

Spectral Analysis of Zooplankton Spatial Heterogeneity

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to the average difference of the two curves in Fig. 1A during the first 5 days. The peak at day zero in Fig. 3A suggests that the relationship described here between the interplanetary field polarity and the size of low-pressure troughs is most effective in the geographic area corresponding to day zero, that is, near 180°W. We are making a new data set to define this geographic area and to search for other possible similar areas such as the Icelandic low.

Figure 3B shows a distribution of 1000 calculations of the ordinate value but with the troughs assigned as away or toward by using a random number generator. The excess areas of away troughs calculated by using the observed direction of the interplanetary magnetic field was equaled in magnitude during less than 1 percent of the random calculations. On the right-hand scale of Fig. 3B, σ represents the standard error of the mean. The observed relationship is about three standard errors removed from a null result.

The relationship reported here has led us to devise an improved data set describing the area of low-pressure troughs. We plan to identify each trough when it first appears in the Northern Hemisphere and then at 12-hour intervals to record the time, latitude, and longitude of the central portion of the trough, the VAI computed with several values of vorticity, and other related quantities such as the maximum value of vorticity within the trough. The limitation in the present data set to wintertime troughs near 180°W will thus be removed. It should be possible to define the geographic area in the Northern Hemisphere in which this relationship exists.

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Spectral Analysis of Zooplankton Spatial Heterogeneity

Abstract. Continuous estimates were obtained of zooplankton abundance, chlorophyll fluorescence, and water temperature along 10- to 100-kilometer transects of the North Sea. Spectral analysis methods were applied to the data. The "patchiness" of the plankton was distributed over all the length scales resolved with no indication of a characteristic patch size. The relative intensity of the zooplankton patchiness was greater than that of the phytoplankton at all spatial scales, with this difference becoming progressively greater for finer-scale features. In the North Sea data, the concentrations of phytoplankton and zooplankton consistently showed negative spatial correlations.

Considerable interest, both theoretical and experimental, has been focused on spatially heterogeneous biological systems. In large part this interest stems from studies showing that spatial heterogeneity is probably both caused by and contributory to the complex nonlinear dynamic behavior of such systems (1). Planktonic systems are particularly useful for experimental observation because the physical structure of the pelagic environment is both relatively weak and transitory in time; persistent biological structure is likely to reflect biological causation at some spatial scale.

Several authors (2) have employed time series (spectral) analysis methods in descriptive studies of phytoplankton patchiness. The advantage of these methods is that they allow the variance

and covariance of serial data to be resolved into component length scales; their disadvantage is that they require long series of closely spaced samples. Chlorophyll fluorescence *in vivo* provides an appropriate method for estimating phytoplankton concentration (3), but until recently there has not been a method comparable in resolution and potential transect length for estimating zooplankton abundance.

We have developed a shipboard sampling system which counts individual particles in a continuous stream pumped from a fixed-depth seawater intake. The particle counter senses the increased resistances resulting from the passage of particles between the sensor electrodes (4, 5). As configured for the work reported here, the system does not discriminate particle size but simply counts the particles larger than threshold size (determined by a sigmoid sensitivity curve centered at 0.375-mm spherical equivalent diameter) and smaller than the sensing tubes (roughly 4-mm equivalent diameter). In all the regions we have sampled, this size range is numerically dominated by small crustacean zooplankton. For the transect reported here, visual counts of concurrent samples collected at the drain of the system showed the population to be composed almost exclusively (~95 percent) of copepods of the genera *Calanus*, *Oithona*, and *Pseudocalanus*. A calibration curve of visual versus electronic counts is given in Fig. 1.

The sampling system also obtains simultaneous records of chlorophyll fluorescence (measured with a Turner Designs fluorometer) and water temperature. Because it is immune to the problem of net clogging, the system al-

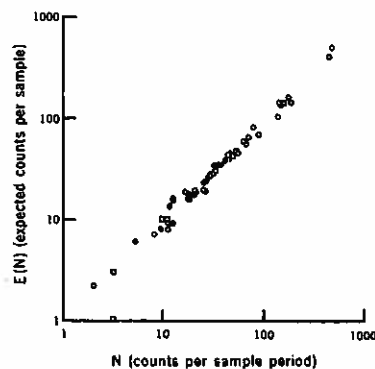


Fig. 1. Expected counts (visual counts of calibration samples weighted by a measured curve of particle size versus counting efficiency) plotted against electronic pulse counts from the sampling system. (●) Laboratory samples, (○) field samples, and (□) samples collected from the Dalhousie University 70-m³ "tower tank."

lows long and detailed transects. At a typical ship's speed of 9 knots, the sample interval is 278 m.

We have performed spectral analyses of our data by using an autocovariance transform routine preceded by pre-whitening and detrending (6). Because we are interested in detecting relatively low levels of squared coherence (typically 0.1 to 0.3) we require extensive frequency-band smoothing to obtain sufficient statistical precision. This results in coarse spectral resolution (large bandwidth). However, we also computed the power spectra with fewer degrees of freedom and did not then find narrow spectral peaks (indicative of characteristic patch sizes) that were lost through smoothing in the wide-band analysis.

Figure 2 shows transect plots of zooplankton abundance, chlorophyll fluorescence, and temperature taken from the Fladen Ground (northern North Sea) in late spring 1976. Power and coherence spectra are shown in Fig. 3. These plots are only representative samples from a larger data set (a total of 19 transect lines with their associated spectra), but they are sufficient to illustrate several important and consistent results (7).

First, the near-surface zooplankton patchiness is extremely intense. Peak abundances ranged to nearly 10^5 per cubic meter, and abundance contrasts of 4- to 5-fold were common. This intensity of aggregation may be relevant to fish biology, since it is now believed that fish (particularly in their early life history) must frequently encounter much greater than average food concentrations for adequate survival (8). Similar strong abundance contrasts appeared only rarely in the fluorescence records and were spread over considerably larger horizontal distances. The intensity of patchiness, expressed as a fractional change of the background (that is, average) abundance, can be estimated by calculating the standard deviation of the logarithm of the plankton concentration. Except in a few cases involving strong hydrographic fronts, this index was typically 1.5- to 6-fold larger for the zooplankton than for the fluorescence transects.

Second, although the heterogeneity of both phytoplankton and zooplankton is distributed smoothly over all the length scales resolved in our analyses (with small patches superimposed on or modulated by much larger ones), the small spatial scale contribution to the total patchiness is relatively much greater for zooplankton than for phytoplankton. As a result, the zooplankton power spectra have weaker wavenumber dependence

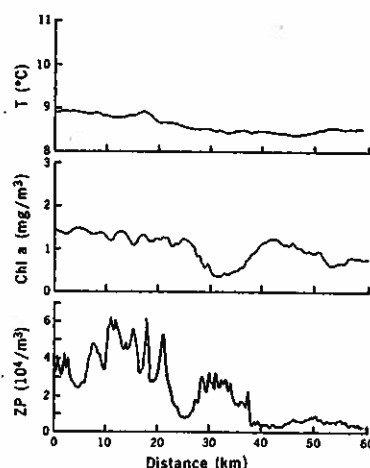


Fig. 2. Plots of the North Sea transect, 27 May 1976, showing water temperature, chlorophyll fluorescence, and zooplankton abundance as functions of distance along the transect. The decrease in abundance of the zooplankton near the end of the transect is due in part to their diel downward migration from the surface layer.

(are less steeply sloped) than the corresponding fluorescence spectra. This means that the zooplankton form a more finely grained pattern and suggests that they must have a stronger mechanism for formation of small-scale aggregations, or equivalently a better mechanism for resisting turbulent diffusion. Most analytical models describing phytoplankton patch formation have employed a per-

turbation analysis of the scale-dependent balance between turbulent diffusive flux and exponential reproductive growth (9). This type of model is inapplicable for explaining the zooplankton heterogeneity over these scales. Since the intrinsic rate of increase (r in most contexts) is normally much lower for zooplankton than for phytoplankton, the zooplankton should be able to form and maintain only very large scale abundance features. A mechanism with a shorter characteristic time scale (probably behavioral in origin) is required to explain the observed intensity of small-scale zooplankton patchiness.

Third, the spatial patterns of phytoplankton and zooplankton frequently show significant correlation. Since feeding and growth rates of zooplankton are dependent on their food concentration, this correlation has obvious ecological implications. The Fladen Ground data consistently yield correlations that are negative (phase spectrum $\sim 180^\circ$), indicating that peaks of zooplankton abundance are concurrent with local minima of phytoplankton fluorescence. This spatial pattern can easily be seen in Fig. 2.

The negative correlations may be explained by spatial variations in grazing stress; by this mechanism the zooplankton patchiness could cause some of the phytoplankton patchiness. Calculations employing suggested filtering rates of zooplankton (10) together with the observed contrasts in zooplankton abundance show that 5 to 30 percent varia-

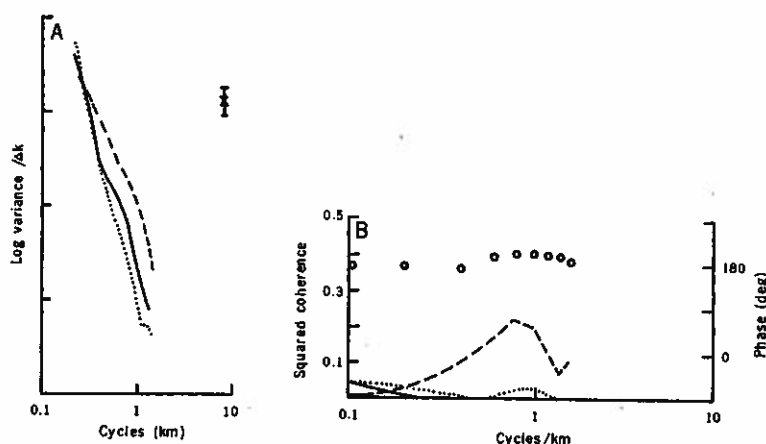


Fig. 3. Spectra calculated for the transect in Fig. 2. (A) Power spectra (logarithmic scales) of zooplankton (dashed line), chlorophyll (solid line), and temperature (dotted line). The zooplankton spectrum incorporates a correction for the amount of variance added by random sampling from a discrete population. The vertical line at the upper right shows the 95 percent confidence interval for a single spectral estimate. (B) Coherence spectra of zooplankton abundance with temperature (solid line), chlorophyll with temperature (dotted line), and zooplankton abundance with chlorophyll (dashed line). Only the latter pairing consistently exceeds the theoretical 95 percent confidence level for nonzero squared coherence (~ 0.05 for the ratio of lags to record length that we selected). The chlorophyll-zooplankton phase spectrum is indicated by the open circles; the consistent 180° phase relationship indicates negative spatial correlation.

tions in phytoplankton stock would develop during a 4-hour nocturnal grazing period. This is consistent with the observed small-scale coherences. Greater depletions of phytoplankton accompanied zooplankton patches of larger spatial scale, implying more prolonged contact between the zooplankton peaks and phytoplankton troughs (although the coherence was weaker for these larger features).

A possible mechanism for maintaining the observed zooplankton and phytoplankton patterns is the intense (in this region) diel vertical migration of the zooplankton. Pearre (11) has suggested in a study based on gut content analyses that the daily downward migration of carnivorous zooplankton can be triggered by satiation. Mackas and Bohrer (12) found similar evidence for herbivorous copepods. Evans *et al.* (13) constructed a mathematical model coupling this migratory pattern with a vertical current shear. Their model output showed intensifying zooplankton patches that are negatively correlated with the spatial pattern of the phytoplankton, a result that is consistent with (although not proved by) our observations.

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Mercury Distribution in the Gulf Stream

Abstract. Measurements of reactive mercury in ocean water in the Gulf Stream at depths from 250 to 4460 meters revealed lower and more consistent concentrations than have been reported in the western Atlantic. The mean and standard deviation of 24 values in a vertical profile were 4.1 ± 1.0 nanograms per liter. A correlation was found between variations in mercury and silicate, suggesting a common link in their marine geochemistry.

Information on the natural occurrence and cycle of Hg in the ocean is important in evaluations of man's role in mobilizing this potentially toxic metal. Contamination has been a major obstacle to obtaining reliable concentrations of Hg in seawater (1). Earlier studies have not shown a consistent correlation between the Hg concentration and the distributions of other chemicals in the ocean (2-7). We have used a sensitive method for the shipboard analysis of Hg in seawater which minimizes contamination. Results for a vertical profile of samples taken from the Gulf Stream show lower concentrations than those measured in earlier work and systematic variations with silicate.

With this analytical technique it was possible to measure the so-called reactive Hg (inorganic Hg plus a portion of the organic Hg) in seawater. Five milliliters of 10 percent stannous chloride were added to 250 ml of seawater, which had been acidified with 2 ml of concentrated Hg-free HNO₃ to avoid loss after collection; we brought the sample into equilibrium with room temperature by allowing the sample to sit for approximately 2 hours before analysis. Nitrogen was bubbled through the sample at the rate of 290 ml/min for 15 minutes to transfer the elemental Hg to a preconcentration trap consisting of Au-coated quartz sand. The Hg was released from the Au by heating to $350 \pm 25^\circ\text{C}$ as measured by an iron-constantan thermocouple placed inside the preconcentration trap. The Hg then was swept through a cold vapor atomic absorption instrument (Spectro Products HG-3). Further bubbling of the sample and heating of the preconcentration trap did not show any detectable signal; this result indicated the complete recovery of the Hg. Analyses were carried out within about 6 hours of collection to minimize loss or contamination of Hg associated with storage. The method provided a 100-fold concentration factor between the Hg initially stripped from the seawater and that passing through the analysis instrument. The technique is a modification of the one given by Fitzgerald *et al.* (5).

In the calibration of the method we

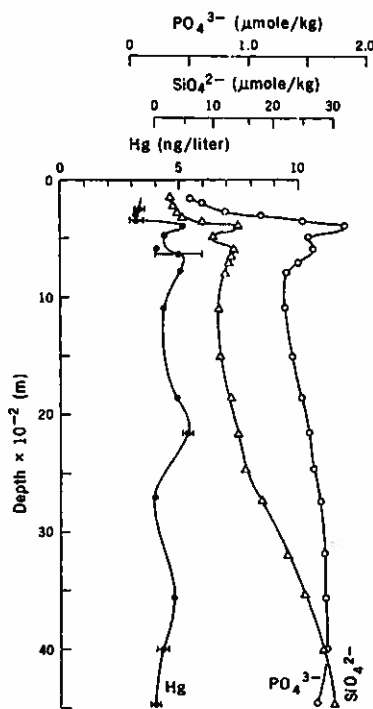


Fig. 1. Depth profiles for reactive Hg (●), reactive silicate (Δ), and phosphate (○). The error bars for Hg are equal to 2σ in total magnitude, average $1\sigma = 0.5$ ng/liter. The sea floor is 4670 m deep at this station.