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Phil. Trans. R. Soc. Lond. B 1997 **352**, 633-642
doi: 10.1098/rstb.1997.0043

Spatial variance of mobile aquatic organisms: capelin and cod in Newfoundland coastal waters

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CONTENTS

SUMMARY

Spatial variance in the distribution of aquatic mobile organisms differs from that of passive tracers such as phytoplankton or water temperature. On average, spatial variance of phytoplankton scales with sample unit as L^2 or equivalently with frequency as f^{-2}. Limited evidence suggests that spatial variance in the distribution of mobile organisms is concentrated at relatively small scales, with little increase over larger scales: spatial variance scales as f^{-1} or less. We investigated whether spatial variance in distributions of a mobile predator, Atlantic cod (*Gadus morhua*), and a schooling prey, capelin (*Mallotus villosus*), also scale with frequency as f^{-1}. Acoustic surveys showed that at short time scales spatial variance in cod and capelin densities, as measured by spectral density, peaked at various scales ranging from 20 m to 10 km. At longer time scales, spatial variance of cod scaled as $f^{-1.08}$ at resolutions finer than 90 m, while scaling as $f^{-0.18}$ at coarser scales. Spatial variance of capelin scaled as $f^{-1.1}$ at resolutions finer than 400 m, while scaling as $f^{-0.21}$ at coarser scales. Spatial variance plots of krill and marine birds showed similar transitions from shallow to steep scaling. Shoaling, schooling and the aggregative response by predators to concentrations of prey were three processes hypothesized to influence spatial variance in distributions of mobile organisms. Numerical experiments showed that shoaling injects variance at large to intermediate scales, resulting in scalings flatter than f^{-1}. Additional experiments showed that schooling produces a transition from shallow to steep scaling as frequency increases. Spatial variance patterns in cod density were not due to aggregative responses by the predator to concentrations of capelin—there was no association, on average, at resolution scales from 20 m to 10 km. Exponent values for aquatic or terrestrial mobile organisms are predicted to be approximately two at the scale of an individual organism, 0.2 at scales that contain aggregations, and two at scales larger than that of populations. These findings suggest that relations between mobile organisms and large scale habitat variables will be difficult to detect, that stratified survey designs used to estimate commercial population sizes will be inefficient, and that rates of interaction between predator and prey will be underestimated if local observations are averaged over the spatial scale of the population.

1. INTRODUCTION

Heterogeneity in spatial distributions of organisms is a long recognized attribute of both terrestrial (Watt 1925, 1947) and aquatic (Hensen 1911; Hardy 1935, 1936) ecosystems. Quantifying spatial heterogeneity as a function of scale has been used to judge the applicability of small scale experiments to larger scale natural settings (Mercer & Hall 1911) to separate scale domains of equivalent spatial variability (Fairfield Smith 1938) to identify scales of maximum heterogeneity (Greig-Smith 1952; Kershaw 1957) and to provide clues to the biological or physical processes that generate observed patterns (Greig-Smith 1983; Denman & Powell 1984; Legendre & Demers 1984; Mackas *et al.* 1985).

A simple yet useful way to characterize the scale dependence of spatial variability in biological or

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physical variables is to quantify the rate of change in spatial variance using a power law. To illustrate by way of example, kinetic energy generated at large scales by physical structures in fluid environments (e.g. eddy, gyre) is transferred to successively smaller scales until viscous dissipation becomes important (Kolmogorov 1941). This 'turbulent cascade of variability' (cf. figure 2, Mackas *et al.* 1985) can be summarized by scaling the variance in a quantity of interest Var(Q) with sample unit or length scale L

$$\mathrm{Var}(Q) = cL^{\beta}.$$

Variability in the same series can also be described in the frequency domain using the power spectra P (squared magnitude of the Fourier transform) to quantify variance (i.e. spectral density) as a function of frequency f

$$P(f) = cf^{-\beta},$$

where c is a proportionality constant. When the logarithm of the power spectrum is plotted as a function of logarithm of frequency, the slope of the line is equal to the scaling factor β.

Theoretical values of β collected from a diverse set of disciplines range from zero to over two. If the variance in a series of measurements is independent of frequency, or its inverse—spatial scale—then the value of β equals zero. This is known as white noise (cf. Schroeder 1991). When variance in a series is proportional to the inverse of the frequency the value of β is one. The amplitude of the variance will be proportional to the scale of observation. In classic Brownian diffusion processes (i.e. series that lack serial correlation between successive measures) β is equal to two.

In aquatic ecosystems, efforts to quantify spatial variance as a function of scale have traditionally focused on particles or organisms that move passively with the surrounding fluid. In a dimensional analysis of spatial variance in phytoplankton density distributions, Denman & Platt (1976) found that $\beta = \frac{5}{3}$ for passive organisms. Empirical examples where the variance is proportional to approximately the square of the length scale include surface water temperature (Saunders 1972; Fasham & Pugh 1976; Richerson *et al.* 1978; Star & Mullin 1979), sea level (Wunsch 1972) and plankton distributions (Platt *et al.* 1970; Platt 1972; Powell *et al.* 1975; Denman 1976; Horwood 1978).

Spatial variance in the distribution of at least one mobile aquatic organism differs from that of passive organisms or particles. At the temporal scale of a survey transect, Weber *et al.* (1986) found that spatial variance of Antarctic krill (*Euphausia superba*) density was concentrated at single spatial scales. But these concentrations of spatial variance did not always occur at the same scale among transects. When transects were averaged to increase the temporal scale, the slope of the spatial variance plot was less than that of surface temperature or phytoplankton over length scales of 1–100 km (Weber *et al.* 1986; Levin *et al.* 1989). Increased spatial variance in krill distribution at smaller scales was attributed to an unspecified behavioural mechanism (Weber *et al.* 1986) or the movement of krill into swarms (Levin *et al.* 1989). Similar spatial variance patterns have been observed for pelagic fish (Horne 1994; Schneider 1994). The generality of these patterns and potential variance generating mechanisms have not been systematically investigated for mobile aquatic organisms.

Physical, biological and a combination of physical and biological processes have been hypothesized to generate spatial variance in distributions of mobile aquatic organisms. By definition mobile organisms have the ability to move independently of the fluid, so spatial variance patterns are not expected to be heavily influenced by large scale water motions. Among biological processes the most commonly proposed mechanism that creates spatial variance at small scales is locomotory behaviour (Mackas & Boyd 1979; Star & Mullin 1981; Mackas *et al.* 1985). Weber *et al.* (1986) proposed that behaviour was responsible for small scale variability in krill biomass distribution that could not be attributed to physical processes. Rose & Leggett (1988*a*, 1989) suggested that a combination of biological and physical processes influence the distribution and resulting spatial variance of Atlantic cod (*Gadus morhua*). Distribution of cod was attributed to an aggregative response by predators to concentrations of prey, constrained by water column thermal structure.

We hypothesize that at least three biological processes potentially generate spatial variance in the distribution of mobile aquatic organisms: shoaling, schooling and the aggregative response by predators to concentrations of prey. Shoaling, defined as the convergence of organisms independent of fluid motion, is predicted to increase spatial variance at intermediate scales by altering local densities and causing a reduction in the value of β. Schooling is distinguished from shoaling by the coordinated movement of a group of aquatic organisms (Pitcher 1986). At scales smaller than the size of an aggregation, even spacing of individuals within groups (Weihs 1973, 1975; Pitcher 1986) should reduce spatial variance of schooling organisms. This would result in a steeper slope in the spatial variance plot below the scale of an aggregation and an increase in the value of β. Experiments using live fish to test the changes in spatial variance due to shoaling or schooling have not been conducted (cf. Pitcher & Parrish 1993). A third process that potentially influences patterns of spatial variance among mobile organisms is aggregative responses by predators to concentrations of prey (Holling 1965, 1966; Murdoch & Oaten 1975). Convergence of predators in areas of high prey density will increase spatial variance of predator distribution at the scale of a prey aggregation. If cod are tracking capelin to maximize encounter rates then spatial variance patterns in cod distribution will match those of capelin and peaks in predator spatial variance will coincide with those of prey. Predator spatial variance potentially decreases at smaller or larger scales. Alternatively, spatial association between predator and prey may peak at a scale that maximizes net energetic benefit to the predator.

We used relative density estimates of capelin (*Mallotus villosus*) and Atlantic cod (*Gadus morhua*) from acoustic surveys to evaluate whether spatial variance patterns reported for krill apply to other mobile aquatic organisms. Capelin are a pelagic, schooling fish species whose adults (aged not less than three years) migrate from offshore to coastal waters to spawn on gravel beaches during June and July (Templeman 1948; Carscadden 1983). During this same period Atlantic cod, a demersal species, complete a post-spawning migration to coastal waters where they forage on capelin (Akenhead *et al.* 1982; Lilly 1987). Examining spatial variance in the distribution of cod and capelin also allows us to determine if: (1) mobile aquatic organisms will not be concentrated at a characteristic spatial scale, as observed in euphausiids; (2) spatial variance in the distribution of a predator matches that of its prey; and (3) association between predators and prey occur at a characteristic spatial scale.

2. METHODS

(*a*) *Sampling procedure*

Acoustic surveys were conducted along the western coast of Conception Bay, Newfoundland during the latter half of July and the first week of August, 1991. Linear transects were oriented parallel to the coast within the 100 m depth contour when possible. Stationary fishing gear adjacent to the coast restricted proximity of transects to shore. The majority of transects were run during the day but collectively transects spanned all 24 h in a day. Transect length among the 19 transects used in the analysis varied from 5.5 to 22.7 km. Capelin and cod relative density distributions were surveyed by using a 120 kHz echosounder (Model 105, Biosonics, Seattle, WA, USA) with a single-beam 22° transducer mounted in a towed V-fin. Pulse width was 0.8 ms and generated at $2\ \mathrm{s}^{-1}$. Data were heterodyned to 10 kHz using a Biosonics model 171 interface and stored on digital audio tapes for echo integration processing. A calibration tone was recorded at the beginning of each day to standardize playback amplitude levels. The V-fin was towed at a depth of approximately 1.5 m and at a speed of $2.5\ \mathrm{m\ s}^{-1}$. A pair of 95 N expansion springs were used to decouple motions of the boat from that of the V-fin in an effort to enhance transducer stability. Surface temperature was continuously monitored using a towed thermistor and electronically recorded at 100 m intervals.

(*b*) *Analysis*

Acoustic data were integrated using a Biosonics 221 echo integrator which digitally samples voltages at 25 kHz. Relative fish density (RD) estimates were calculated from $20 \log R$ amplified target voltages (V) using an equation from Burczynski (1982)

$$RD_{i,x,z} = \frac{\left(\sum V_i^2\right)_{x,z} K_{TVG} K_{\mathrm{S}}}{P_x N_{x,z}},$$

where $RD_{i,x,z}$ is the relative fish density of species i in horizontal bin x (m) at depth interval z (m), $(\sum V_i^2)_{x,z}$ is the squared sample voltages of species i in horizontal bin x at depth interval z, K_{TVG} is an empirically determined constant that compensates the $20 \log R + 2\alpha R$ amplifier gain for the attenuation of sound α in seawater over R m, K_{S} is an empirically determined constant that corrects system parameters to theoretical values, P_x is the number of echo sounder pulses in each horizontal bin and $N_{x,z}$ is the number of sampled voltages in horizontal bin x at depth interval z.

Data were stratified in 10 m horizontal by 5 m vertical bins to a maximum depth of 112 m. To prevent integration of surface noise or bottom echoes the top 2 m and bottom 1 m of the water column were not included. Relative capelin and cod densities were integrated vertically to a maximum depth of 112 m and then summed for each 10 m horizontal distance. Cod were distinguished from capelin by: (a) classification of targets by signal properties as viewed on an oscilloscope (Rose & Leggett 1988*b*); (b) simultaneous viewing of near-surface capelin aggregations in the water and traces on oscilloscope and echograms; (c) capture of capelin and cod using hook and line while recording traces on echograms; (d) observation and sampling of capelin and cod as the overwhelmingly dominant species in commercial traps in the sampling area; and (e) similarity of echogram traces with those of capelin and cod reported in northwest Atlantic waters (Atkinson & Carscadden 1979; Whitehead 1981; Piatt 1990; Rose 1992). Uni- and bivariate spectral analyses were used to quantify scale-dependent spatial variability of cod and capelin density distributions (Jenkins & Watts 1968; Koopmans 1974; Platt & Denman 1975). This technique estimates scale-dependent variance of a continuously recorded variable over a range of frequency bands. The frequency band range extends from half the length of the series to twice the sample resolution. The power spectra of each species as well as the coherence and phase between capelin and cod were estimated for each transect using the BMDP statistical package (Dixon 1983). Coherence measures the strength of association between two variables as a function of frequency and is analogous to a squared correlation. Potential values range from zero to one. Phase indicates the sign of correlation between the two series. Two series that are less than 90° out of phase are positively correlated and termed in phase. Two series that are greater than 90° out of phase are negatively correlated and termed out of phase. A smoothing window of $0.01\ \mathrm{cycles\ m}^{-1}$ was used in comparative analyses to provide the best compromise between accuracy and smoothness. All spectral density estimates were standardized to permit direct comparison of survey transects (Denman 1975). To increase the temporal scale of observation, spectral density estimates of capelin, cod and surface temperature from all transects were averaged over 0.001 cycle m^{-1} bins to produce average spectral density plots. Linear regressions were used to quantify slopes (i.e. β values) of spectral density plots. If residuals from a single regression equation were not acceptable (i.e. uniformly distributed with no apparent pattern), the data was divided in two sections and regression equations were fit to each section. Location of the data division was determined by the fit of regression equations to the data, and the distribution of residuals.

To assess the generality of spatial variance patterns among mobile organisms, average spectral density estimates of phytoplankton, Antarctic krill, capelin, Atlantic cod and two marine birds—common murres (*Uria aalge*) and Atlantic puffins (*Fratercula arctica*)—were plotted in a single diagram. Murres and puffins nest on rocky areas along the Newfoundland coastline where they feed extensively on capelin while rearing chicks (Brown & Nettleship 1984). Spectral density estimates of murres and puffins (bandwidth 0.1) from 35 transects were standardized and then averaged over 0.01 cycle km^{-1} bins (D. Schneider, unpublished data).

3. RESULTS

A characteristic scale of maximum spatial variance for cod or capelin was not observed in the 19 transects surveyed in Conception Bay. At short time scales (*ca.* 1 h), peaks in spectral density plots of capelin and cod spatial variance occurred at scales ranging from 20 m to 10 km. Scales of maximum spatial variance differed among spatially separated transects or within any series of repeated transects. Within the 20 m to 10 km range of analysed spatial scales, distinct peaks of capelin spatial variance occurred in five of 19 transects. Broader peaks of spatial variance were observed in seven of 19 transects. No peaks of spatial variance were observed in the remaining seven transects. Among the cod spectral density plots, only two transects contained sharp peaks of spatial variance. An additional seven transects contained peaks in spectral density spread over a broader range of spatial scales. A group of four transects provide representative plots of spatial variance patterns. Spectral density estimates of capelin and cod from a 20 km transect were plotted as a function of frequency. In three of four transects spatial variability of capelin (figure 1*a*) was similar at all scales ranging from 5000–100 m and then rapidly decreased at smaller scales. Small peaks in spatial variance were observed in spectral density plots of single transects at scales less than 90 m. In contrast, two distinct patterns were present in the plots of cod spectral densities (figure 1*b*). Two transects had slight negative slopes down to spatial scales of approximately 80 m. Spatial variance decreased at smaller scales. Spatial variance of the remaining two transects was approximately uniform across the range of sampled scales.

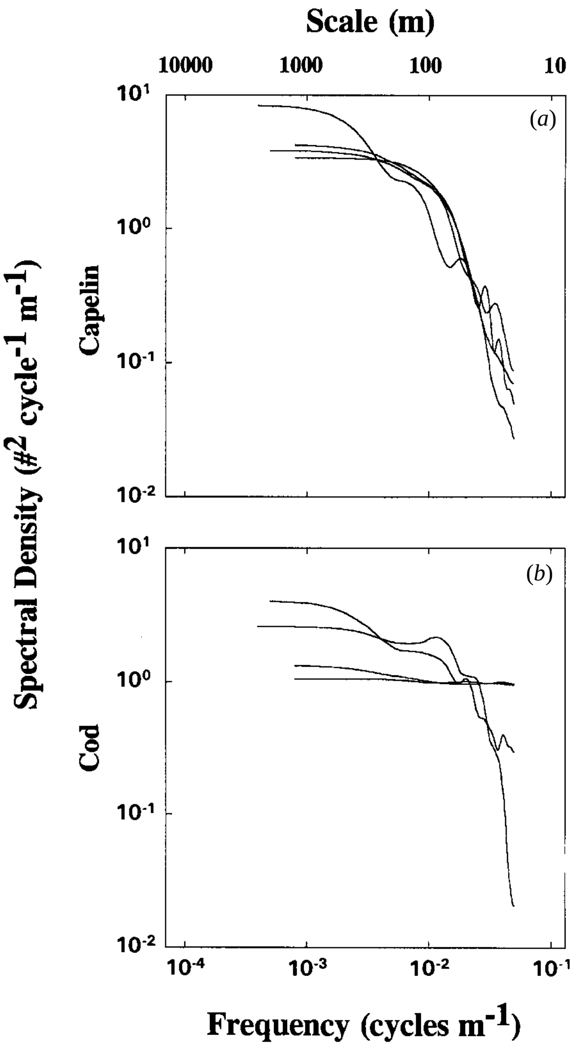

Figure 1. Spectral density estimates of (*a*) capelin and (*b*) Atlantic cod (bandwidth 0.01, centred, normalized) plotted as a function of frequency. Periods (m) are shown on the upper x-axis. Each graph contains four repetitions of a 20 km transect, sampled at a resolution of 10 m, along the western shore of Conception Bay, Newfoundland, Canada.

Spatial variance patterns of capelin and cod over longer temporal scales were examined by averaging spectral density estimates and plotting them as a function of frequency (figure 2). A peak in spatial variance, indicative of a characteristic scale of aggregation, was not observed in the average power spectra of capelin or cod. Capelin and cod average spectral density plots contained two ranges of scales that differed in slope. From large to intermediate scales, slopes of spectral density plots were slightly negative (capelin -0.21, $r^2 = 0.951$, $n = 6$; cod -0.18, $r^2 = 0.795$, $n = 11$). At scales smaller than a transition region (capelin *ca.* 400 m; cod *ca.* 90 m), slopes of spectral density plots increased (capelin -1.1, $r^2 = 0.997$, $n = 46$; cod -1.08, $r^2 = 0.993$, $n = 41$).

To compare spatial variance patterns of capelin and cod to those of passive tracers, an averaged sea surface temperature plot was added to the same

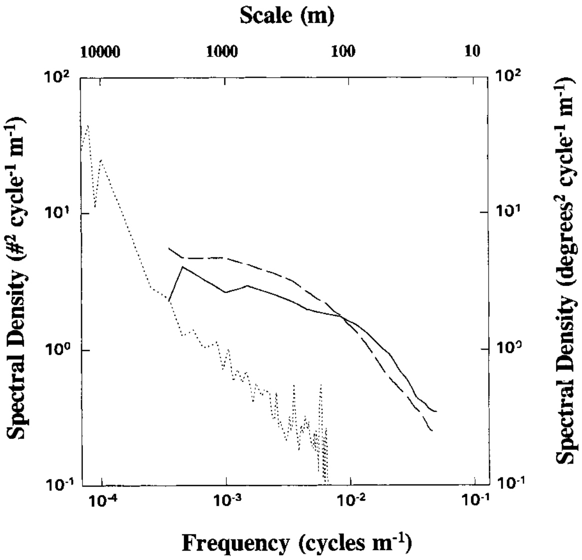

Figure 2. Average capelin (broken line), Atlantic cod (solid line), and surface temperature (dotted line) spectral density estimates (bandwidth 0.01, centred, normalized) plotted as a function of frequency. Periods (m) are shown on the upper x-axis. Data for capelin and cod spectral density estimates from Horne & Schneider (1994).

graph (figure 2). The steep monotonic slope of the surface temperature power spectrum (-1.06, $r^2 = 0.944$, $n = 71$) was steeper than slopes of capelin and cod power spectra at large to intermediate scales and matched slopes at scales smaller than transition regions.

Scales of transition regions identified in average spectral density plots (figure 2) were compared to tabulations of capelin and cod aggregation sizes. Cumulative frequency distributions of capelin (figure 3*a*) and cod (figure 3*b*) aggregation sizes (defined as the number of contiguous 10 m blocks with fish present) showed that 98% of capelin aggregations were not more than 400 m ($n = 2247$) and 91% of cod aggregations were not more than 100 m ($n = 642$). Distances between aggregations of capelin averaged 46.3 m (±2.0 s.e.) compared to 242.5 m (±24.5 s.e.) for cod.

Patterns of capelin and cod average spatial variance were consistent with those of other mobile marine organisms (figure 4). Over large to intermediate scales, spectral density slopes of capelin, cod, puffins and murres were shallower than that of phytoplankton. The dip in the power spectra of common murres coincides with the observed association of murres with upwelling events at the spatial scale (5 km) of a Rossby radius (cf. Schneider 1989). Among mobile organisms shallow spectral density slopes reduce spatial variance at large scales and increase spatial variance at intermediate scales relative to the distribution of spatial variance in passive tracers.

The scaling of spatial variance in cod resembled that of its primary prey, capelin (figure 2). However, this was not due to aggregative responses by the predator to concentrations of prey. At the temporal scale of all 19 transects (*ca.* 2 weeks) there was no association, on average, at resolution scales ranging from 20 m to 10 km (cf. figure 3, Horne & Schneider 1994). This result was also observed at the temporal scale of single transects (figure 5). In general, coherence of cod with capelin was less than 0.2 within any of these transects. Only three of the 19 transects exhibited recognizable peaks of coherence at any scale. In the absence of any consistent spatial association, no attempt was made to determine the form of a functional aggregative response by the predator to its prey.

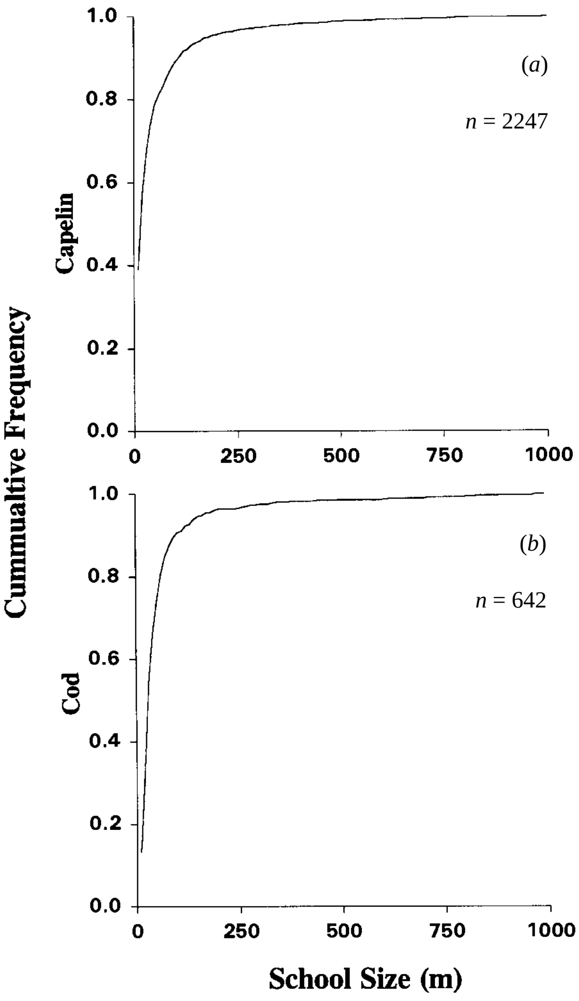

Figure 3. Cumulative frequency histograms of (*a*) capelin and (*b*) Atlantic cod shoal sizes. Shoal sizes are tabulated in bins of 10 m. A shoal is defined as the number of contiguous 10 m horizontal blocks with fish present.

4. DISCUSSION

Spatial variance patterns of mobile, aquatic organisms did not follow the f^{-2} scaling proposed for passive tracers of the surrounding fluid. Among single transects, recurring peaks at the same spatial scale in spectral density plots, indicative of characteristic patch sizes, were not observed for capelin or cod. Similar episodic concentrations of spatial variance over a range of scales have been reported among benthic megafauna (Grassle *et al.* 1975), krill (Weber *et*

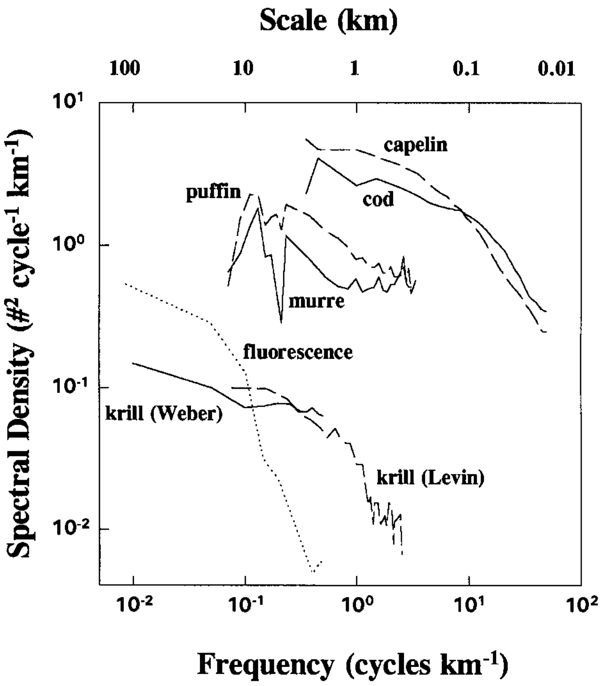

Figure 4. Average spectral density estimates of capelin (broken line), Atlantic cod, Atlantic puffin (broken line), common murre, Antarctic krill (data from Weber *et al.* 1986), Antarctic krill (dotted line) (data from Levin *et al.* 1989), and fluorescence as an index of phytoplankton (data from Weber *et al.* 1986) plotted as a function of frequency. Phytoplankton is plotted as a dotted line to distinguish spectral density plots of mobile organisms from passive tracers of the surrounding fluid. Periods (km) are shown on the upper x-axis.

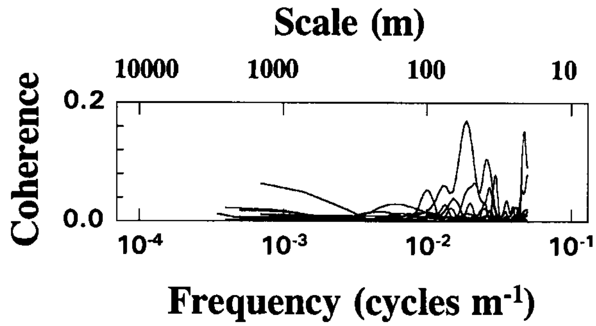

Figure 5. Coherence of capelin and Atlantic cod plotted as a function of frequency. Periods (m) are shown on the upper x-axis.

al. 1986; Levin *et al.* 1989), marine birds (Schneider & Duffy 1985; Schneider 1989) and fish (Schneider 1989; Rose & Leggett 1990). With the exception of the study by Weber *et al.* (1986), these patch size studies were based on a single or a limited number of survey transects. At larger temporal scales, capelin and cod spatial variance decreased slightly from large to intermediate scales. The slight negative slopes of capelin and cod spectra ($\beta \approx -0.2$) contrasted to the slope of the average surface temperature spectral density plot ($\beta \approx -1$), used as an example of a passive tracer of the surrounding fluid. At scales smaller than transition regions, β values in fish and surface temperature spectral density plots were approximately -1. This pattern was maintained when spatial variance plots of other mobile, aquatic animals were compared to a plot of phytoplankton spatial variance.

All spectral density plots of mobile organisms contained two regions of differing slopes. The slight negative slope at large to intermediate spatial scales is consistent with the hypothesized injection of spatial variance due to the convergence of individuals into shoals. The sharp drop in spectral density plots at scales smaller than transition regions is consistent with the hypothesized reduction in spatial variance due to the even spacing of schooling animals. To determine if these mechanisms would produce observed patterns, we randomly replaced values of a continuously recorded, surface temperature data series with zeros. The intent of this exercise was to see if spatial variance patterns observed among passive particles can be altered to those observed for mobile organisms through biologically meaningful data manipulations. The division of a continuous data series into discrete patches by introducing a single zero creates distribution patterns that are analogous to shoaling by organisms. In each of eight numerical experiments, a single value from a 10 km sea surface temperature record (resolution 233 m, $n = 44$ data points) was randomly replaced with a zero. Spectral density estimates from each series were standardized by the variance and plotted as a function of frequency in a common log–log plot. The slope of the spectral density plot from the original temperature series (figure 6*a*) was -2.57 ($r^2 = 0.962$, $n = 22$) compared to an average slope of -0.36 ($r^2 = 0.727$, $n = 176$) in the manipulated temperature series (figure 6*b*). Spectral analysis of the manipulated surface temperature series confirms that the presence of zeros in a data series reduces slopes of spatial variance plots at large to intermediate scales.

In a similar set of numerical experiments, effects of schooling on β values were investigated by randomly substituting two consecutive zeros in the original surface temperature data series. Introduction of consecutive zero counts creates patterns that resemble those of organisms actively forming mobile aggregations and creating 'empty' areas along survey transects. The substitution of two consecutive zeros in the original surface temperature series (figure 6*c*) resulted in an increase in spatial variance at intermediate scales and a sharp drop in spatial variance at scales smaller than a transition scale of approximately 400 m. Transitions in spectral density plots of mobile aquatic organisms, marked by an increase in β values, can be replicated by creating strings of unoccupied locations in a continuous data series.

Virtually all counts of mobile organisms contain zeros. Zero counts in transect data can arise from high resolution sampling or convergent behaviour of animals. High resolution sampling combined with low organism abundance lowers the mean abundance per sample and increases the probability of a zero count. The probability of a zero count increases as the ratio of organism body size to sample quadrat size increases. Sampling patchily distributed organisms

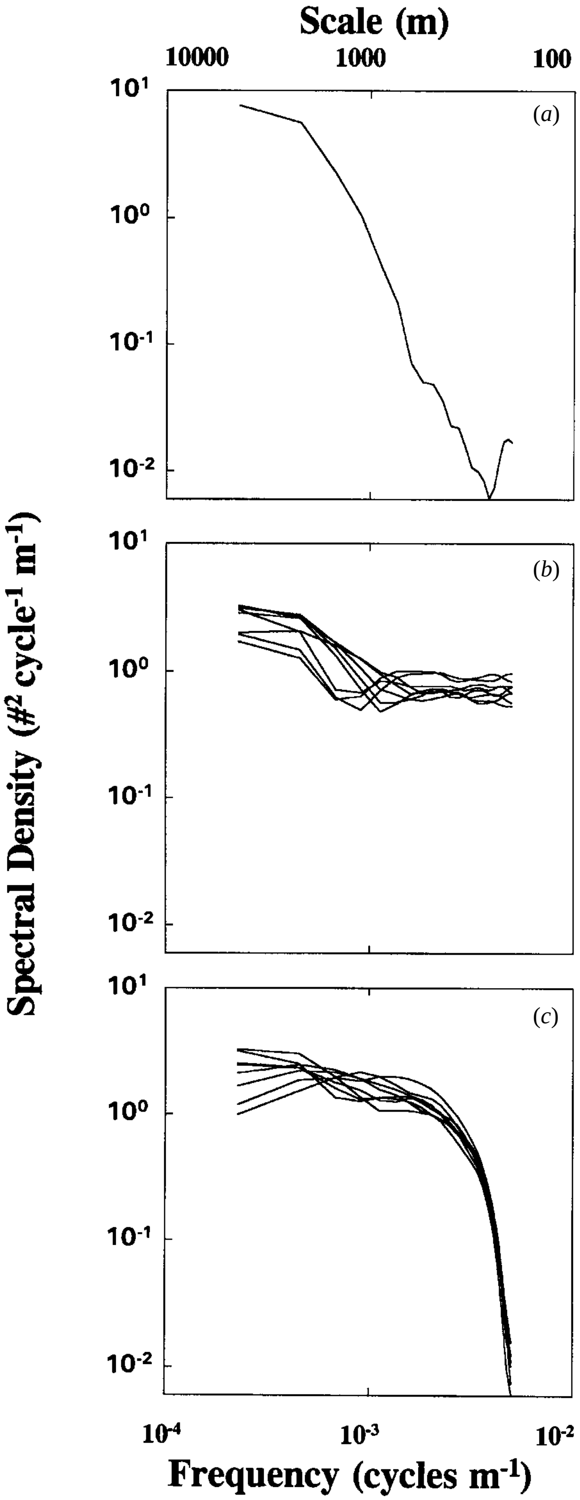

Figure 6. Spectral density estimates of (*a*) original surface temperature series (length 10 km, resolution 233 m), (*b*) eight repetitions of surface temperature series with a single zero randomly substituted, and (*c*) eight repetitions of surface temperature series with two zeros randomly substituted as a block.

such as capelin will also result in a higher proportion of zeros when compared to counts of uniformly distributed animals. This effect is amplified when mean densities are low. The presence of zeros in count data potentially introduces an additional source of variance when analysed with spectral decomposition techniques. Slopes of spectral density plots have been shown to decrease as the mean count per sample decreases (Fasham 1978).

A process that potentially influences spatial variance of mobile aquatic organisms is the aggregative response by predators to concentrations of prey. We predicted that a characteristic scale of maximum association between predator and prey would occur within the range of a few body lengths to the spatial scale of a small bay. Contrary to predictions we found that, on average, capelin were not associated with cod over spatial scales ranging from 20 m to 10 km. This was an unexpected result. Capelin are a major component of cod diet (Popova 1962; Lilly 1987, 1991) especially during late spring through early summer (Thompson 1943; Methven & Piatt 1989). Coherence between adult capelin and Atlantic cod has been observed (Rose & Leggett 1990) at the spatiotemporal scale of a foraging bout (length less than 5 m, duration less than 1 h) during a short (185 m) daytime transect when cod were actively feeding on capelin. The present study includes samples from all hours of the day to ensure sampling occurred when cod were actively feeding on capelin.

We do not believe that the lack of spatial association between capelin and cod was due to analytic or data acquisition procedures. Failure to detect a characteristic scale of coherence between capelin and cod was not due to sampling over a limited range of spatial scales. Spatial variance of fish density distributions and predator–prey interactions were examined over four orders of sampling magnitude (10 m to 20 km). A sampling range of this size is rare within a single study. Failure to detect a characteristic scale of spatial association between capelin and cod was also not due to the use of spectral decomposition techniques. A similar approach using spectral analysis showed that it is possible to detect a scale of maximum spatial association between marine birds and pelagic fish (Schneider 1989). The existence of association scales between marine birds and fish were confirmed using variance to mean ratios (Piatt 1990).

Using spectral decomposition techniques to detect scales of association between two count series does have limitations. One limitation is the inability of spectral analysis to detect nonlinear interactions between predator and prey. Spectral analysis fits a linear relationship between two variables. Aperiodic or nonlinear interactions are underestimated and result in lower coherence estimates (Star & Cullen 1981). Coherence estimates between predator and prey may also be influenced by the vertical integration of relative fish density data prior to estimating spectral densities. Two-dimensional transects were analysed as one-dimensional data series. This potentially increases fish aggregation sizes and would increase the scale of maximum association between predator and prey. At small scales this may lower coherence between the two species but strong spatial associations would remain detectable in spectral density plots. A two-dimensional spectral analysis was not computed because it requires a square data matrix to be used in the algorithm (Ripley 1981). The disproportionate length to depth ratio of survey transects would require a large number of zeros to be added to 'square' a data matrix. As discussed above, the addition of zeros lowers the overall mean density in a data series and changes spectral density estimates (cf. Fasham 1978). Coherence values can also be lowered by random sampling error of a Poisson process (Mackas 1977). As a compromise between high data resolution and reducing the probability of getting a zero count, data resolution in this study was set at 10 m. A fourth factor that potentially affects coherence is the choice of bandwidth used in spectral analyses. Bandwidth influences coherence by setting the number of adjacent periodograms averaged to estimate the magnitude of variance in each frequency band (Chatfield 1980). A wide bandwidth smooths the curve by averaging a larger number of periodogram estimates (Diggle 1990). A narrow bandwidth may lower coherence values but was used in this study to minimize bias due to smoothing among frequency bands.

A simple biological explanation for the low coherence between cod and capelin is that cod do not need to be spatially coupled with capelin at the space and time scales of our study. If energetic costs of tracking prey over large distances exceed net energy gained by consuming prey, then spatial coupling of cod to capelin is potentially restricted to scales greater than 10 km or smaller than 20 m. Bioenergetic calculations show that movement is not restricted by energetics when cod forage on capelin (Horne & Schneider 1994). The energetic costs of swimming by cod represent a small proportion (10–14%) of the total energy used to obtain and assimilate a ration of capelin. The absence of a characteristic scale of spatial association combined with the large energetic gain of cod glut feeding on capelin (Horne & Schneider 1994) suggests that cod can function successfully as 'sit and wait' predators. The lack of an aggregative response by cod to concentrations of capelin at small to intermediate scales may be true of other predators. Aggregative functional responses by predators may prove to be strongly scale-dependent in other mobile predator–prey systems.

Scale-dependent spatial variance in the distribution of mobile aquatic organisms did not match the 'turbulent cascade of variability' proposed for passive tracers ($\beta \approx 2$). For mobile organisms the decrease in spatial variance with increasing scale is very small (i.e. $\beta = 0.2$). Spatial variance is concentrated at local scales, with little increase in patchiness at larger scales. Transitions in slopes of spectral density plots will arise from any factor, including social behaviour, that increases the number of unoccupied locations along a transect. Transitions that define domains of homogeneous spatial variance (cf. Horne & Schneider 1995) will occur at the spatial scale of an individual organism, at the scale of an aggregation and at the scale corresponding to the range of an organism. In general, β values for mobile organisms are predicted to be two at small spatial scales due to the presence or absence of individuals, 0.2 at intermediate scales that contain aggregations and two at scales larger than the range of the animal due to the presence or absence of populations.

We predict that similar β values and transitions will be observed in aquatic and terrestrial populations at spatial resolutions high enough to result in unoccupied locations along continuously surveyed transects. This hypothesis could be tested in a laboratory setting by comparing spatial variance patterns of dispersed animals to those of shoaling and schooling animals. It could also be tested as a natural field experiment by comparing spatial variance patterns of animals that aggregate during daylight hours to those that disperse during night foraging. A computer simulation of animal shoaling and schooling is a third method to test this hypothesis (e.g. Horne 1995).

We found that spatial variance of mobile organisms at local scales (i.e. the scale of an aggregation) did not dramatically increase at large scales (i.e. the scale of a survey). One implication of this finding is that relations between mobile organisms and large scale habitat variables will be difficult to detect. Large sample sizes will be required to detect spatial associations of mobile organisms with important physical and biological features of the environment because of the intensity of local variation relative to larger scale variation. A second implication of this finding is that stratified survey designs, which are often used to estimate population size in commercial fish species, such as cod and capelin, will be inefficient. Stratification typically occurs at the scale of tens or hundreds of km. Our results suggest that variance at the scale of strata will be small relative to variance within strata, and that stratification will do little to reduce the variance in an estimate of population size.

Our finding that spatial variance in mobile organisms depends on measurement scale has implications for ecological theory. Lotka–Volterra models (Lotka 1925; Volterra 1926, 1931) assume that rates of contact between predators and their prey depends on the number of predator–prey pairs, not on scale or distance between organisms. Quantifying spatial variance in counts of predators and prey can be used to measure the number of potential contacts among organisms at any scale (cf. Schneider *et al.* 1987). Our finding that spatial variance of mobile organisms does not dramatically increase with scale means that there is little additional potential for interaction between predators and their prey with increasing scale. This suggests that population interactions among mobile organisms are highly localized and do not extend much beyond the spatial scale of an aggregation. This may lead to an underestimate of population interaction rates if field observations are made at the scale of predator–prey interactions and subsequent models are averaged over the spatial scale of a population (e.g. Anderson & May 1985; Mason & Brandt 1996). Our estimates of spatial variance as a function of scale are a step toward a better understanding of how contact-dependent interactions such as predation, competition and habitat selection vary in intensity with spatial scale.

This work was supported in part by the Ocean Production Enhancement Network (National Centres of Excellence, Canada), by the Natural Sciences and Engineering Research Council of Canada, and by the National Science Foundation (OCE-9415740). P. Normore and C. Tuck assisted in the field. We thank D. Mackas and P. Pepin for discussion and comments that improved the manuscript. This is Ocean Sciences Centre contribution 279.

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Received 12 August 1996; accepted 14 January 1997