Journal of Oceanography
Vol. 51, pp. 261 to 266. 1995

Fractal Distribution of an Oceanic Copepod *Neocalanus cristatus* in the Subarctic Pacific

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(Received 13 April 1994; in revised form 28 June 1994; accepted 30 August 1994)

Horizontal distribution of the copepod *Neocalanus cristatus* was shown to be fractal on the scale between tens of meters and over 100 km. The fractal dimensions ranged between 1.68–1.89, significantly higher than those of oceanic turbulence and phytoplankton distribution.

1. Introduction

Heterogeneity in the horizontal distribution of zooplankton has been recognized for many years (e.g. Hardy, 1936). The phenomenon, however, has seldom been described precisely, although zooplankton patchiness is relevant to many aspects of biological oceanography. Recent studies reveal that copepod patches do not exhibit characteristic lengths (Mackas and Boyd, 1979; Tsuda *et al*., 1993) and that the patterns of copepod distribution are self-similar and independent of the scale of observation (Tsuda *et al*., 1993). These findings suggest that copepod distributions may be fractal.

Mandelbrot (1967) introduced the concept of fractals for temporally or spatially irregular phenomena which show self-similarities over a wide range of scales. Many fractal objects have been found in nature (Mandelbrot, 1982), and the theory has been applied to some ecological studies (Morse *et al*., 1985; Pennycuick and Kline, 1986; Dicke and Burrough, 1988; Sugihara and May, 1990; McKinney and Frederick, 1992). In the oceans, environmental turbulence itself has fractal facets in many aspects (Mandelbrot, 1982; Sreenivasan and Meneveau, 1986). Therefore, plankton living in the medium should also have fractal facets. In fully developed turbulence, a given order of eddy generates smaller eddies by nonlinear interactions (Richardson, 1922). This recurring scheme produces a hierarchy of eddies in the sea. A hierarchical structure similar to the ambient flow was observed in the distribution of copepods (Tsuda *et al*., 1993). Spectral analysis has been used for examining irregular time series, and a relationship between fractal analysis and power spectrum analysis has been reported (Berry and Lewis, 1980; Fox, 1989; Higuchi, 1990). However, use of the fractal concept provides a better intuitive sense of the spectral data (Steele, 1989; Sugihara and May, 1990) and some fractal measures provide a more stable estimation of dimension than that of power law index in spectral analysis when the number of data is limited (Higuchi, 1990). The goal of the present study is to test the hypothesis that the horizontal distribution of the oceanic copepod, *Neocalanus cristatus*, is fractal.

2. Materials and Methods

All samplings were carried out during the KH-91-3 cruise of the *Hakuho Maru*, Ocean Research Institute, University of Tokyo in the western subarctic Pacific. Seawater was pumped up from the ship bottom intake and an oceanic copepod, *Neocalanus cristatus* copepodite stage V, was continuously counted with an electronic particle counter along the cruise track (meso/mega scale observation) and around Stn. A (micro-scale observation) (Fig. 1). The ship speed was

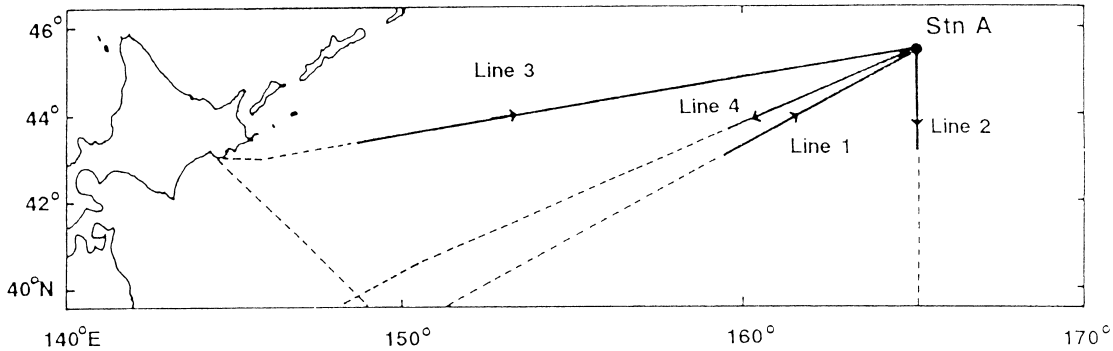

Fig. 1. Cruise track and location of the micro-scale sampling station (A). Thick lines indicate the area used for the analysis characterized by low temperature (<5.4°C). Arrows indicate ship's heading direction.

maintained at ~30.6 km hr^{-1} along the track, and the sampling interval of copepod counting was 1 min (510 m). For the micro-scale observation, periods with low ship speed (0.6–1.8 km hr^{-1}) were selected from the data around Stn. A; sampling interval of micro-scale observation ranged between 10 and 30 m. Although the micro-scale observation was discontinuous, robustness of the fractal estimates to the random gaps in serial data was confirmed by the numerical experiments by McKinney and Frederick (1992). Details of sampling methods and a general description of the copepod distribution are presented elsewhere (Tsuda *et al.*, 1993; Tsuda and Sugisaki, 1994).

To test whether or not the copepod distribution is fractal, we first applied the box-counting algorithm which is a widely used method with practical advantages (Mandelbrot, 1982). Since the data consists of a time series in one dimension, we divided it into segments with various times of length r, and let $N(r)$ be the number of segments that contain copepods. If the relationship between r and $N(r)$ in a log-log plot is linear with the slope $-D$, then D can be interpreted as the fractal dimension (capacity dimension) of the copepod distribution:

$$N(r) \propto r^{-D}.$$

Secondly, we calculate the information dimension. The total information ($I(r)$) is defined as;

$$I(r) \equiv \sum_i P_i(r) \times \log P_i(r)$$

where $P_i(r)$ is the probability of finding a copepod in the i-th segment with length r. Total information decreases with increasing scale of resolution. If the distribution is fractal, a linear relationship with slope $-D$ will be obtained between $\log(r)$ and $I(r)$. Then D can be interpreted as the fractal dimension (information dimension);

$$I(r) = I_0 - D \cdot \log r.$$

The above calculations were made using data from both meso/mega- and micro-scale observations.

Only night time data were used so errors caused by diel vertical migration (Tsuda *et al.*, 1993) were not introduced.

3. Results and Discussion

Sample calculations are presented in Fig. 2. Linear relations between r and $N(r)$, and r and $I(r)$ were obtained both in the meso/mega scale and the micro-scale data. No significant deviations from linearity are found in the transect line data. Note that all segments have copepods when r is very large, and thus the slope of the regression lines in the box-counting algorithm coincides with the Euclidean dimension i.e. $D = 1.0$. This is obviously an artifact and these points were excluded in the calculation of the capacity dimension. Consequently, linear regressions were performed for each transect line of the scales of 2 to 8 km for box counting and 2–128 km for the information dimension. Estimated fractal dimensions are listed for each transect line in Table 1. The dimensions of capacity and information for transect lines ranged from 0.72 to 0.85, and 0.83 to 0.89, respectively. Similar but slightly lower dimensions were obtained for the micro-scale observation at Stn. A. These results suggest that fractal facets in copepod distribution prevailed over scales from tens of meters to over 100 km. The estimated capacities were somewhat lower and more variable than the information dimensions. This might be due partly to the difference in range of scales.

Estimated dimensions can be converted to fractal dimensions on a horizontal plane

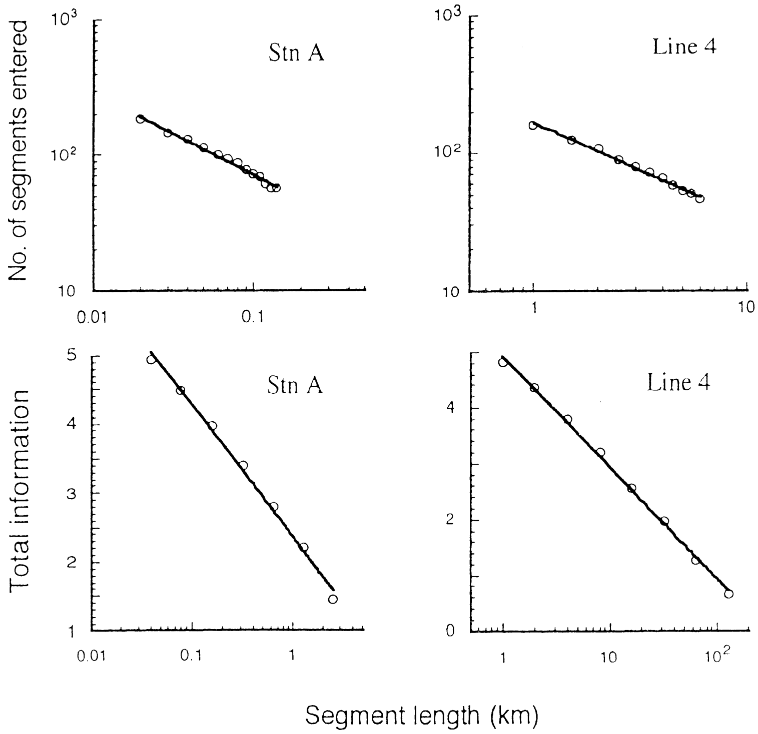

Fig. 2. Relationships between segment length and number of segments with copepods (upper) and total information (lower) for the meso/mega scale observation along cruise track and micro-scale observation at Stn. A. The sampling intervals in minutes were converted to lengths using mean ship speeds.

Table 1. Estimated fractal dimensions of 1 dimensional distribution of *Neocalanus cristatus* for meso/mega scale and micro-scale observations. Parentheses indicate standard error.

	Meso/mega scale				Micro scale
	line 1	line 2	line 3	line 4	Stn. A
Capacity dimension	0.83 (0.01)	0.85 (0.01)	0.72 (0.02)	0.76 (0.04)	0.68 (0.02)
Information dimension	0.84 (0.03)	0.89 (0.02)	0.83 (0.02)	0.89 (0.04)	0.84 (0.03)
Power law index of power spectrum	–0.33	–0.47	–0.38	–0.23	—

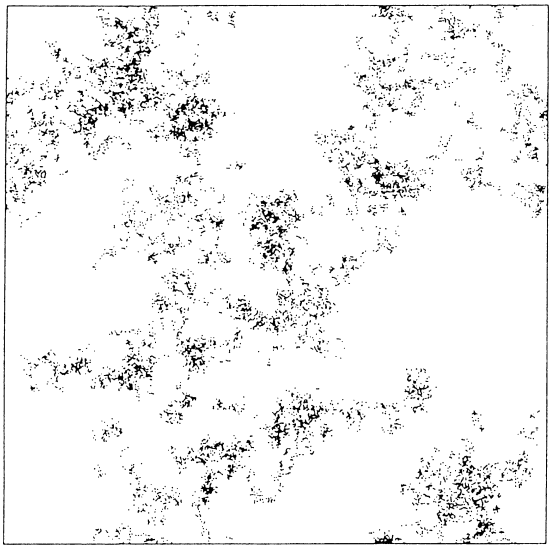

Fig. 3. Lévy dust simulated with fractal dimension of 1.8 on 2 dimensional plane.

(Euclidean dimensions = 2) by adding 1.0 to the estimated dimensions from the line transect, if we assume isotropy in the horizontal direction (Sreenivasan and Meneveau, 1986). Some support for isotropy is provided by the similarity of the estimated dimension of line 2 (S-N direction) with those of other lines (WSW-ENE) (see Table 1). A simulation of the copepod horizontal distribution based on the estimated fractal dimension of 1.8 is presented in Fig. 3. The fractal point pattern is realized by the so-called Lévy dust (Mandelbrot, 1982). When we regard a point as an individual copepod and assume an *in situ* abundance of 41 copepods m^{-3}, typical for the surface layer (Tsuda *et al*., 1993), the figure gives a bird's-eye view of a $50 \times 50 \times 0.1$-m distribution.

Power law indices of the power spectra are also shown in Table 1. Although the relationship between the power law index and the fractal dimension is not clear over the range of the present study, they do not deviate from the predicted value estimated by numerical investigations (Fox, 1989; Higuchi, 1990).

Reported fractal dimensions of two dimensional oceanic turbulence range from 1.2 to 1.4 (Osborne *et al.*, 1989; Osborne and Caponio, 1990; Sanderson and Booth, 1991). Therefore, the estimated fractal dimensions for copepod distribution are considerably higher than those of oceanic turbulence. Since phytoplankton are expected to behave passively with turbulence (Denman and Platt, 1976), their distribution possesses the same fractal dimensions as oceanic turbulence (A. Okubo, personal communication). On the other hand, copepod distribution showed higher fractal dimensions than turbulence, even though zooplankton share the same environment with phytoplankton. Higher fractal dimension corresponds with weaker wave-number dependence in the power spectrum. Copepods and phytoplankton differ in their size and mobility. I ignore the reproduction of copepods in my analysis, because the copepods were pre-dormant stage (Miller *et al.*, 1984). We speculate that copepod behaviors such as diel migration, phototaxis, rheotaxis, and social behaviors should cause the larger fractal dimensions (flatter power spectrum) in comparison with phytoplankton. Steele and Henderson (1992) derived a flatter spectrum for zooplankton in a numerical experiment based on the Lotka-Volterra equations with diffusion terms. They suggest that a zooplankton mortality term (predation) given as a stochastic variant, causes a difference in the spectra of phytoplankton and zooplankton under appropriate diffusion coefficients. They mentioned that the predation term should not be interpreted only as stochastic predation, but may also include random redistribution which could occur as a result of diel vertical migration combined with vertical shear. In other words, because zooplankton have more random processes determining their distribution than phytoplankton, zooplankton show a more fragmented and plane-filling distribution.

Fractal dimension of food particles (or prey) is very important to grazers (or predators), because the food availability changes depending on the dimension. Low dimension means smooth and predictable distribution or particles gathered in small numbers of flocks, and high dimension means rough, fragmented, plane-filling and unpredictable distribution. Therefore, when a predator has some information on the location of the prey or can remotely detect them, foods with low dimension should be more efficient. In contrast, when a predator has no information or detection ability, foods with high dimension should be relatively better, because available food quantity or encounter rate approaches proportional to searched volume with increase of fractal dimension.

Heterogeneity of zooplankton distribution has been a complicated problem to study and patchy distributions are often represented using four or more parameters (e.g. Fasham *et al.*, 1974). The simulation in the present study, however, demonstrates that only two parameters, average abundance and fractal dimension, are sufficient for accurately describing and reconstructing the patchy nature of the horizontal distribution of copepods. As shown by some studies (Morse *et al.*, 1985; Caddy and Stamatopoulos, 1990), I believe that fractals are the simplest expression of irregular distribution of some objects in ecological models.

Acknowledgements

I greatly appreciate Dr. Akira Okubo for critically reading this manuscript and for various discussions. I am also grateful to Drs. M. J. Dagg and C. B. Miller for their critical reading and encouragements. I thank Dr. H. Sugisaki and the scientists aboard for their cooperation in sampling and discussion, the crew members of R/V *Hakuho Maru* for the ship operation, Drs. Y.

Ogata and S. Nakamoto for the discussion, Messrs M. Toyokawa and J. Nishikawa for drawing the figures, and to Dr. H. Takayasu for motivating the present study through his essays on fractal.

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