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Theme session on "The Influence of Intermediate-Scale Physical Processes on the Transport and Food Environment of Fish"

Patchiness of plankton and abiotic variables: at what scales and turbulence levels do distributions differ?

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Abstract:

The distribution of plankton is non-random and characterized by patterns of aggregation at various spatial scales. The size of these aggregations is influenced by biotic (e. g., reproduction, predation) and abiotic (e. g., turbulence intensity, circulation features) factors. In this study, we compare the spatial variability of abiotic variables (temperature, conductivity) with those of simultaneously-measured zooplankton distributions. Our working hypothesis is that zooplankton patch structure will differ from that of the physical variables due to zooplankton swimming behaviour and other biological processes. We present preliminary transect results of optical particle counts and physical variables that were measured in the southern Baltic Sea as part of an EU/AIR project investigating environmental effects on cod recruitment and reproductive success. Data were collected at sampling intervals of < 10 m allowing us to resolve spatial patterns at scales of 10's - 100's of metres. We have found that patch structure of zooplankton at these scales differs substantially from that for the temperature or conductivity measurements. However, the conditions of turbulence under which such aggregations form and persist require further theoretical and empirical study. We compare our findings to related observations in the literature that have been made in other environments and at other scales of resolution.

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Introduction

A paradox of fisheries oceanographic research is that larval fish in nature appear to grow and survive at high rates even though prey levels are much less than those required to produce the same growth rates in laboratory experiments (Anderson 1988). This discrepancy is partly due to zooplankton being distributed in patches whose sizes are smaller than the tow distances (1000's of metres) typically used to estimate zooplankton abundances (Owen 1989, Jenkins 1989, MacKenzie et al. 1990), but which may be important for larval fish feeding (e. g., Hunter and Thomas 1974, Lasker 1975, Munk and Kjørboe 1985). Hence prey abundances derived from integrative plankton samplers will frequently underestimate prey availability for larval fish, and give no indication of the small-intermediate scale distribution of such prey.

Plankton distributions can however be resolved at small spatial scales (< 10 's of m) with automated particle counters (e. g., Mackas et al. 1985) and with unobtrusive video microscopy (Davis et al. 1992). Results obtained using these instruments show that spatial variability of both plankton and water temperature is distributed across a wide range of scales (Platt and Denman 1975, Mackas and Boyd 1979, Mackas et al 1985), and that variance spectra are typically characterized by high variability at large scales and a logarithmic decline in variability towards smaller scales. The shape of temperature spectra depends mainly on the degree of turbulent mixing between water masses, whereas the shape of plankton spectra is due to the interaction of biological processes (e. g., mortality, reproduction, swimming behaviour) with the turbulence (Platt and Denman 1975, Mackas et al 1985). Hence, under different scenarios, the spectra of temperature and plankton could be similar or different, depending on the relative importance of biological processes (e. g., plankton swimming speed, reproduction rate) and turbulence intensity.

In the case of zooplankton, whose patch structure in the vertical dimension differs greatly over time (Lasker 1975, Owen 1989), we hypothesize that in moderate to highly turbulent conditions, its spectra will closely resemble that for water temperature at most resolvable spatial scales. However, in the horizontal dimension and in calmer conditions, or more generally in situations where biological processes can overcome the velocity of turbulent water motion, we hypothesize that zooplankton patch structure will differ from the temperature spectra. In general therefore, we anticipate that the coherence between plankton and temperature spectra will be related to the intensity of turbulence during and shortly prior to sampling.

We have begun to test these hypotheses using a towed optical particle counter as part of fieldwork within a larger European Union project investigating recruitment and reproductive success in Baltic cod. We have intentionally focussed our sampling and analyses on processes operating at small-intermediate scales (10's-100's of metres) because it is these scales which are of most relevance to larval and 0-group fish feeding, and because of the relative scarcity of data describing processes at such scales. Our general objective is to determine under what conditions small-intermediate scale plankton patchiness is determined by biological and physical processes.

Materials and Methods

General:

Our sampling plan was designed to sample different hydrographic situations to compare plankton particle distributions under contrasting levels of turbulence. We also were interested in comparing the degree of horizontal patchiness with that vertically. To meet both of these requirements, we deployed an optical particle counter (OPC) equipped with a CTD along a cruise track which sampled vertically as well as horizontally at different fixed-depths.

Sampling site and methods:

Sampling was conducted in the centre of the Bornholm Basin in the southern Baltic on the evening of August 10, 1994 (Figure 1). A CTD profile taken at the western end of the transect < 30 minutes before OPC deployment showed that the water column was highly stratified and consisted of three layers. A surface wind-mixed layer overlaid the summer thermocline, which was located at depths 18-25 m. An intermediate mixed layer separated the seasonal thermocline from the permanent halocline, which was located at 46-70 m. This water column structure is typical for this region (Møller and Hansen 1994). During the deployment period, and the preceding 72 hours, wind speeds were low (Fig. 2; mean = 3.1 m/s), and the sea was calm.

Tow depths for horizontal sampling were located within the surface mixed layer, within the thermocline, and at the base of the thermocline (Fig. 3). Tow speed was ca. 3 knots, which in combination with the sample interval of the OPC resulted in a spatial sampling interval of 3 m. Tow distances in the horizontal sections of the track were ca. 800-1000 m.

Particle size and abundance was recorded in situ by the OPC. The basic operating principle involves the enumeration of particles as they pass across a beam of light. Shadow size during passage through the light beam is used to estimate body size, which is reported as equivalent spherical diameter (esd).

The sizes of particles in which we were interested are those similar in size to prey consumed by larval and 0-group cod (i. e., copepod nauplii and copepodite; Bainbridge and McKay 1968, Kane 1984). We conducted most of our analyses on two size groups of plankton (356 and 449 μm esd), which overlap the range in length of copepod nauplii and copepodites found in the southern Baltic (Krajewska-Soltys and Linkowski 1994).

Data analyses:

Particle abundances from the four horizontal transects of the OPC track were subject to time series statistical methods. These consisted of autocorrelation and spectral analyses (Chatfield 1989). All statistical procedures were conducted using programs in the SAS language (SAS 1986). Spatial series were first truncated to the same length (789 m; 263 observations) and then evaluated for stationarity using standard linear regression methods. If a significant slope ($P < 0.05$) was present for the series, the residuals from the fitted regression line were used in time series analyses rather than the raw values.

Spectral analyses were used to identify the scales of spatial variability. Briefly, this statistical technique is an exploratory analysis of variance in which the total series

variance, σ^2 , is partitioned into frequencies ranging from the lowest frequency associated with the series length ($1/789 \text{ m} = 0.0013 \text{ m}^{-1}$) up to the Nyquist frequency ($1/2 \cdot \Delta x = 1/(2 \cdot 3) = 0.166 \text{ m}^{-1}$). The periodogram estimates at each frequency were then smoothed with a triangular window. Spectra were then evaluated with a Kolmogorov-Smirnov statistic to determine if they differed significantly from the spectrum of a random spatial series (SAS 1986). If plankton and temperature spectra from the same transect differed significantly from spatial random distributions, the squared coherence between the two series was then calculated to determine whether variability in one series coincided with variability in the other series at identical spatial scales. Scales of significant association ($P < 0.10$) between the two series were determined as those at which the squared coherence differed significantly from 0. The minimum significant squared coherence (0.13) used for our comparisons was calculated according to Koopmans (1974) with $n = 18$.

Results:

The vertical distribution of the small size class of plankton particles shows a marked peak in abundance in the middle of the principle thermocline (Fig. 4). Abundance was about 2-fold higher in the thermocline than a few metres above, and about 5-fold higher than a few metres below. Similar results (not shown) were also seen with the other size class and the sum of the two size classes.

Abundance of the smaller size class was generally about two-fold larger than that of the larger size class (Fig. 5). The temperature profile measured during the particle count transect is similar to that obtained immediately before the track began.

The horizontal transects showed little upward or downward trend within each series (Fig. 6). The coefficient of variation (SD/mean) for particle abundances was low (ca. 20-40%), but, in two instances, the spatial distribution of this variability differed significantly from a random distribution (Table 1, Fig. 7). In these cases, the variability in abundance was greatest and relatively constant at large scales (ca. 100 - 800 m), and lowest and also constant at small scales (6 - 50 m). Variability decreased by the largest amount at scales of 50 - 100 m.

In all transects, both temperature and salinity spectra showed strong evidence of non-random spatial variability. In these cases, the variability was greatest and relatively constant at large spatial scales (100 - 750 m), and was lowest and relatively constant at the smaller scales (6 - 25 m). At intermediate scales (25 - 100 m), variability in temperature decreased most dramatically.

The pattern of significant variability in particle abundances and temperature suggests that fluctuations in these series may be correlated at some spatial scales. The squared coherence between these variables shows that variability in the two series is significantly coherent at some scales, and that the spatial scales of this variability differed between transects. In the thermocline transect I, squared coherence was significant at small and intermediate scales (Fig. 8), whereas in the sub-thermocline transect P, squared coherence was most significant at the largest spatial scales (Fig. 9).

Discussion:

General

The particle abundances measured in our transects are similar to abundances of copepod nauplii and copepodite enumerated from net plankton tows during the same time of year in the same area. Krajewska-Soltys and Linkowski (1994) observed abundances of 5-10 individuals l^{-1} in the 0-15 m depth range, 15-30 l^{-1} in the 15-30 m depth range, and < 5 l^{-1} in the 60-90 m range. These values overlap the range in abundances recorded at similar depths by the OPC (Fig. 4), and suggest that it can assist in describing distributions of plankton.

Scales of patchiness

Horizontal variability in particle abundance during our survey was relatively small, and generally was distributed randomly across spatial scales. This distribution pattern is substantially different from that of our temperature and salinity distributions, which showed significant and strong departures from randomness. This pattern has been observed by others working at larger scales of resolution (e. g. Mackas and Boyd 1979: 556 m; Weber et al. 1986: 1000 m), and is consistent with the fact that temperature and salinity are conservative tracers of water motion, whereas plankton particle distributions can also be affected by biotic processes.

The scales of greatest temperature variability indicate that temperature is most influenced by processes occurring at spatial scales of at least 100 m. At scales below 100 m, temperature variability decreases, and appears constant between scales of 6 - 25 m. These observations, coupled with the fact that the abiotic and biotic variables were only weakly and inconsistently coherent across spatial scales, suggests that the plankton distributions were largely independent of the variability in temperature and salinity.

The uncoupling of variability in the particle abundances from the physical variability may be due to the relatively calm conditions which prevailed during and prior to our survey. Although we have no direct measures of dissipation rate during our study, wind-generated turbulence would have been low in the surface layer (estimated dissipation rate at 10 m depth for a 3 m/s wind speed would be ca. $5.7 \times 10^{-9} \text{ m}^2 \text{ s}^{-3}$; MacKenzie and Leggett 1993), the high level of stratification in the thermocline would have further reduced any mixing due to wind, and tidal mixing in the Baltic is essentially nil (Møller and Hansen 1994). It is possible that residual current flows (Møller and Hansen 1994) could have generated sufficient turbulence to induce the temperature variability seen in our spectra. Nevertheless, regardless of the source of the turbulence, the spectral results suggest that there was sufficient turbulence to generate significant spatial variability in temperature records, but it was insufficient to overcome the swimming ability of the particles enumerated by the OPC and to cause mixing of particles layered at different depths (Fig. 2). Alternatively, particles may have been distributed in patches at scales smaller than those resolved with our OPC. For example, Davis et al. (1992) observed copepods in patches at scales < 20 cm coastal waters off Massachusetts.

We suspect that more of our particle distributions would have deviated from randomness, and been coherent with the physical variables across a wider range of spatial

scales, if conditions had been more turbulent. This is because there was strong vertical differences in particle abundances, which mixing would have re-distributed throughout the water column. In addition, turbulence-related circulation features (e. g., Langmuir cells, internal wave motion) could also have created distributions that would differ from randomness. This hypothesis should be investigated under more turbulent conditions.

Our finding that particle distributions at these spatial scales (6-789 m) were randomly distributed and mostly incoherent with temperature and salinity is similar to some previous studies. For example, Weber et al. (1986) found that spectra of Antarctic krill distributions were similar to random distributions, whereas Mackas and Boyd (1979) observed that zooplankton spectra were flatter than both temperature and chlorophyll spectra, and not significantly coherent with the temperature spectra. They suggested that the difference in slope could be associated with zooplankton swimming behaviour, which also appears to be a cause of randomness in our particle distributions.

Although the general pattern of variability in our particle distributions was random, we did observe two instances where particles were distributed in significant aggregations. In these cases, the spectra tended to be most variable at large spatial scales and least variable at small spatial scales. In contrast, in the cases where spectra resembled a flat or "white-noise" spectrum, there were no significant scales of aggregation observed along the tow path.

The spatial scales of particle variability that we report can be interpreted as patches of different sizes superimposed on each other. For example, the variability in two of our particle abundance spectra (e. g. Fig. 7) was greatest at larger scales. This suggests that the OPC travelled through patches having a linear dimension of at least 100 m. Once inside such a patch, particle distributions appeared to be relatively uniform with little variability at smaller scales; hence, the large decrease in variability at progressively smaller scales. In those cases where the spectra were similar to a random distribution of particles, we conclude that the OPC was in a patch whose linear dimension exceeded the largest spatial scale traversed by our instrument (i. e., > 789 m).

Plankton patchiness and larval fish foraging strategy:

From the perspective of a larval fish foraging for prey, the most effective strategy would be to explore the water column vertically rather than horizontally, at least under the calm conditions observed during this study. By moving vertically 15 m, larvae could encounter a 5-fold range in particle abundance. However, by moving horizontally, such variability would not be encountered unless the larva swam distances larger than those covered during our transects (i. e., greater than 789 m). At spatial scales between 6 and 789 m, and based on our spectra, the probability of finding a 5-fold variability in particle abundance is essentially nil.

Conclusions:

We observed a significant decoupling of distributions of plankton particles from distributions of abiotic variables under calm conditions in the Baltic Sea. This uncoupling was observed at spatial scales of 6 - 789 m which are smaller than those used in some previous related studies. We attribute the decoupling to the swimming ability of plankton which was sufficient to overcome the weak conditions of turbulence which prevailed during the study, and which enabled plankton to form layers at different depths. It is hypothesized

that additional sampling under more turbulent conditions would indicate patchier distributions of plankton due to mixing of these layers.

Acknowledgements:

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Table 1. Summary of results of Kolmogorov-Smirnov white-noise tests for spectra of particle abundance, temperature and conductivity measured on 4 sections of the transect shown in Figure 3. Values with asterisks indicate distributions which differ significantly from randomness ($P < 0.10$).

	Transect			
Variable	H	I	M	P
Small zoopl. (356 μm)	.0641	.1155	.0671	.1234*
Large zoopl. (449 μm)	.0778	.1004	.0738	.0543
356 & 449 μm	.0717	.1414*	.0914	.0971
Temperature	.1981*	.1714*	.8312*	.6257*
Salinity	.8485*	.7634*	.7457*	.8712*

Figure Captions:

Figure 1. Map of southern Baltic showing depth contours, and position of optical particle counter transect.

Figure 2. Wind speeds recorded at 3 hour intervals during the month of August, 1994. "ZP" denotes time when particle counter was deployed. Mean wind speeds during the 24, 48, and 72 hours previous to this point were 3.1, 2.5 and 2.6 m s⁻¹ respectively.

Figure 3. Left panel: Tow track of the optical particle counter. Data analyses are based on the sections labelled with letters. Right panel: temperature and salinity at the beginning of the OPC deployment.

Figure 4. Solid line: abundance of particles in the 356 and 449 μm size-groups measured with the OPC. Dotted line: temperature profile. The arrows and corresponding letters refer to the depths where the OPC was towed horizontally (see positions in Figure 3).

Figure 5. Mean and 2 x standard error of the abundance of particles in the 356, 449 μm and summed size-groups at 4 depths in the Bornholm Basin during August 1994.

Figure 6. Raw spatial series of temperature and particle abundances on transect I (Figure 3). Particle abundances are the sum of those in the 356 and 449 μm size classes.

Figure 7. Spectra of the summed abundance of particles in the 356 and 449 μm size classes (solid line), and for the water temperatures (dashed line) on transect I (see also Fig. 6).

Figure 8. Squared coherence of the transect I particle abundances and water temperature (Fig. 6). The dotted line is the minimum squared coherence significant at the 10% probability level.

Figure 9. Squared coherence of the transect P particle abundance in the 356 μm size class and water temperature. The dotted line is the minimum squared coherence significant at the 10% probability level.

Figure 1

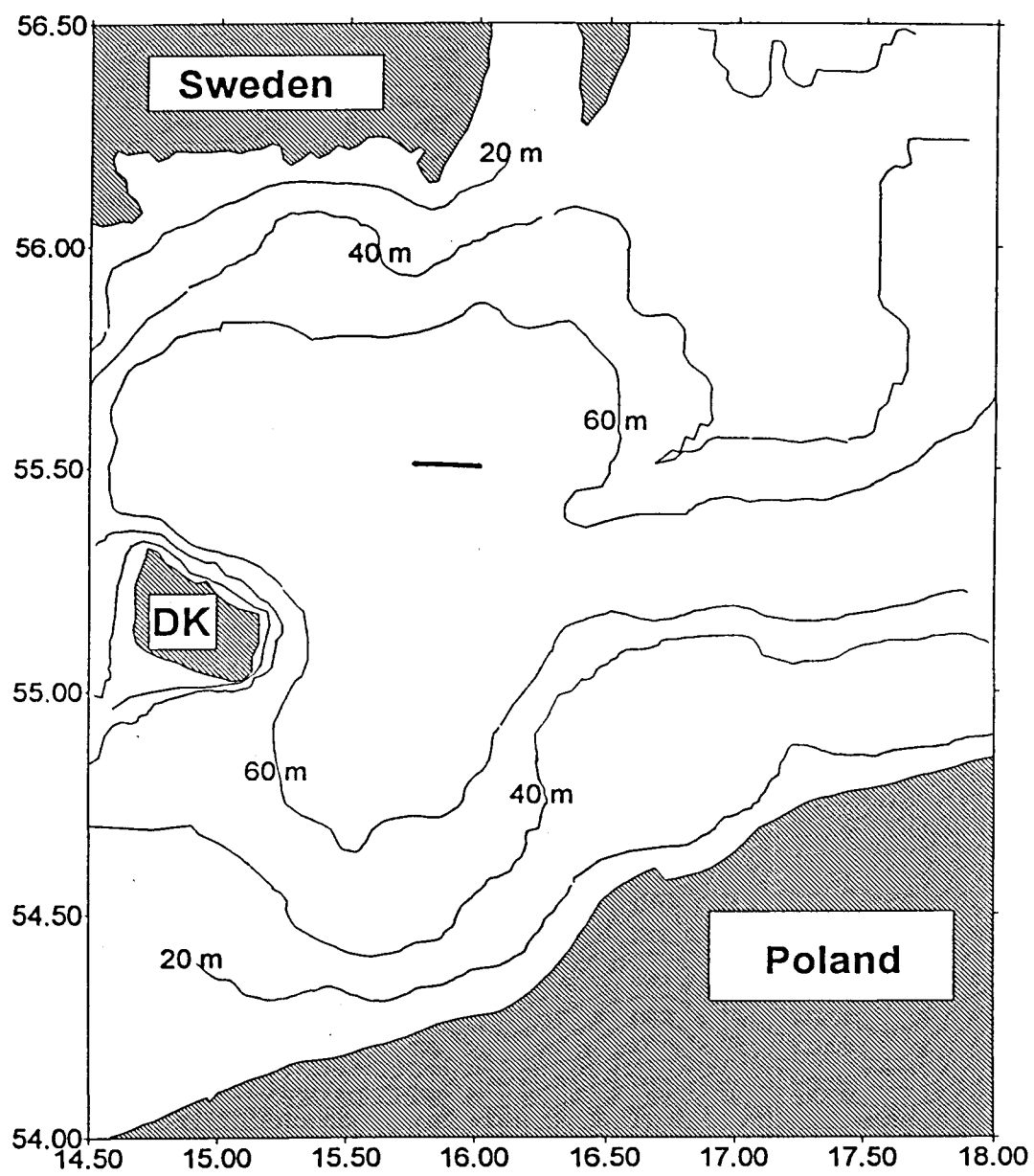


Figure 2

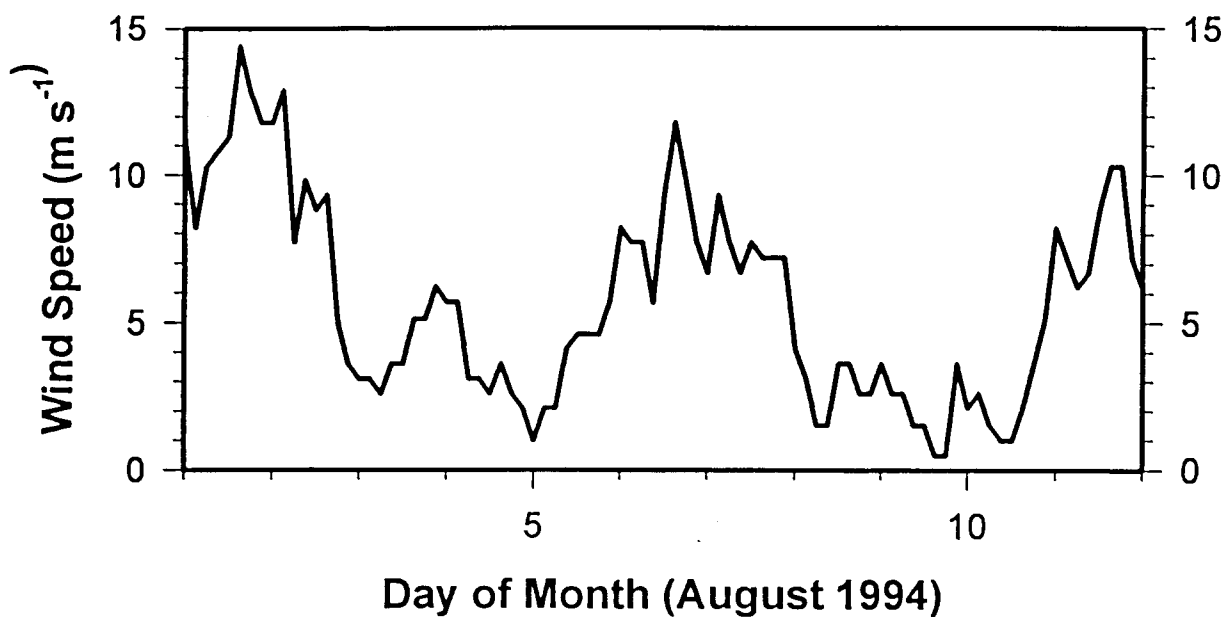


Figure 3

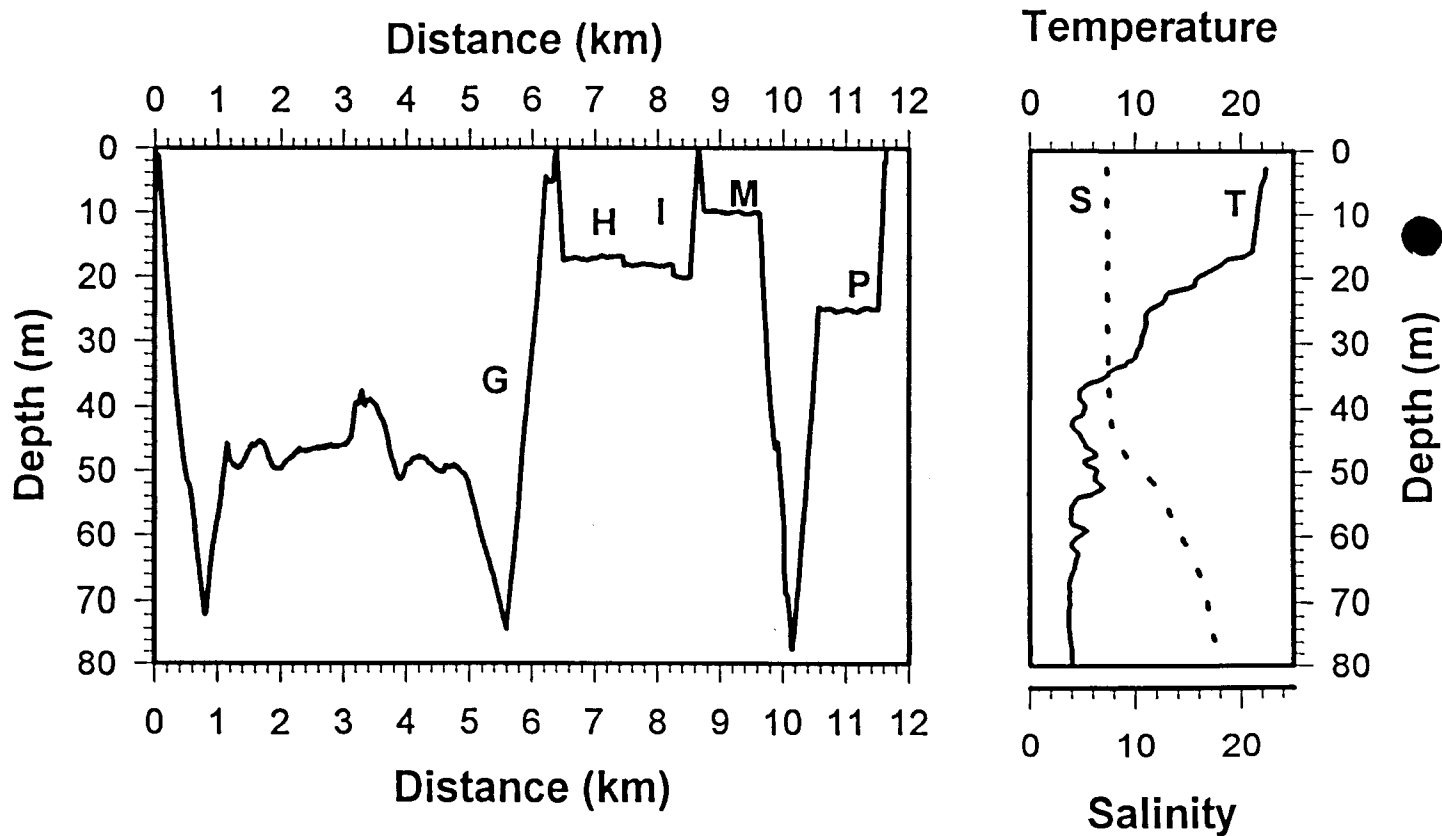


Figure 4

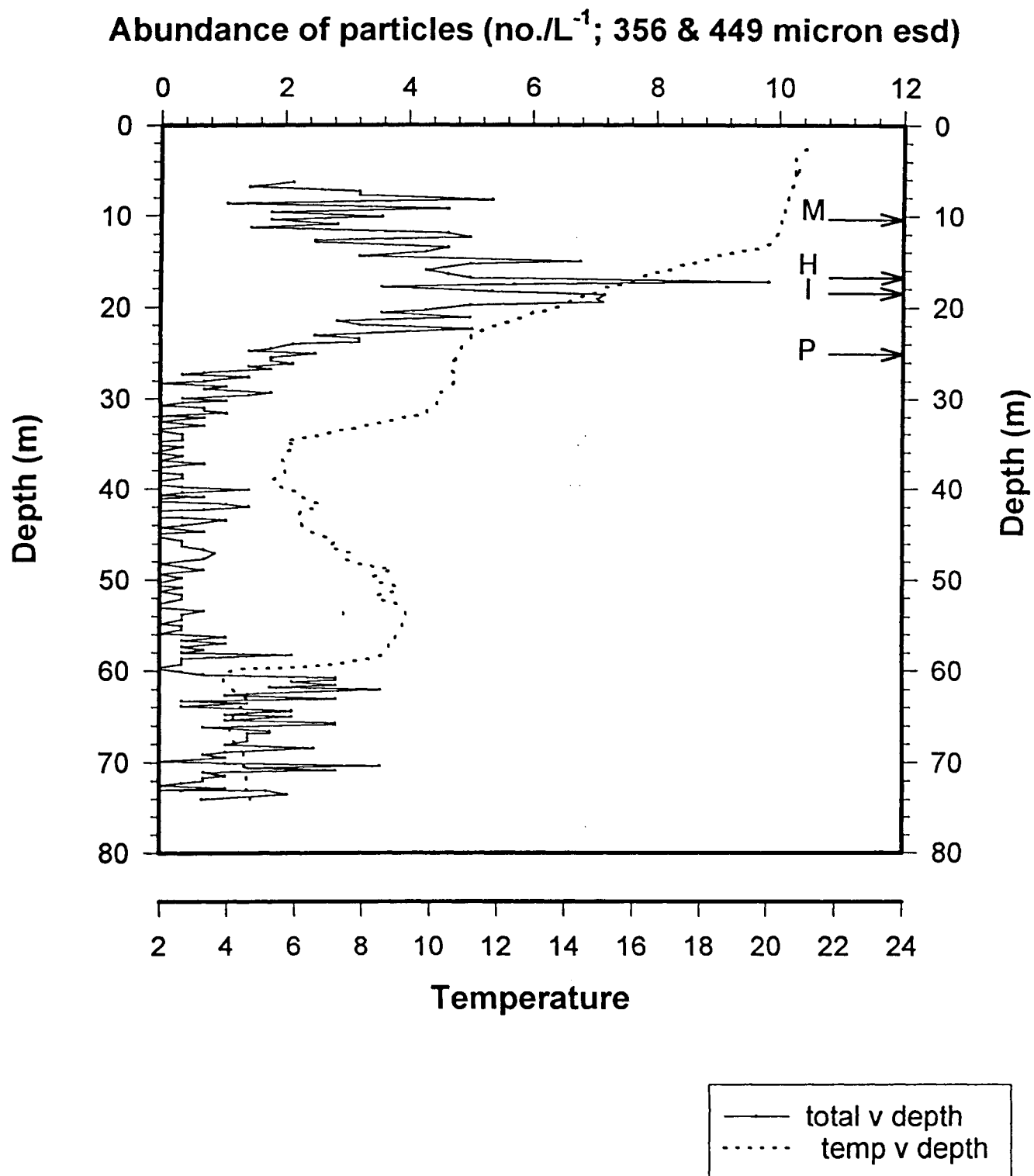


Figure 5

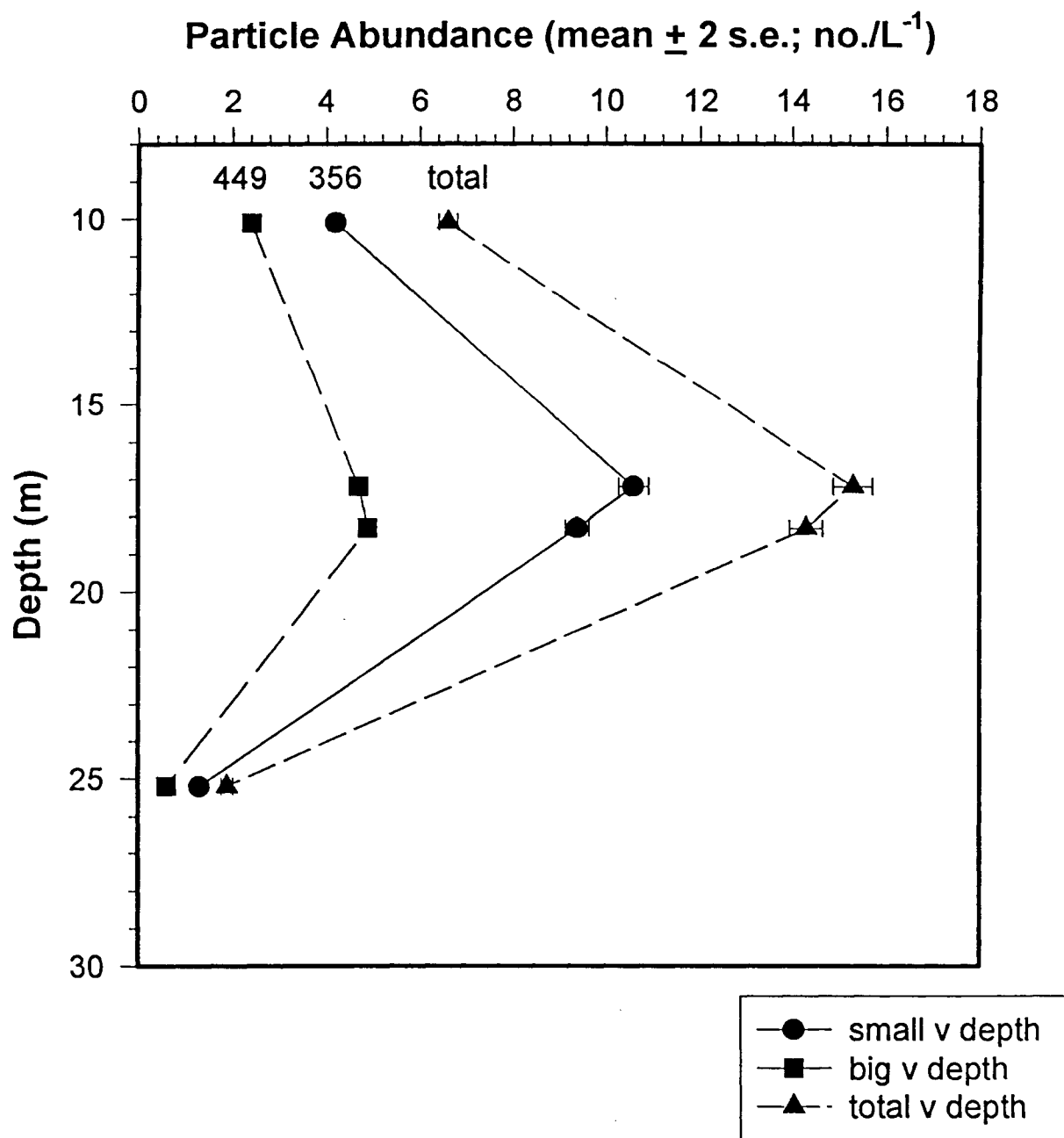


Figure 6

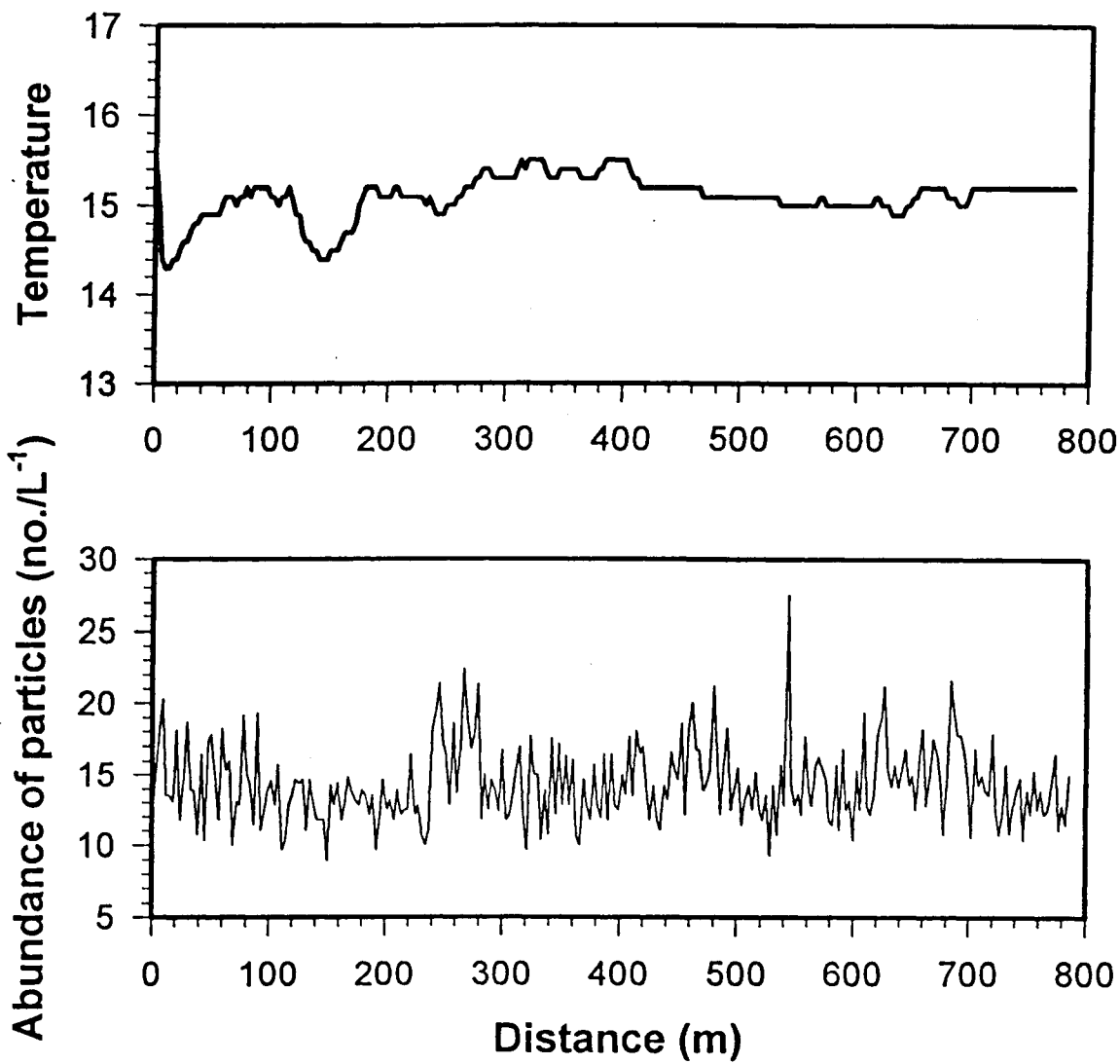


Figure 7.

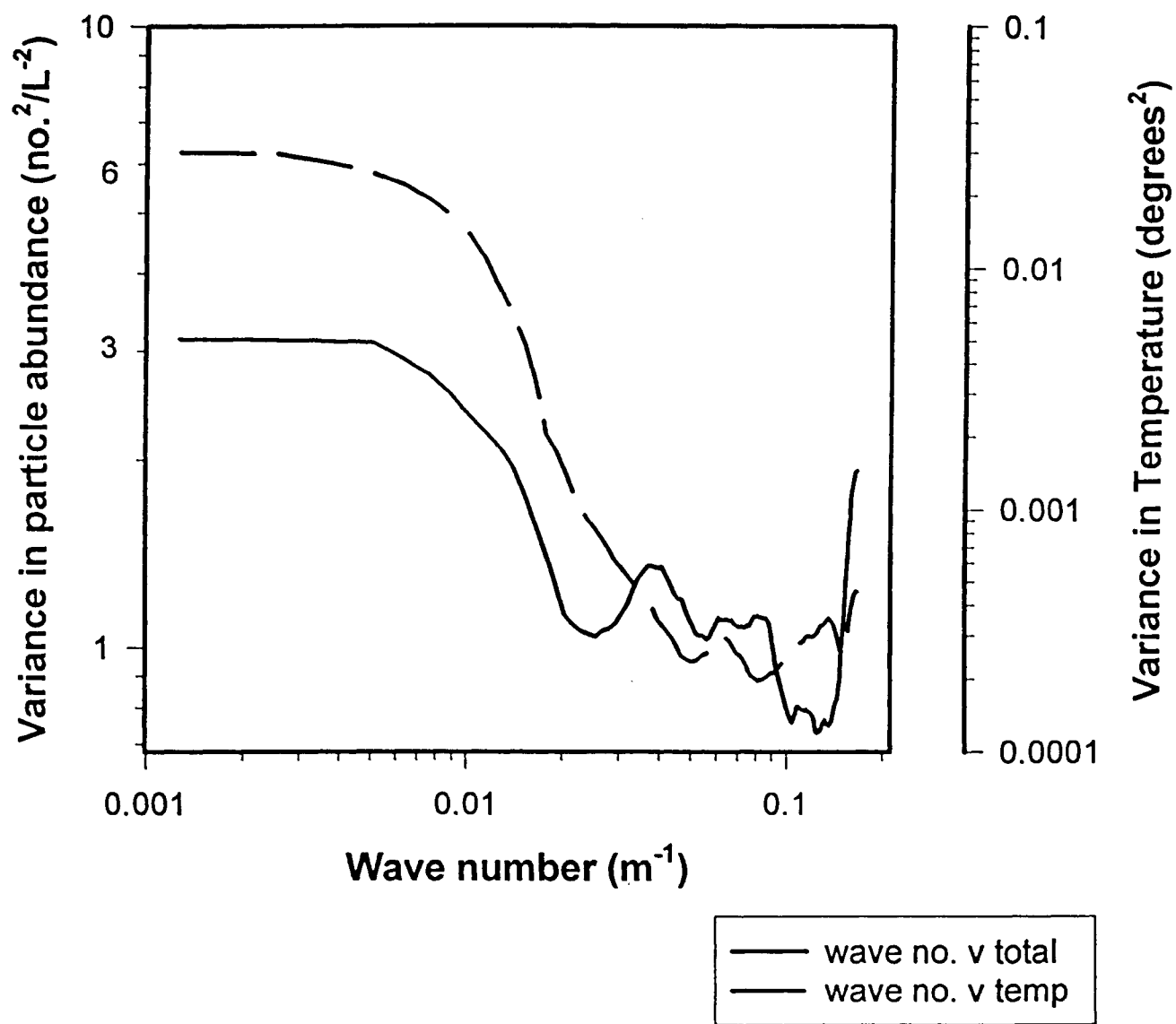


Figure 8

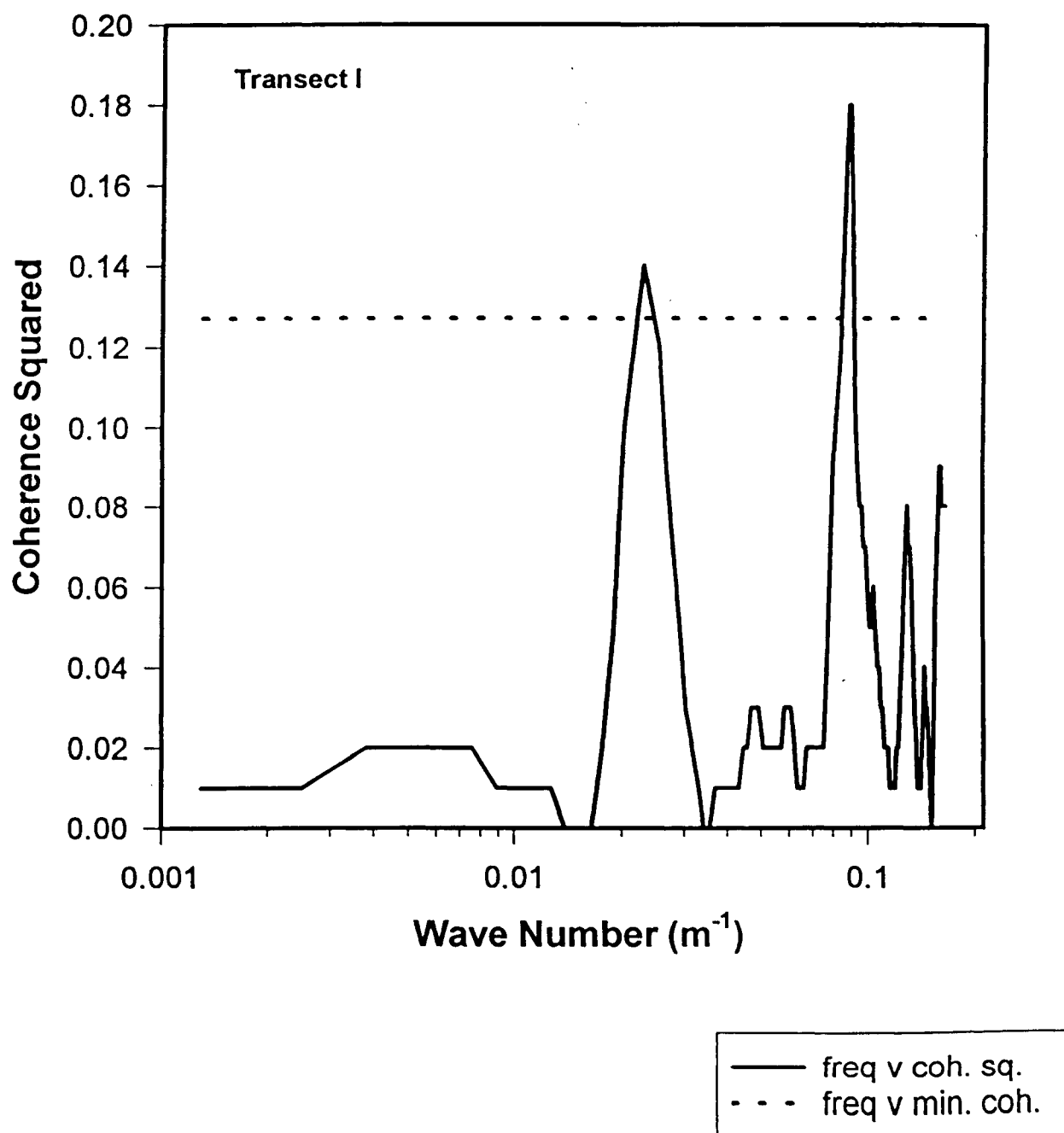
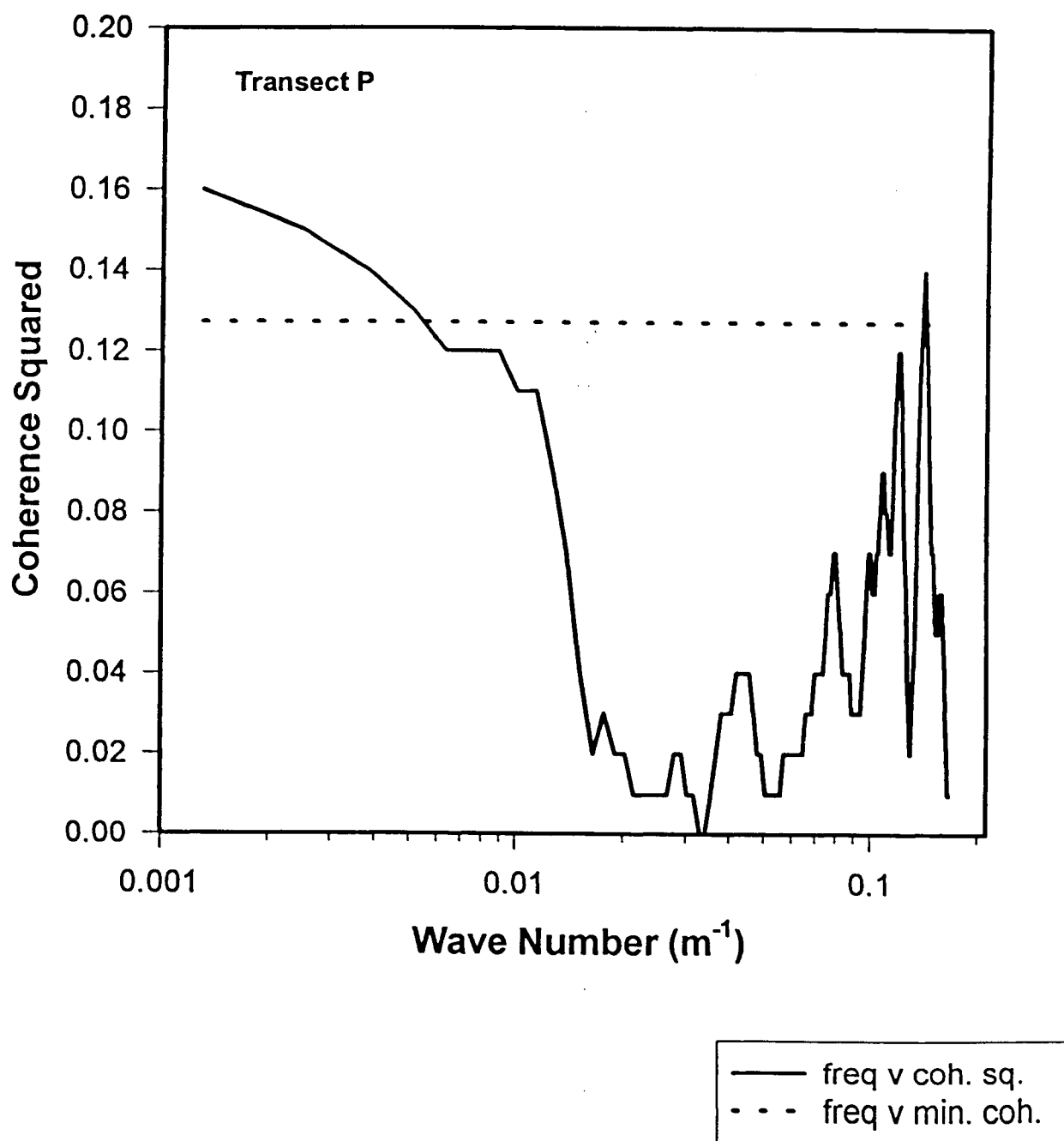


Figure 9



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