, Johnston & Forman 1989). Thus, whether a prey patch is used depends on the overall quality of the 'region' within which the prey patch is embedded. Guillemots, apparently did not select relatively dense prey patches in transect segments where average prey densities were below a biomass corresponding to the top third of maximum prey biomass recorded during this study. This pattern was evident for bin sizes of 0.3–2.0 km, but was most pronounced at the largest bin sizes. We interpret this result to indicate that unless a region had a relatively high biomass of prey, the guillemots made little effort to prospect it for patches of high density (see also Veit *et al.* 1993). This may be similar to the foraging by 'expectation' shown by Gibb (1962), or it may represent threshold foraging, where the threshold is set for a region rather than for an individual patch. Threshold foraging behaviour at different prey densities has been suggested for capelin predators such as common guillemots *Uria aalge* and Atlantic puffins *Fratercula arctica* (Piatt 1990) and guillemots *Uria* spp. (Erikstad *et al.* 1990), and for baleen whales (Piatt & Methven 1992).

The numerical aggregative response curves (Fig. 6) between guillemot and prey density were sensitive to spatial scale. Consistent responses were not obtained at small spatial scales (< 1 km), but strong positive responses were evident at larger scales. The response curves could not be classified as being hyperbolic (type II) or sigmoidal (type III) within the range of prey densities observed in this study. As pointed out by Hassell & May (1974), it is difficult to resolve the shape of the upper part of the response curve without an adequate number of data points representing high prey density. It is likely that Brünnich's guillemots in the study area sometimes encounter higher prey densities than those observed by us. Under such circumstances the aggregative response curve might level off and approach the sigmoidal type, which is most common for higher vertebrates (Goss-Custard 1970, 1977; Hassell & May 1974; Piatt & Methven 1992). Our results are similar to those obtained in a study of several shorebird species (Bryant 1979), in which strong correlations were obtained between invertebrate prey density and the density of foraging birds. Bryant (1979) also observed no levelling off of the aggregative response curves at high prey densities.

Our results illustrate that the aggregative response of predators to different prey densities should be studied at a range of spatial scales (Horne & Schneider 1994). Only a single spatial scale was considered in the original descriptions of the aggregative response curve between predator and prey density (Holling 1959, 1965; Hassell & May 1974). Piatt (1990) chose a single spatial scale of 2.5 km in his study of spatial association between two capelin predators, common

guillemot and Atlantic puffin, and their prey. He found a sigmoidal aggregative response in about one-third of his transects and suggested that the response was best resolved at spatial scales similar to the scale of aggregations (≈ 2 –4 km). Our data showed a similar strong aggregative response within this range of spatial scales.

Ecologists have long recognized that predators are sensitive to the distribution and availability of prey. By using a continuous record of predator and prey numbers over long transect lengths, we have been able to demonstrate the range of distance scales over which predators show sensitivity to variation in prey density. Using these techniques we have also been able to demonstrate that 'regional' prey abundances affect local use of patches. Detection of these effects would have been problematic using survey methods with discontinuous sampling. Our results are important because they not only confirm that there is a lower limit to the grain size that predators will discriminate, but also that predators respond to the major variations in their resource landscape, which correspond to the size and spacing of the major aggregations of prey.

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References

- Bradshaw, G.A. & McIntosh, B.A. (1994) Detecting climate-induced patterns using wavelet analysis. *Environmental Pollution*, **83**, 135–142.
- Bradshaw, G.A. & Spies, T.A. (1992) Characterizing canopy gap structure in forests using wavelet analysis. *Journal of Ecology*, **80**, 205–215.
- Brown, R.G.B. (1980) Seabirds as marine animals. *Behavior of Marine Animals*, Vol. 4. *Marine Birds* (eds J. Burger, B.L. Olla & H.E. Winn), pp. 1–39. Plenum Press, New York.
- Bryant, D.M. (1979) Effects of prey density and site character on estuary usage by over-wintering waders (Charadrii). *Estuarine and Coastal Marine Science*, **9**, 369–384.
- Coulson, T., Albon, S., Guinness, F., Pemberton, J. & Clutton-Brock, T. (1997) Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). *Ecology*, **78**, 852–863.
- Daubechies, I. (1988) Orthonormal bases of compactly supported wavelets. *Communications on Pure and Applied Mathematics*, **41**, 909–996.
- Erikstad, K.E., Moum, T. & Vader, W. (1990) Correlations

- between pelagic distribution of common and Brünnich's guillemots and their prey in the Barents Sea. *Polar Research*, **8**, 77–87.
- Fairweather, P.G. (1988) Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology – Progress Series*, **45**, 237–243.
- Fairweather, P.G., Underwood, A.J. & Moran, M.J. (1984) Preliminary investigations of predation by the whelk *Morula marginata*. *Marine Ecology – Progress Series*, **17**, 143–156.
- Fretwell, S.D. & Lucas, H.L. Jr (1970) On territorial behaviour and other factors influencing habitat distribution in birds. *Acta biotheoretica*, **19**, 16–36.
- Gibb, J.A. (1962) L. Tinbergen's hypothesis of the role of specific search images. *Ibis*, **104**, 106–111.
- Goss-Custard, J.N. (1970) The responses of redshank (*Tringa totanus* (L.)) to spatial variations in the density of their prey. *Journal of Animal Ecology*, **39**, 91–113.
- Goss-Custard, J.N. (1977) Responses of redshank, (*Tringa totanus*), to the absolute and relative densities of two prey species. *Journal of Animal Ecology*, **46**, 867–874.
- Griffiths, A.M., Siegfried, W.R. & Abrams, R.W. (1982) Ecological structure of a pelagic seabird community in the southern ocean. *Polar Biology*, **1**, 39–46.
- Hassell, M.P. & May, R.M. (1974) Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology*, **43**, 567–594.
- Holling, C.S. (1959) The components of predation as revealed by a study of small mammal predation on the European pine sawfly. *Canadian Entomologist*, **91**, 293–320.
- Holling, C.S. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada*, **45**, 1–60.
- Horne, J.K. & Schneider, D.C. (1994) Lack of spatial coherence of predators with prey: a bioenergetic explanation for Atlantic cod feeding on capelin. *Journal of Fish Biology*, **45** (Suppl. A), 191–207.
- Hunt, G.L. (1990) The pelagic distribution of marine birds in a heterogeneous environment. *Polar Research*, **8**, 43–54.
- Hunt, G.L., Gould, P.J., Forsell, D.J. & Peterson, H. (1981) Pelagic distribution of marine birds in the Eastern Bering Sea. *The Eastern Bering Sea Shelf: Oceanography and Resources*, Vol. 2 (eds D.W. Hood & J.A. Calder), pp. 689–718. NOAA, Office of Marine Pollution Assessment, Washington, DC.
- Hunt, G.L. Jr & Harrison, N.M. (1990) Foraging habitat and prey taken by least auklets at King Island, Alaska. *Marine Ecology – Progress Series*, **65**, 141–150.
- Hunt, G.L. Jr, Harrison, N.M. & Cooney, T. (1990) The influence of hydrographic structure and prey abundance on foraging of least auklets. *Studies in Avian Biology*, **14**, 7–22.
- Hunt, G.L., Heinemann, D. & Everson, I. (1992) Distributions and predator–prey interactions of macaroni penguins, antarctic fur seals, and antarctic krill near Bird Island, South Georgia. *Marine Ecology – Progress Series*, **86**, 15–30.
- Hunt, G.L. & Schneider, D.C. (1987) Scale-dependent processes in the physical and biological environment of marine birds. *Seabirds: Feeding Biology and Role in Marine Ecosystems* (ed. J.P. Croxall), pp. 7–41. Cambridge University Press, Cambridge, UK.
- Kotliar, N.B. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Logerwell, E.A., Hewitt, R. & Demer, D.A. (1998) Scale-dependent spatial variance patterns and correlations of seabirds and prey in the southeastern Bering Sea as revealed by spectral analysis. *Ecography*, **21**, 212–223.
- McClatchie, S., Hutchinson, D. & Nordin, K. (1969) Aggregation of avian predators and zooplankton prey in Otago shelf waters, New Zealand. *Journal of Plankton Research*, **11**, 361–374.
- Mehlum, F. & Bakken, V. (1994) Seabirds in Svalbard: status, recent changes and management. *Seabirds on Islands: Threats, Case Studies & Action Plans* (eds D.N. Nettleship, J. Burger & M. Gochfeld), pp. 155–171. Bird-Life Conservation Series, no. 1.
- Mehlum, F., Hunt, G.L., Klusek, Z., Decker, M.B. & Nordlund, N. (1996) The importance of prey aggregations to the distribution of Brünnich's guillemots in Storfjorden, Svalbard. *Polar Biology*, **16**, 537–547.
- Milne, B.T., Johnston, K. & Forman, R.T.T. (1989) Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model. *Landscape Ecology*, **2**, 101–110.
- Morris, D.W. (1987) Ecological scale and habitat use. *Ecology*, **68**, 362–369.
- Piatt, J.F. (1990) The aggregative response of common murre and Atlantic puffins to schools of capelin. *Studies in Avian Biology*, **14**, 36–51.
- Piatt, J.F. & Methven, D.A. (1992) Threshold foraging behavior of baleen whales. *Marine Ecology – Progress Series*, **84**, 205–210.
- Pocklington, R. (1979) An oceanographic interpretation of seabird distributions in the Indian Ocean. *Marine Biology*, **51**, 9–21.
- Ray, C. & Hastings, A. (1996) Density dependence: are we searching at the wrong spatial scale? *Journal of Animal Ecology*, **65**, 556–566.
- Rose, G.A. & Leggett, W.C. (1990) The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. *Ecology*, **71**, 33–43.
- Russell, R.W., Hunt, G.L. Jr, Coyle, K.O. & Cooney, T. (1992) Foraging in a fractal environment: Spatial patterns in a marine predator–prey system. *Landscape Ecology*, **7**, 195–209.
- Sakshaug, E., Bjørge, A., Gulliksen, B., Loeng, H. & Mehlum, F. (1994) Structure, biomass distribution, and energetics of the pelagic ecosystem in the Barents Sea: a synopsis. *Polar Biology*, **14**, 405–411.
- Schmitt, R.J. (1982) Consequences of dissimilar defenses against predation in a subtidal marine community. *Ecology*, **63**, 1588–1601.
- Schmitt, R.J. (1985) Competitive interactions of two mobile prey species in a patchy environment. *Ecology*, **66**, 950–958.
- Schneider, D.C. (1993) Scale-dependent pattern and species interactions in marine nekton. *Aquatic Ecology: Scale, Pattern and Process* (eds P.S. Giller, A.G. Hildrew & D. Raffaelli), pp. 441–467. Blackwell Science, Oxford.
- Schneider, D.C. (1994) *Quantitative Ecology: Spatial and Temporal Scaling*. Academic Press, San Diego.
- Schneider, D.C. & Duffy, D.C. (1985) Scale-dependent variability in seabird communities. *Marine Ecology – Progress Series*, **25**, 211–218.
- Schneider, D.C. & Piatt, J.F. (1986) Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Marine Ecology – Progress Series*, **32**, 237–246.
- Shuntov, V.P. (1974) *Sea Birds and the Biological Structure of the Ocean*. Translated from Russian by I. Allardt. National Technical Information Service, US Department of Commerce, Springfield, Virginia.
- Skarsfjord, H. (1995) *Multiskala-analyse av romlige og numeriske sammenhenger mellom pelagisk sjøfugl og byttedyr*. Cand. scient. – thesis. University of Tromsø, Tromsø Norway. (In Norwegian).
- Smith, P.E. (1978) Biological effects of ocean variability: time and space scales of biological response. *Rapport et*

- Pocès-verbaux des Réunions du Conseil Permanent Internationale pour L'Exploration de la Mer*, **173**, 117–127.
- Statsoft, Inc. (1995) *Statistica for Windows, Release 5.0*. Statsoft Inc., Tulsa, Oklahoma.
- Tasker, M.L., Hope Jones, P., Dixon, T. & Blake, B.F. (1984) Counting seabirds from ships: a review of methods employed and a suggestion for a standardized approach. *Auk*, **101**, 567–577.
- Veit, R.R. (1988) *Spatial dispersion patterns of Antarctic Seabirds*. PhD thesis, University of California, Irvine, Irvine.
- Veit, R.R., Silverman, E.D. & Everson, I. (1993) Aggregation patterns of pelagic predators and their principal prey, Antarctic krill, near South Georgia. *Journal of Animal Ecology*, **62**, 551–564.

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Appendix 1

We defined an echo sample as $u_{i,j}$ (where i = ping number, j = sample number in the ping) expressed in voltage, which could be transformed to acoustic pressure). For discriminating between dense concentrations of targets (echo type A – aggregated) and the second, dispersed targets (echo type D – dispersed)

we applied the following procedure. At the first stage the value $s_{i,j}$ was calculated as:

$$s_{i,j} = \frac{1}{9} \sum_{k=-1}^{k=1} (\text{pf}1_{i+k} + \text{pf}2_{i+k} + \text{pf}3_{i+k})$$

where $s_{i,j}$ is a two-dimensional (3×3) moving average of voltages of echo signals around the point with i, j indices, and $\text{pf}1$ = value of previous echo profile, $\text{pf}2$ = value of present echo profile, $\text{pf}3$ = value of next profile.

Echoes were classified as aggregated if the following conditions were fulfilled:

1. the $s_{i,j}$ values were larger than the thresholds $\text{pg}1$ and $\text{pg}2$ (Mehlum *et al.* 1996).
2. the minimum number of samples surrounding the $u_{i,j}$ sample (among 8 surrounding samples) higher than $\text{pg}2$ equalled 5.

Otherwise, the echoes were classified as dispersed. The first condition used the fact that the level of echo from an aggregated patch was usually higher than the echoes from dispersed targets; the second and third conditions that a patch of aggregated targets could be emersed in a layer of dispersed targets.