

Foraging in a fractal environment: Spatial patterns in a marine predator-prey system

Robert W. Russell¹, George L. Hunt, Jr.^{1,*}, Kenneth O. Coyle² and R. Ted Cooney²

¹*Department of Ecology and Evolutionary Biology, University of California, Irvine, California 92717, USA;* ²*Institute of Marine Science, University of Alaska, Fairbanks, Alaska 99775-1080, USA*

Keywords: fractal dimension, spatial correlation, predators, consumers, resources, seabirds, zooplankton, foraging, animal movements

Abstract

Spatial relationships between predators and prey have important implications for landscape processes and patterns. Highly mobile oceanic birds and their patchily distributed prey constitute an accessible model system for studying these relationships. High-frequency echosounders can be used together with simultaneous direct visual observations to quantitatively describe the distributions of seabird consumers and their resources over a wide range of spatial scales, yielding information which is rarely available in terrestrial systems.

Recent fine-scale investigations which have used acoustics to study the distribution of foraging marine birds have reported weak or ephemeral spatial associations between the birds and their prey. These results are inconsistent with predictions of optimal foraging, but several considerations suggest that traditional foraging models do not adequately describe resource acquisition in marine environments. Relative to their terrestrial counterparts, oceanic 'landscapes' are structurally very simple, but they generally lack visual cues about resource availability.

An emerging view assumes that perceptually constrained organisms searching for food in multiscale environments should respond to patterns of resource abundance over a continuum of scales. We explore fractal geometry as a possible tool for quantifying this view and for describing spatial dispersion patterns that result from foraging behavior. Data on an Alaskan seabird (least auklet [*Aethia pusilla*]) and its zooplanktonic food resources suggest that fractal approaches can yield new ecological insights into complex spatial patterns deriving from animal movements.

1. Introduction

The landscape ecological perspective focuses on interactions between spatial patterns and the ecological processes influencing and influenced by patterns at different scales (Risser *et al.* 1984; Risser 1987). Predator-prey interactions constitute an important class of such ecological processes because: 1) most organisms live in environments where food resources are distributed heterogeneously (Wiens

1976); 2) the distribution of resources influences the movement of consumers across landscapes (Smith 1974; O'Neill *et al.* 1988); and 3) the spatial configuration of prey utilization by predators has important consequences for the dynamics of nutrient and energy fluxes in ecosystems (Wiens *et al.* 1985; Schneider *et al.* 1987). Unfortunately, empirical investigations of predator-prey interactions over a broad range of scales have been limited by obvious logistical and methodological difficulties.

* Author to whom reprint requests should be addressed

Strictly defined, landscape ecology is concerned with land areas; however, its principles and concepts apply equally to aquatic and terrestrial environments (Forman and Godron 1986). The ocean can be viewed as a 'landscape' in the sense that it can be described by patterns with different temporal and spatial scales (Haury *et al.* 1978; Steele 1989). Oceanic birds and their marine prey constitute an excellent model system for examining the interplay between resource distribution, foraging behavior, and trophic exchange. Seabirds are highly mobile, fly at speeds faster than dispersal rates of their prey, and can theoretically respond quickly to spatial variations in prey distribution. Despite its outwardly 'minimalist' appearance, the ocean is an exceptionally heterogeneous environment (*e.g.*, Steele 1976; Haury *et al.* 1978; Hunt and Schneider 1987; Hunt 1990; Nero *et al.* 1990), and marine resources such as plankton exhibit patchiness over a continuum of scales (Platt 1972; Mackas and Boyd 1979; Mackas *et al.* 1985). Unlike terrestrial environments, where complex landscape structure may be an important constraint on movement (*e.g.*, rock piles, dense vegetation, mountains, bodies of water), the oceanic environments of seabirds are vast and open; consequently, the movements of foraging seabirds are potentially directly reflective of their assessment of spatial variation in resource abundance or availability.

Efforts to understand interactions between higher trophic-level organisms and their resources usually focus on habitat selection. If resource exploitation is the primary function of habitat selection, then the spatial distribution of a predator should follow the dispersion of its prey at fine spatial scales (Morris 1987). On the other hand, if habitat selection serves other purposes, or if perceptual constraints prohibit accurate resource assessment, then the distribution of predators may or may not reflect that of their prey.

Patterns of spatial distribution of many marine organisms exhibit variation over a wide range of scales (Haury *et al.* 1978; Schneider and Duffy 1985; Hunt and Schneider 1987; Pinckney and Sandulli 1990; Rose and Leggett 1990), and research offers frequently focus on finding a 'characteristic scale' at which predator-prey correlations are maximized (*e.g.*, Schneider and Piatt 1986; Heinemann

et al. 1989; Erikstad *et al.* 1990; Piatt 1990). This approach may partly reflect the prevalence of an optimization paradigm in ecology (Cody 1974; Maynard Smith 1978; Gould and Lewontin 1979; Krebs and McCleery 1984; Rapport 1991), but it neglects important realities of marine and other environments.

In this paper we begin to explore an emerging perspective which explicitly acknowledges the multiscale patchiness characterizing most ecological systems (Senft *et al.* 1987; Kotliar and Wiens 1990). We examine the possible use of fractal geometry for analyzing spatial dispersion patterns of marine birds, and argue for the use of the fractal dimension as a descriptor of spatial distribution. Examples are provided from case studies of planktivorous seabirds in the northern Bering Sea. Further development of the approaches advocated here could yield many new insights into spatial dispersion patterns which result from complex animal movements.

2. A brief overview of seabird ecology

2.1. The marine distribution of seabirds

Numerous studies have shown that the marine distribution of seabirds is closely related to physical oceanographic structure over intermediate to broad spatial scales (Shuntov 1974; Pocklington 1979; Brown 1980; Griffiths *et al.* 1982; Hunt and Schneider 1987; Veit 1988). Different species assemblages are often associated with adjacent water masses, suggesting that seabirds are able to respond to subtle differences in their marine habitat (Hunt *et al.* 1990b). However, in some cases, associations between seabirds and physical factors have been lacking (Abrams and Griffiths 1981).

More recently, interest has shifted to biological structure. Acoustic technology (Barraclough *et al.* 1969; Andersen and Zahuranec 1977; Pieper 1983; Pieper and Holliday 1984; Pieper *et al.* 1990) has allowed marine ecologists to combine quantification of plankton and fish prey populations with simultaneous shipboard observations of birds. The resulting data sets provide continuous records of both consumer and resource distributions, a situation unavailable in most terrestrial systems.

Recent fine-scale (< 5 km) investigations employing this technology to study the foraging distribution of planktivorous seabirds have typically reported weak or ephemeral associations with their prey (Woodby 1984; Obst 1985; Heinemann *et al.* 1989; Hunt *et al.* 1990a; but see McClatchie *et al.* 1989). In contrast, studies and analyses conducted at larger scales (Jespersen 1930; Bailey 1966; Heinemann *et al.* 1989; Ryan and Cooper 1989; Hunt *et al.* 1990a) and studies of piscivorous birds (Schneider and Piatt 1986; Safina and Burger 1988; Erikstad *et al.* 1990; Piatt 1990) and fish (Rose and Leggett 1990) have frequently documented stronger correlations. These observations have led some workers to hypothesize that it may not be energetically efficient for some planktivores to seek out the most dense prey patches in areas of high overall prey abundance (Woodby 1984; Hunt *et al.* 1990a), and that planktivores may select their foraging habitat in a coarse-grained fashion, primarily on the basis of physical oceanographic features presumed to enhance prey accessibility (Hunt *et al.* 1990a).

2.2. Relationship to optimal foraging theory

The seemingly weak spatial relationship between planktivorous seabirds and their prey is inconsistent with relevant foraging models which generalize the concept of 'ideal free distribution' (Fretwell and Lucas 1970) to environments where resource distributions are continuous but arbitrary. These models predict strong correlations above some threshold prey density, irrespective of basal metabolic costs, searching costs, handling costs, locomotion costs, or the need to return to a central place (Arditi and Dacorogna 1985, 1987, 1988). This discrepancy between theory and observations suggests either that seabirds do not forage optimally or that these models do not adequately describe foraging behavior in the marine environment.

While the optimal foraging models yield specific predictions about the spatial distribution of optimal foragers, we believe that they ignore important aspects of resource acquisition in marine and other environments. Patchiness is an important

characteristic of most ecological systems (Wiens 1976). However, the behavioral response of an animal to patchy resources depends on the scale at which patches occur, the richness of the patches, and the animal's mobility relative to the persistence of the patches (Morse and Fritz 1982). These factors are not generally incorporated into traditional optimal foraging models, which generate predictions about resource acquisition in single-scale or scale-insensitive environments.

High prey densities are, at times, associated with certain physical features of the ocean, such as hydrographic fronts (see reviews in Hunt and Schneider 1987, Hunt 1990). However, patterns of attendance by seabirds at features such as fronts can be quite variable (reviewed by Schneider 1990a). While such features are sometimes visible to a bird flying over the ocean's surface (*e.g.*, Brown 1980; Briggs *et al.* 1984; Hunt and Harrison 1990), there are frequently no obvious surface clues to the presence of either the subsurface physical structure or the associated prey patch, and marine predators are not omniscient (Obst 1985). Thus, it seems likely that a foraging seabird may perceive much of its environment to be, *a priori*, essentially uniform (*cf.* McNamara 1982); only after it has sampled an area or observed the behavior of other foraging animals can *a posteriori* decision rules be implemented.

3. An alternative view

3.1. Fractal geometry

A relatively new tool for the analysis of multiscale spatial structure in natural systems is fractal geometry (Mandelbrot 1982). Fractal geometry is an appropriate framework for analyzing dispersion patterns of seabirds and their prey because these patterns are predicted (and observed) to exhibit variation over a continuum of scales. The fractal dimension has been described as 'a useful indicator of the complexity of autocorrelations over many scales for natural phenomena' (Burrough 1981, p. 242). A fractal is technically defined as a series in which the Hausdorff-Besicovitch (fractal) dimen-

sion (D) exceeds the topological dimension (D_t) (Mandelbrot 1982). In non-technical terms, fractals are temporal or spatial phenomena which have detail at all scales, and which show partial correlations over many scales (Burrough 1981; Palmer 1988). A graph of an environmental variable such as bird density plotted as a function of distance along a transect may be linear ($D = D_t = 1$), implying strict spatial dependence; it may be highly erratic, with the entire plane filled with points ('white noise'; $D = 2$); or it may fall somewhere in between ($1 < D < 2$) (Palmer 1988). Phenomena with fractal geometries fall into the latter category.

3.2. 'Behavioral cascades'

Keeping in mind the constraints discussed in section 2.1, we may explore an alternative view of the foraging behavior of marine predators. At horizontal scales ranging from 10 m to 20 km (depending in part on the kinetic energy level of the environment), turbulent diffusion is an important determinant of the spatial distribution of phytoplankton (Platt 1972; Denman and Platt 1976; Legendre and Demers 1984; Mackas *et al.* 1985), and consequently should influence the movements and dispersion of organisms which exploit phytoplankton (Frontier 1987). The geometry of turbulence is fractal; that is, turbulence consists of eddies which dissipate continuously into smaller ones, down to the scale of viscosity (Mandelbrot 1982; Frontier 1987). As a consequence, patchiness in the distribution of plankton is not discrete but continuous (Frontier 1987); variation occurs at many spatial scales, and the definition of a patch is therefore ambiguous (Wiens 1976; Kotliar and Wiens 1990).

It seems intuitively reasonable to assume that consumers, foraging under information constraints on continuously distributed resources such as plankton, should themselves employ a multiscale search strategy. Initially, a marine bird may broadly explore a large area where food is known to be particularly abundant or accessible (Hunt and Harrison 1990; Hunt *et al.* 1990a). Within that broad-scale search area, the individual can search for flocks of conspecifics or other predators that might

signal the presence of food (*e.g.*, Ryder 1957; Hoffman *et al.* 1981; Evans 1982; Ridoux 1987; Hunt *et al.* 1988; Obst and Hunt 1990; Au 1991; Harrison *et al.* 1991). When prey are eventually located, the probability of finding more prey in the immediate vicinity is thereby increased (by definition of a patchy distribution), and the broad exploratory strategy should be replaced by more specific searching behaviors at a smaller spatial scale (Smith 1974; Frontier 1987; Kareiva and Odell 1987). Frontier (1987) conjectured that such a strategy should result in a cascade of levels of behavior occurring in response to the fractal pattern of the prey distribution. Under this hypothesis, the spatial dependence of foraging behavior is successively transferred to smaller scales during a foraging bout in conformance with scaling patterns of the resource. We suggest that if such 'behavioral cascades' accurately describe the responses of individual predators to prey distribution across a wide range of scales, then an ensemble of such predators should collectively exhibit a spatial distribution with a fractal dimension that is correlated to the fractal dimension of the prey distribution. We also hypothesize that the subtle patterns of spatial association that are likely to result from such behavioral cascades may elude detection by simple correlational analyses, since predator and prey distributions would be expected to match spatially only in an asymptotic sense.

4. Methods

4.1. Observations at sea

We studied the foraging ecology of the planktivorous least auklet (*Aethia pusilla*), one of the most abundant Alaskan seabirds (Sowls *et al.* 1978). During 1985–1986 we conducted shipboard transects of the Chirikov Basin in the northern Bering Sea, near islands where these birds breed (Hunt *et al.* 1990a; Hunt and Harrison 1990). The oceanography of the region and its influence on breeding auklets is described in detail elsewhere (Springer and Roseneau 1985; Springer *et al.* 1987; Hunt and Harrison 1990; Hunt *et al.* 1990). Here, we employ correlational and fractal techniques to

Table 1. Description of the transect data used in analyses

Transect name	Date (m/d/y)	Starting point	Direction	Length (km)	Minimum sampling interval (km)	Total auklets observed
KING8	8/1/85	64.97°N 169.79°W	E	74	0.4	465
LRNC1	8/7/85	63.71°N 170.15°W	N	41	0.4	510
LRNC2	8/8/85	63.70°N 170.14°W	NE	74	0.4	822
LRNC5	8/10/85	63.70°N 170.14°W	N	74	0.4	3039
KONE1	8/14/86	64.17°N 169.07°W	SW	31	0.2	3610
KNGD1	8/16/86	64.96°N 168.10°W	W	74	0.2	1241

examine spatial patterns of association between auklets and their acoustically measured food resources, using data from six transects near King and St. Lawrence Islands (Table 1). These transects constitute a sample from a larger data set, and were selected for analysis on the basis of the quality and lengths of the acoustic records.

Auklet dispersion was assessed from a moving vessel by shipboard observers who counted foraging birds continuously within an arc from 300 m ahead of the vessel to 90° off the beam. Data were entered directly into a handheld microcomputer to the nearest 0.1 minute to facilitate comparisons between birds and acoustic survey data. Only birds observed sitting on the water are included in analyses, since birds in flight were probably commuting between foraging areas.

We measured the distribution of the biomass of the large calanoid copepods on which the auklets feed using a Biosonics™ Model 101 echosounder (200 kHz) and echointegrator with the transducer towed beside the ship at about 6 knots (11 km hr⁻¹). Subsurface interactions between the acoustic beam and planktonic biomass result in backscattered sound waves; the amount and characteristics of the backscattering depend on the volume and size distribution of material in the water column. Vertical net tows indicated that the copepod *Neocalanus plumchrus*, the auklets' preferred prey (Hunt and Harrison 1990), was the dominant zooplankton in our study area, suggesting that most of the acoustic scattering was due to its presence. Horizontal profiles of the acoustic data indicated that most of the prey biomass was concentrated at or above the thermocline (ca. 10–15 m below the surface; Hunt *et al.* 1990a). We therefore

integrated measures of acoustic scattering vertically between 7 m below the surface (the minimum possible due to interference from air bubbles entrained near the surface) and 15 m below the surface. Each integration sequence covered either 0.1 or 0.2 nautical miles (ca. 0.2/0.4 km) of transect. Possible sources of error in our acoustic sampling methods are discussed extensively by Hunt *et al.* (1990a).

We did not attempt to convert acoustic survey data (units = -dB) to estimates of actual biomass, due to uncertainties about the exact relationship between target strength and body size. Thus, the data used in these analyses should be interpreted as relative indices of total zooplanktonic biomass. For simplicity of presentation, we will hereafter use the term 'prey' in reference to the acoustic scattering data.

4.2. Fractal analysis

We used a method (Burrough 1981; Phillips 1985; Palmer 1988) based on geostatistics and regionalized variable (RV) theory (Journel and Huijbregts 1978) to calculate fractal dimensions of bird and prey distributions for each of the six transects. RVs are continuous spatial variables whose variation is too complex to be described by traditional mathematical functions (Phillips 1985). Their spatial variation is 'deterministic in the sense that nearby samples will have similar values, but stochastic in that the value at a given point cannot be precisely calculated from neighboring samples' (Phillips 1985, p. 97).

Geostatistical methods (Journel and Huijbregts 1978) are used for analyzing patterns of variation in

RVs. The semivariance $V(h)$ of an RV at a scale of h distance units is defined as half of the variance of increments (*i.e.*, the expected squared difference of the value of the function) h units apart:

$$V(h) = 1/2 E[(W(x) - W(x+h))^2] \quad (1)$$

where x represents the straight-line distance along a transect and $W(x)$ is the value of the RV at point x . The semivariance is an estimator of the average rate of change of an RV over a given distance (Phillips 1985). If second-order stationarity is a reasonable assumption, then semivariance is closely related to autocorrelation, and each may be computed from the other; however, semivariance is less sensitive to nonstationarity than autocorrelation (since it is calculated from differences between observations), and is therefore more versatile in many applications (Phillips 1985).

A plot of semivariance on the vertical axis against distance between pairs of samples on the horizontal axis is called a semivariogram. Because the semivariance has, under certain conditions, the form of a fractal function that scales with h^{4-2D} at the origin (Berry and Lewis 1980), the fractal dimension D of $W(x)$ can be estimated from the slope m of a log-log plot of the semivariogram of $W(x)$ (Burrough 1981):

$$D = (4 - m)/2 \quad (h \neq 0). \quad (2)$$

If the fractal dimension is scale-dependent, the log-log semivariogram is nonlinear and m is not constant. For more detailed discussions of geostatistics, the relationships between semivariograms and fractals, and other applications of fractals in ecology, the reader is referred to Journel and Huijbregts (1978), Burrough (1983a,b), and Sugihara and May (1990), respectively.

We estimated fractal dimensions of bird and prey distributions using simple least squares regression and equations (1) and (2). Because semivariograms tend to deteriorate with increasing spatial lag, an objective criterion is needed for deciding upon an appropriate range of h to include in the regressions. We simply used the values of h which maximized the coefficients of determination (r^2) of the regressions. This method yields a minimum range of spatial lags over which fractal scaling applies. How-

ever, it does not allow us to address possible transitions in pattern at scales broader than this minimum range.

5. Results

5.1. Spatial distributions of auklets and their prey

The distributions of auklets and their prey along each transect are shown in Fig. 1. On four of the transects, very few birds were present along one or both ends of the transect, probably because the birds flew over areas where preferred prey were absent or where lack of vertical stratification in the water column reduced the availability of the prey (Hunt *et al.* 1990a; Hunt and Harrison 1990). For three of these transects (KINGS, KNGD1, LRNC1), we only consider data from a segment of the transect that includes 95 percent of all birds observed, thereby focusing on the marine habitat of the auklets (*i.e.*, the portion of transect where both auklets and appropriate prey, as judged from the behavior of the auklets, were present). In the fourth case (KONE1), bird distribution was sharply demarcated (Fig. 1), so we simply focus on data from that portion of the transect where birds were present.

5.2. Spatial correlations between auklets and their prey

Correlations between the abundances of auklets and their prey were weak or negative at the most finely resolved spatial scale in all six transects (Fig. 2). Consistent with previous studies (Schneider and Piatt 1986; Heinemann *et al.* 1989; Erikstad *et al.* 1990; Hunt *et al.* 1990a; Piatt 1990; Rose and Leggett 1990), the spatial correlation between predators and prey depended upon the scale at which data analysis was carried out (Fig. 2). This widespread observation has been interpreted as evidence that seabirds select foraging habitat in a coarse-grained fashion, and are not good at identifying the highest-density prey patches at small spatial scales (Heinemann *et al.* 1989; Hunt *et al.* 1990a). How-

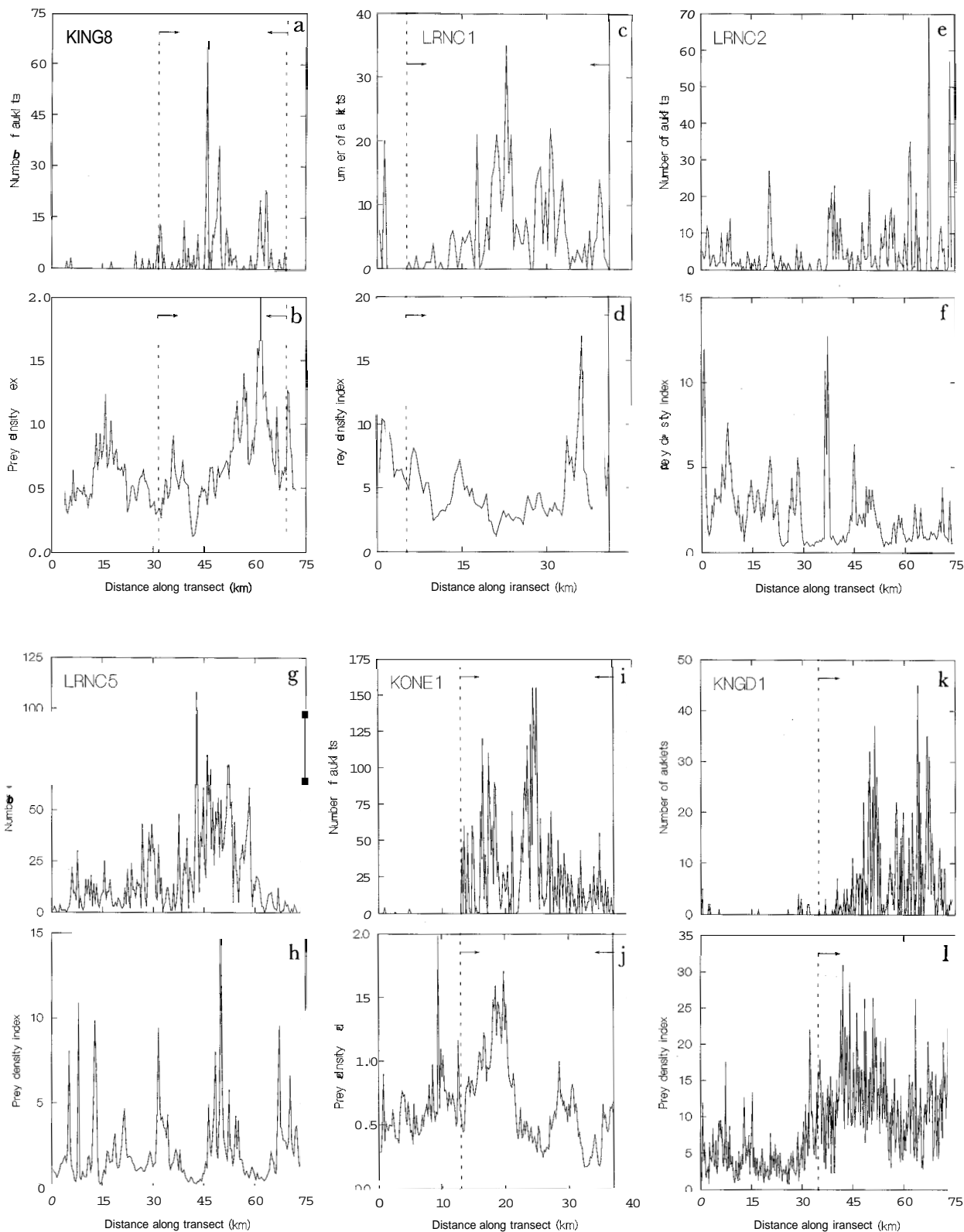


Fig. 1. The distribution of auklets (above) and their prey (below) along each transect. Arrows and vertical lines demarcate the ranges of transect data used in analyses. Solid vertical lines show where a transect ended; dotted lines indicate boundaries enclosing 95% of bird abundance (see section 5.1 for more details).

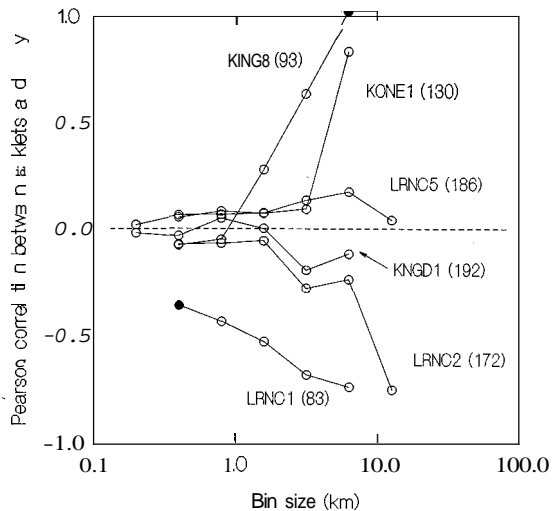


Fig. 2. Scale-dependence of the spatial correlation between auklets and their prey across the six transects. The scale on the horizontal axis reflects the distance over which data were lumped for analysis. Correlations were computed with data at the most finely resolved spatial scale, then adjacent bins of data were combined into double-sized bins and correlations were recomputed, then adjacent double-sized bins of data were combined into quadruple-sized bins and correlations were recomputed, etc. Sample sizes for correlations computed at the finest scale are shown; sample sizes for broader-scale correlations are successively halved. For comparative purposes, statistically significant correlations (adjusted for a type I family-wide error rate of $p = 0.05$) are indicated on the figure by filled circles. Note, however, that statistical significance is likely to be inflated by the lack of independence in spatially dependent data, so 'significance' should be interpreted cautiously.

ever, on some of our transects there were negative correlations (Fig. 2). Furthermore, intensification of correlations with increasing scale, irrespective of the sign of the correlation, suggests that factors in addition to 'coarse-grained habitat selection' are probably implicated.

5.3. Fractal dimensions of auklet and prey distributions

Semivariograms for bird and prey distributions together with the best-fitting lines are shown in Fig. 3. In most instances, linearity is evident as the spatial lag increases up to about 10 km. Beyond 10 km, semivariograms tend to deteriorate as the lag increases because the number of point pairs de-

creases. Coefficients of determination ranged between 0.668 and 0.999 for zooplankton, and between 0.781 and 0.902 for auklets (except in one anomalous case of a nearly flat semivariogram where r^2 was 0.319; see LRNC2 in Fig. 3).

The mean fractal dimension of auklet distributions was $1.90 (\pm 0.02 \text{ SE}, N = 6)$, and the mean of prey distributions was $1.82 (\pm 0.05 \text{ SE}, N = 6)$. Although the range of observed fractal dimensions was quite small, especially in the case of the auklets, Fig. 4 shows that fractal dimensions of bird and prey distributions tended to be positively correlated across the six transects. The regression is not statistically significant when all six data points are included ($r^2 = 0.126, p = 0.490$), but is significant when the transect with the flat semivariogram (LRNC2) is excluded ($Y = 1.59 + 0.17 * X, r^2 = 0.78, F = 10.76, p = 0.046$).

6. Discussion

6.1. Fractal dimensions of predator and prey distributions

As discussed earlier, previous analyses of seabird dispersion have typically focused on discovering a characteristic scale of patchiness (e.g., Schneider and Duffy 1985; Schneider 1990b; Schneider *et al.* 1990) or characteristic scale of correlation between seabirds and prey resources (e.g., Schneider and Piatt 1986; Heinemann *et al.* 1989; Hunt *et al.* 1990a; Piatt 1990; Hunt *et al.* MS). Implicit in this approach is an assumption that predator-prey correlations are noisy at smaller scales due to failure of predators to find all small-scale prey patches, but that these matching errors should diminish at larger scales, as reflected in higher correlations and aggregation intensity. In contrast, the behavioral cascade perspective deemphasizes the ecological significance of matching errors, and focuses instead on understanding how individual search strategies might be translated into predator dispersion patterns via the autocorrelation structure of the environment.

Although no obvious pattern of direct correlation between predator and prey densities emerged

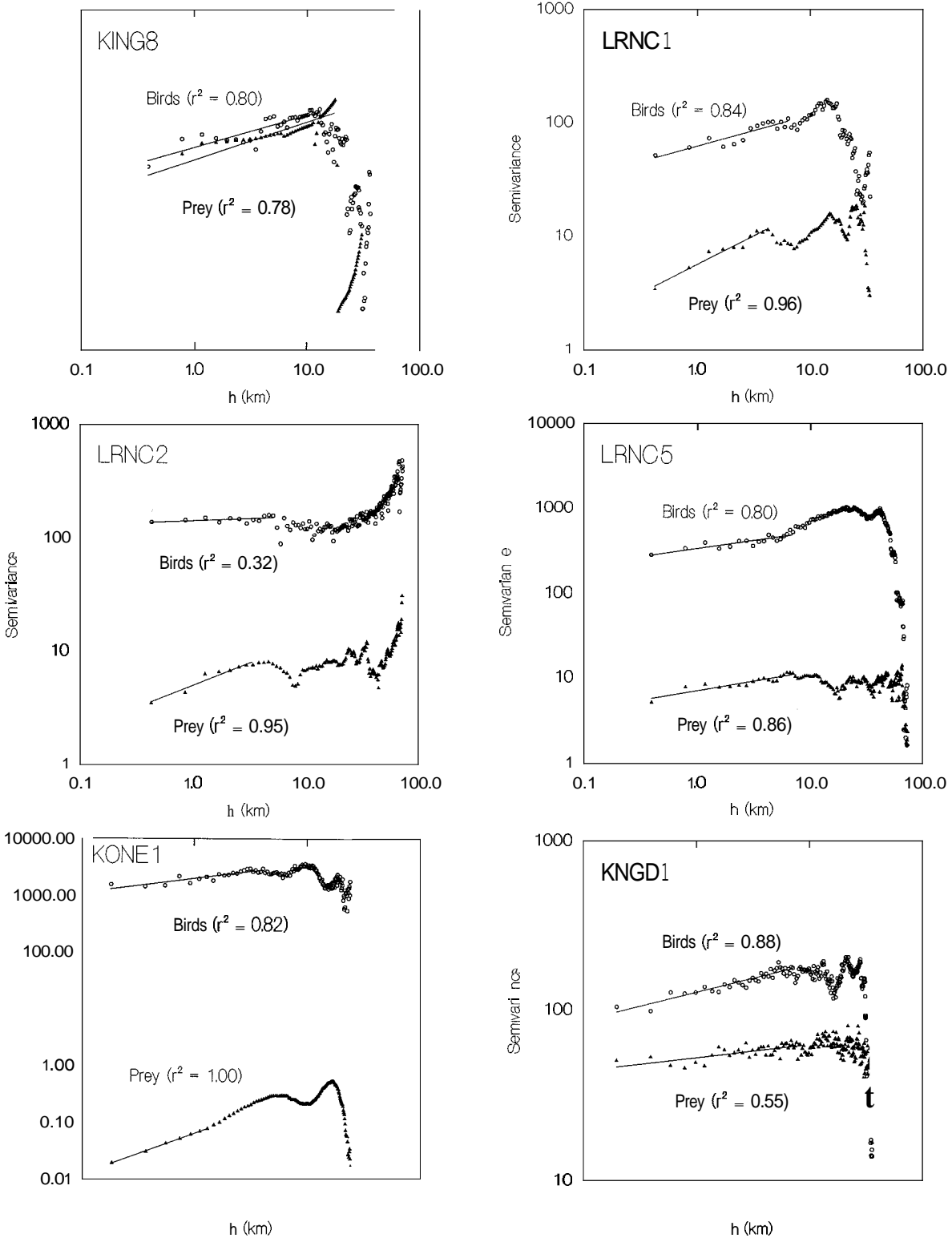


Fig. 3. Semivariograms for bird and prey distributions along each transect. Best-fitting lines with r^2 values are shown (see section 4.2 for details).

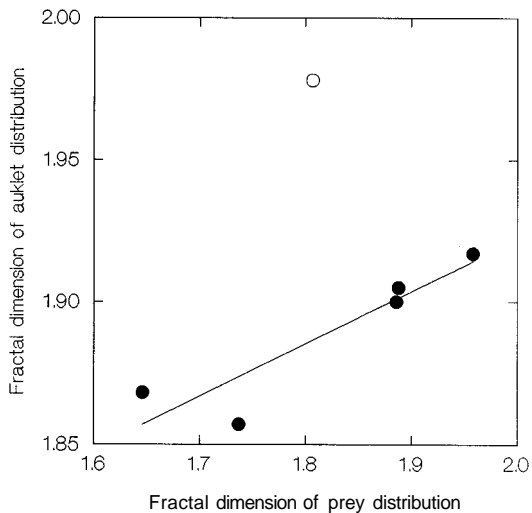


Fig. 4. The relationship between fractal dimensions of auklet and prey distributions across the six transects. The regression through all six points is not statistically significant. Exclusion of the weakly determined data point associated with the flat semi-variogram (indicated on the figure by an open circle) yields a significant regression (see text for statistics).

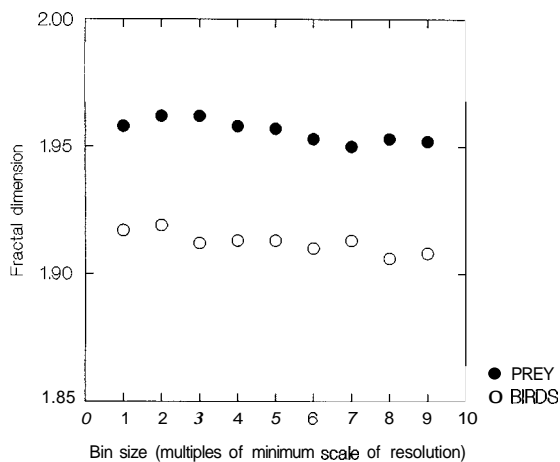


Fig. 5. Example of the apparent self-similarity of the horizontal distributions of both auklets and zooplankton biomass over a range of fine scales. These data are from transect KNGD1. Note that the vertical scale here is the same as in Fig. 4.

in our analyses, there was some evidence of a relationship between fractal dimensions of their spatial distributions. This observation suggests, albeit indirectly, that the birds did respond directly to variation in the spatial dependence of prey resources within their marine habitat, and supports the hypo-

thesis that important trophic linkages may not always be manifested in strong predator-prey correlations.

Pinckney and Sandulli (1990) obtained similar results in an analysis of meiofaunal and microalgal populations on an intertidal sandflat. Although they found no correlation between meiofaunal abundance and microalgal biomass, the two groups nonetheless showed similar spatial patterns as revealed by autocorrelation analyses. These findings were interpreted as evidence of a common scale linkage between the two groups.

We repeated our fractal analyses with the data grouped into bins of increasingly larger size. This kind of data aggregation essentially increases the observational scale of our study, but in retrospect. These analyses showed that fractal dimensions were relatively constant (e.g., Fig. 5), indicating that spatial patterns of auklet and zooplankton distributions were nearly scale-invariant over the range of relatively fine scales examined here.

If the fractal dimension is not a constant function of scale, however, then the pattern it describes is not scale-invariant. For instance, in Fig. 3, there are apparent changes in the slopes of several semivariograms at lags of 5–10 km that suggest changes in autocorrelation structure. Under these circumstances, interpretations of spatial variation at one scale cannot necessarily be extrapolated to other scales (Palmer 1988). Some authors have argued that it is these departures from self-similarity, rather than the precise numerical values of the fractal dimension, which may prove to be of most interest to ecologists, because such departures indicate variation in the sources of biological pattern (Bradbury *et al.* 1984). More specifically, abrupt changes in fractal dimension when shifting between scales may demarcate transition zones separating scale ranges dominated by different processes (Mandelbrot 1982), where the environmental properties or constraints acting upon organisms are probably changing rapidly (Frontier 1987). For example, Denman and Platt (1976) predicted, on a theoretical basis, that phytoplankton variability should exhibit a spectral discontinuity at a scale of between 0.2 and 20 km. This critical range represents the scale where the importance of biological

processes (*e.g.*, reproduction) is expected to overcome that of purely physical processes (*i.e.*, turbulent diffusion) in the determination of phytoplankton patchiness. Data from several transects supported these predictions, exhibiting apparent discontinuities at scales of about 0.5 km (Denman and Platt 1976).

6.2. *Advantages of the fractal approach*

The fractal dimension appears to be a useful measure of spatial complexity (Phillips 1985), and provides several advantages over other descriptive indices of ecological patchiness. It is becoming increasingly apparent that more traditional, widely used mathematical descriptors, such as the variance-to-mean ratio, have little meaning in a multiscale spatial context (Palmer 1988; Hurlbert 1990). Furthermore, spatial dependence frequently prohibits rigorous statistical analyses of ecological data, and inference based on autocorrelated observations is risky (Bivand 1980).

Whereas statistical techniques such as analysis of variance (ANOVA) aim to discriminate between sources of variation, the primary goal of fractal analysis and similar techniques such as spectral analysis is to describe variation. Fractal geometry has been usefully applied to a wide variety of problems involving complex patterns in nature, including terrestrial (Burrough 1981) and Martian (Woronow 1981) landscapes, cloud shapes (Lovejoy 1982), taxonomic hierarchies (Burlando 1990), and distributions of nesting bald eagles in rugged landscapes (Pennycuick and Kline 1986). Patterns such as these are generated by the collective operation of a variety of processes at many spatial scales and levels of organization. As a measure of pattern, the fractal dimension has the theoretical advantage that it describes variability at many scales jointly (Hengeveld 1990), and the conceptual advantage that it is relatively easily interpretable in terms of autocorrelation structure.

Although it is difficult or impossible to deduce the biological processes underlying observed spatial patterns from the study of pattern alone (Cale *et al.* 1989; but see Margalef 1985), analysis of pattern

can be valuable in formulating process-oriented hypotheses. Fractal analysis can provide useful information on the spatial configuration of process-pattern interactions (*e.g.*, Krummel *et al.* 1987). Resolution of the scales over which different environmental components are associated is an essential prerequisite for disentangling the factors responsible for spatial heterogeneity in ecological systems (Pieper *et al.* 1990).

Possible sources of bias in the estimation of fractal dimensions must also be considered in attempts to understand what the fractal dimensions actually mean. In this paper we have attempted to estimate and interpret fractal dimensions of the spatial distributions of marine birds and their food resources. We have suggested that variation in fractal dimensions may tell us something about variation in patterns of animal movement that occur in response to different 'landscapes'. In the auklet study, movements of both prey and foraging birds occurred throughout the course of the transects, so that spatial and temporal components of variation in the distributions are inextricably confounded in our data. This confounding of space and time in the 'spatial' coordinates used in the construction of semivariograms (Fig. 3) might be an important source of error in the dimensions we calculated. To date, most studies using fractal approaches have focused on phenomena which are temporally invariant over the time scale of the study (*e.g.*, vegetation patterns, geological formations), and we are not aware of any attempts to document the extent to which temporal changes can affect spatial analyses of fractal structure. Such efforts would clearly be desirable in the future.

6.3. *Conclusions and future directions*

We have shown that spatial patterns of a marine predator and its planktonic prey at scales of up to about 10 km can be described by fractal dimensions. Furthermore, fractal dimensions of predator and prey distributions tended to be correlated, even though there was no consistent pattern of correlation between predator and prey densities within transects. Under many circumstances, it may be

difficult to infer trophic relations from simple correlational analyses of abundance data (see also Pinckney and Sandulli 1990). We suggest that it may be profitable to further investigate the use of fractal geometry as an additional technique for analyzing spatial distributions and relationships deriving from resource acquisition.

More specific interpretations of the patterns we have observed must await the development of a more rigorous theoretical foundation, and our empirical findings should be considered tentative pending replication in other systems. However, the habitats and resources of many organisms have fractal geometries (Morse *et al.* 1985; Frontier 1987; Wiens and Milne 1989; Hegde *et al.* 1991; Scheuring 1991; Williamson and Lawton 1991; Milne 1992), and the ideas presented here can serve as a starting point for posing and testing hypotheses about foraging behavior and animal movements in such complex multiscale environments. Translation of the idea of 'behavioral cascades' from verbal into mathematical statements will facilitate the construction of models, and comparisons of organismal distribution across an array of fractal environments will allow more meaningful generalizations. In the future, the fundamental and important differences between marine and terrestrial ecological systems (*e.g.*, Steele 1985) will need to be addressed.

Acknowledgements

We thank the many co-workers who helped gather the bird and plankton data, and the Captain and crew of the R.V. *Alpha Helix* for facilitating our research at sea. Members of the MacHunt reading group provided useful critical discussion. We are grateful to Bruce Milne, David Schneider, and an anonymous reviewer for providing very helpful reviews of earlier drafts of the paper. Financial support for the project was provided by a grant (DPP-8308232) to G.L. Hunt from the National Science Foundation (Division of Polar Programs).

References

- Abrams, R.W. and Griffiths, A.M. 1981. Ecological structure of the pelagic seabird community in the Benguela Current region. *Mar. Ecol. Prog. Ser.* 5: 269–277.
- Andersen, N.R. and Zahuranec, B.J. (eds.). 1977. *Oceanic Sound Scattering Prediction*. Plenum Press, New York.
- Arditi, R. and Dacorogna, B. 1985. Optimal foraging in non-patchy habitats. I. Bounded one-dimensional resource. *Math. Biosci.* 76: 127–145.
- Arditi, R. and Dacorogna, B. 1987. Optimal foraging in non-patchy habitats. II. Unbounded one-dimensional habitat. *SIAM J. Appl. Math.* 47: 800–821.
- Arditi, R. and Dacorogna, B. 1988. Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am. Nat.* 131: 837–846.
- Au, D.W. 1991. Polyspecific nature of tuna schools: shark, dolphin, and seabird associates. *Fishery Bull. U.S.* 89: 343–354.
- Bailey, R. 1966. The sea-birds of the southeast coast of Arabia. *Ibis* 108: 224–264.
- Barracough, W.E., LeBrasseur, R.J. and Kennedy, O.D. 1969. Shallow scattering layer in the subarctic Pacific Ocean: detection by high-frequency echo sounder. *Science* 166: 611–613.
- Berry, M.V. and Lewis, Z.V. 1980. On the Weierstrass-Mandelbrot fractal function. *Proc. R. Soc. Lond. A* 370: 459–484.
- Bivand, R. 1980. A Monte Carlo study of correlation coefficient estimation with spatially autocorrelated observations. *Quaestiones Geographicae* 6: 5–10.
- Bradbury, R.H., Reichelt, R.E. and Green, D.G. 1984. Fractals in ecology: methods and interpretation. *Mar. Ecol. Prog. Ser.* 14: 295–296.
- Briggs, K.T., Dettman, K.F., Lewis, D.B. and Tyler, W.B. 1984. Phalarope feeding in relation to autumn upwelling off California. *In* *Marine Birds: Their Feeding Ecology and Commercial Fisheries Relationships*. pp. 51–62. Edited by D.N. Nettleship, G.A. Sanger and P.F. Springer. Canadian Wildlife Service, Ottawa.
- Brown, R.G.B. 1980. Seabirds as marine animals. *In* *Behavior of Marine Animals*. Vol. 4: *Marine Birds*. pp. 1–39. Edited by J. Burger, B.L. Olla and H.E. Winn. Plenum Press, New York.
- Burlando, B. 1990. The fractal dimension of taxonomic systems. *J. theor. Biol.* 146: 99–114.
- Burrough, P.A. 1981. Fractal dimensions of landscapes and other environmental data. *Nature* 294: 240–242.
- Burrough, P.A. 1983a. Multiscale sources of spatial variation in soil. I. The application of fractal concepts to nested levels of soil variation. *J. Soil Sci.* 34: 577–597.
- Burrough, P.A. 1983b. Multiscale sources of spatial variation in soil. II. A non-Brownian fractal model and its application in soil survey. *J. Soil Sci.* 34: 599–620.
- Cale, W.G., Henebry, G.M. and Yeakley, J.A. 1989. Inferring process from pattern in natural communities. *BioScience* 39: 600–605.
- Cody, M.L. 1974. Optimization in ecology. *Science* 183: 1156–1164.

- Denman, K.L. and Platt, T. 1976. The variance spectrum of phytoplankton in a turbulent ocean. *J. Mar. Res.* 34: 593–601.
- Erikstad, K.E., Mowm, T. and Vader, W. 1990. Correlations between pelagic distribution of Common and Brunnich's Guillemots and their prey in the Barents Sea. *Polar Res.* 8: 77–87.
- Evans, P.G.H. 1982. Associations between seabirds and cetaceans: a review. *Mammal Rev.* 12: 187–206.
- Forman, R.T.T. and Godron, M. 1986. *Landscape Ecology*. John Wiley & Sons, New York.
- Fretwell, S.D. and Lucas, H.L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16–36.
- Frontier, S. 1987. Applications of fractal theory to ecology. *In* Developments in Numerical Ecology. pp. 335–378. Edited by P. Legendre and L. Legendre. Springer-Verlag, Berlin.
- Gould, S.J. and Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian Paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. B* 205: 581–598.
- Griffiths, A.M., Siegfried, W.R. and Abrams, R.W. 1982. Ecological structure of a pelagic seabird community in the southern ocean. *Polar Biol.* 1: 39–46.
- Harrison, N.M., Whitehouse, M.J., Heinemann, D., Prince, P.A., Hunt, G.L., Jr. and Veit, R.R. 1991. Observations of multispecies seabird flocks around South Georgia. *Auk* 108: 801–810.
- Haurly, L.R., McGowan, J.A. and Wiebe, P.H. 1978. Patterns and processes in the time-space scales of plankton distributions. *In* Spatial Pattern in Plankton Communities. pp. 277–327. Edited by J.H. Steele. Plenum Press, New York.
- Hegde, S.G., Lokesh, R., Ganeshiah, K.N. and Shaanker, R.U. 1991. Seed size distributions in plants: an explanation based on fractal geometry. *Oikos* 62: 100–101.
- Heinemann, D., Hunt, G. and Everson, I. 1989. Relationships between the distributions of marine avian predators and their prey, *Euphausia superba*, in Bransfield Strait and southern Drake Passage, Antarctica. *Mar. Ecol. Prog. Ser.* 58: 3–16.
- Hengeveld, R. 1990. *Dynamic Biogeography*. Cambridge Univ. Press, Cambridge.
- Hoffman, W., Heinemann, D. and Wiens, J.A. 1981. The ecology of seabird feeding flocks in Alaska. *Auk* 98: 437–456.
- Hunt, G.L., Jr. 1990. The pelagic distribution of marine birds in a heterogeneous environment. *Polar Res.* 8: 43–54.
- Hunt, G.L., Jr. and Harrison, N.M. 1990. Foraging habitat and prey taken by least auklets at King Island, Alaska. *Mar. Ecol. Prog. Ser.* 65: 141–150.
- Hunt, G.L., Jr., Harrison, N.M. and Cooney, R.T. 1990a. The influence of hydrographic structure and prey abundance on foraging of Least Auklets. *In* Auks at Sea. pp. 7–22. Edited by S.G. Sealy. Studies in Avian Biology No. 14.
- Hunt, G.L., Jr., Harrison, N.M., Hammer, W.M. and Obst, B.S. 1988. Observations of a mixed-species flock of birds foraging on euphausiids near St. Matthew Island, Bering Sea. *Auk* 105: 345–349.
- Hunt, G.L., Heinemann, D. and Everson, I. MS. The distributions and predator-prey interactions of Macaroni Penguins, Antarctic fur seals, and Antarctic krill near Bird Island, South Georgia. In review, *Mar. Ecol. Prog. Ser.*
- Hunt, G.L., Jr., Heinemann, D., Veit, R.R., Heywood, R.B. and Everson, I. 1990b. The distribution, abundance and community structure of marine birds in southern Drake Passage and Bransfield Strait, Antarctica. *Cont. Shelf Res.* 10: 243–257.
- Hunt, G.L., Jr. and Schneider, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. *In* Seabirds: Feeding Ecology and Role in Marine Ecosystems. pp. 7–41. Edited by J.P. Croxall. Cambridge Univ. Press, Cambridge.
- Hurlbert, S.H. 1990. Spatial distribution of the montane unicorn. *Oikos* 58: 257–271.
- Jespersen, P. 1930. Ornithological observations in the north Atlantic Ocean. *Oceanogr. Rep. Dana Exped.* 7: 1–36.
- Journel, A.G. and Huijbregts, C.J. 1978. *Mining Geostatistics*. Academic Press, London.
- Kareiva, P. and Odell, G. 1987. Swarms of predators exhibit 'prey-taxis' if individual predators use area-restricted search. *Am. Nat.* 130: 233–270.
- Kotliar, N.B. and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253–260.
- Krebs, J.R. and McCleery, R.H. 1984. Optimization in behavioural ecology. *In* Behavioural Ecology: An Evolutionary Approach. pp. 91–121. Sinauer Associates, Sunderland, Massachusetts.
- Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V. and Coleman, P.R. 1987. Landscape patterns in a disturbed environment. *Oikos* 48: 321–324.
- Legendre, L. and Demers, S. 1984. Towards dynamic biological oceanography and limnology. *Can. J. Fish. Aquat. Sci.* 41: 2–19.
- Lovejoy, S. 1982. Area-perimeter relation for rain and cloud areas. *Science* 216: 185–187.
- Mackas, D.L. and Boyd, C.M. 1979. Spectral analysis of zooplankton spatial heterogeneity. *Science* 204: 62–64.
- Mackas, D.L., Denman, K.L. and Abbott, M.R. 1985. Plankton patchiness: biology in the physical vernacular. *Bull. Mar. Sci.* 37: 652–674.
- McClatchie, S., Hutchinson, D. and Nordin, K. 1989. Aggregation of avian predators and zooplankton prey in Otago shelf waters, New Zealand. *J. Plankton Res.* 11: 361–374.
- McNamara, J. 1982. Optimal patch use in a stochastic environment. *Theor. Pop. Biol.* 21: 269–288.
- Mandelbrot, B.B. 1982. *The Fractal Geometry of Nature*. W.H. Freeman, San Francisco.
- Margalef, R. 1985. From hydrodynamic processes to structure (information) and from information to process. *In* Ecosystem Theory for Biological Oceanography. pp. 200–220. Edited by R.E. Ulanowicz and T. Platt. *Can. Bull. Fish. Aquat. Sci.* 213.
- Maynard Smith, J. 1978. Optimization theory in evolution. *Annu. Rev. Ecol. Syst.* 9: 31–56.
- Milne, B.T. 1992. Spatial aggregation and neutral models in fractal landscapes. *Am. Nat.* 139: 32–57.

- Morris, D.W. 1987. Ecological scale and habitat use. *Ecology* 68: 362–369.
- Morse, D.H. and Fritz, R.S. 1982. Experimental and observational studies of patch choice at different scales by the crab spider *Misumena vatia*. *Ecology* 63: 172–182.
- Morse, D.R., Lawton, J.H., Dodson, M.M. and Williamson, M.H. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. *Nature* 314: 731–733.
- Nero, R.W., Magnuson, J.J., Brandt, S.B., Stanton, T.K. and Jech, J.M. 1990. Finescale biological patchiness of 70 kHz acoustic scattering at the edge of the Gulf Stream – *EchoFront* 85. *Deep-sea Res.* 37: 999–1016.
- Obst, B.S. 1985. Densities of Antarctic seabirds at sea and the presence of the krill *Euphausia superba*. *Auk* 102: 540–549.
- Obst, B.S. and Hunt, G.L., Jr. 1990. Marine birds feed at gray whale mud plumes in the Bering Sea. *Auk* 107: 678–688.
- O'Neill, R.V., Milne, B.T., Turner, M.G. and Gardner, R.H. 1988. Resource utilization scales and landscape pattern. *Landscape Ecol.* 2: 63–69.
- Palmer, M.W. 1988. Fractal geometry: a tool for describing spatial patterns of plant communities. *Vegetatio* 75: 91–102.
- Pennycuik, C.J. and Kline, N.C. 1986. Units of measurement for fractal extent, applied to the coastal distribution of bald eagle nests in the Aleutian Islands, Alaska. *Oecologia* 68: 254–258.
- Phillips, J.D. 1985. Measuring complexity of environmental gradients. *Vegetatio* 64: 95–102.
- Piatt, J.F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *In Auks at Sea*. pp. 36–51. Edited by S.G. Sealy. *Studies in Avian Biology* No. 14.
- Pieper, R.E. 1983. Quantitative estimates of euphausiid biomass determined by high-frequency acoustics. *Biol. Oceanogr.* 2: 133–149.
- Pieper, R.E. and Holliday, D.V. 1984. Acoustic measurements of zooplankton distributions in the sea. *J. Cons. int. Explor. Mer* 41: 226–238.
- Pieper, R.E., Holliday, D.V. and Kleppel, G.S. 1990. Quantitative zooplankton distributions from multifrequency acoustics. *J. Plankton Res.* 12: 433–441.
- Pinckney, J. and Sandulli, R. 1990. Spatial autocorrelation analysis of meiofaunal and microalgal populations on an intertidal sandflat: scale linkage between consumers and resources. *Estuar. Coast. Shelf Sci.* 30: 341–353.
- Platt, T. 1972. Local phytoplankton abundance and turbulence. *Deep-sea Res.* 19: 183–187.
- Pocklington, R. 1979. An oceanographic interpretation of seabird distributions in the Indian Ocean. *Marine Biol.* 51: 9–21.
- Rapport, D.J. 1991. Myths in the foundations of economics and ecology. *Biol. J. Linn. Soc.* 44: 185–202.
- Ridoux, V. 1987. Feeding association between seabirds and killer whales, *Orcinus orca*, around subantarctic Crozet Islands. *Can. J. Zool.* 65: 2113–2115.
- Risser, P.G. 1987. Landscape ecology: state of the art. *In Landscape Heterogeneity and Disturbance*. pp. 3–14. Edited by M.G. Turner. Springer-Verlag, New York.
- Risser, P.G., Karr, J.R. and Forman, R.T.T. 1984. Landscape ecology: directions and approaches. III. *Nat. Hist. Surv. Spec. Pub. No. 2*.
- Rose, G.A. and Leggett, W.C. 1990. The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. *Ecology* 71: 33–43.
- Ryan, P.G. and Cooper, J. 1989. The distribution and abundance of aerial seabirds in relation to Antarctic krill in the Prydz Bay region, Antarctica, during late summer. *Polar Biol.* 10: 199–209.
- Ryder, R.A. 1957. Avian-pinniped feeding associations. *Condor* 59: 68–69.
- Safina, C. and Burger, J. 1988. Ecological dynamics among prey fish, bluefish, and foraging common terns in an Atlantic coastal system. *In Seabirds & Other Marine Vertebrates*. pp. 95–173. Edited by J. Burger. Columbia Univ. Press, New York.
- Scheuring, I. 1991. The fractal nature of vegetation and the species-area relation. *Theoret. Pop. Biol.* 39: 170–177.
- Schneider, D.C. 1990a. Seabirds and fronts: a brief overview. *Polar Res.* 8: 17–21.
- Schneider, D.C. 1990b. Spatial autocorrelation in marine birds. *Polar Res.* 8: 89–97.
- Schneider, D.C. and Duffy, D.C. 1985. Scale-dependent variability in seabird abundance. *Mar. Ecol. Prog. Ser.* 25: 211–218.
- Schneider, D.C., Hunt, G.L., Jr. and Powers, K.D. 1987. Energy flux to pelagic birds: a comparison of Bristol Bay (Bering Sea) and Georges Bank (Northwest Atlantic). *In Seabirds: Feeding Ecology and Role in Marine Ecosystems*. pp. 259–277. Edited by J.P. Croxall. Cambridge Univ. Press, Cambridge.
- Schneider, D.C. and Piatt, J.F. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Mar. Ecol. Prog. Ser.* 32: 237–246.
- Schneider, D.C., Pierotti, R. and Threlfall, W. 1990. Alcid patchiness and flight direction near a colony in eastern Newfoundland. *Stud. Avian Biol.* 14: 23–35.
- Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37: 789–799.
- Shuntov, V.P. 1974. *Sea Birds and the Biological Structure of the Ocean*. Translated from Russian by I. Allardt. National Technical Information Service, U.S. Department of Commerce, Springfield, Virginia.
- Smith, J.N.M. 1974. The food searching behaviour of two European thrushes. II: The adaptiveness of the search patterns. *Behaviour* 49: 1–61.
- Sowls, A.L., Hatch, S.A. and Lensink, C.J. 1978. Catalog of Alaskan Seabird Colonies. Biological Services Program FWS/OBS – 78/78. Fish Wildl. Serv., U.S. Dept. Interior, Washington, D.C.
- Springer, A.M. and Roseneau, D.G. 1985. Copepod-based food webs: auklets and oceanography in the Bering Sea. *Mar. Ecol. Prog. Ser.* 21: 229–237.
- Springer, A.M., Murphy, E.C., Roseneau, D.G., McRoy, C.P. and Cooper, B.A. 1987. The paradox of pelagic food webs in the northern Bering Sea – I. Seabird food habits. *Cont. Shelf*

Res. 7: 895–911.

- Steele, J.H. 1976. Patchiness. *In* *The Ecology of the Seas*. pp. 98–115. Edited by D.H. Cushing and J.J. Walsh. Blackwell Scientific Publications, Oxford.
- Steele, J.H. 1985. A comparison of terrestrial and marine ecological systems. *Nature* 313: 355–358.
- Steele, J.H. 1989. The ocean 'landscape'. *Landsc. Ecol.* 3: 185–192.
- Sugihara, G. and May, R.M. 1990. Applications of fractals in ecology. *Trends Ecol. Evol.* 5: 79–86.
- Veit, R.R. 1988. Spatial dispersion patterns of Antarctic seabirds. Ph.D. thesis, University of California, Irvine.
- Wiens, J.A. 1976. Population responses to patchy environments. *Annu. Rev. Ecol. Syst.* 7: 81–120.
- Wiens, J.A., Crawford, C.S. and Gosz, J.R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45: 421–427.
- Wiens, J.A. and Milne, B.T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. *Landsc. Ecol.* 3: 87–96.
- Williamson, M.H. and Lawton, J.H. 1991. Fractal geometry of ecological habitats. *In* *Habitat Structure: The Physical Arrangement of Objects in Space*. pp. 69–86. Edited by S.S. Bell, E.D. McCoy and H.R. Mushinsky. Chapman and Hall, London.
- Woodby, D.A. 1984. The April distribution of murrelets and prey patches in the southeastern Bering Sea. *Limnol. Oceanogr.* 29: 181–188.
- Woronow, A. 1981. Morphometric consistency with the Hausdorff-Besicovitch dimension. *Math. Geol.* 13: 201–216.