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Spatio-temporal dynamics of chlorophyll in the open Baltic Sea

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Abstract. Five charts of the chlorophyll and hydrographic fields by vertical profiles of *in situ* fluorescence and CTD were made on a stationary grid of 20 x 25 nautical miles with a 5-mile spacing in the open Baltic Sea. Both chlorophyll levels and variability were maximal close to the spring bloom. High chlorophyll levels in summer are sustained by recurrent nutrient injections from the deep saline layer. Two of the surveys showed close coupling between the coarse-scale (~ 10 km) chlorophyll distribution and the hydrographic structure determining the intensity of nutrient transfer. Vigorous advection, stirring and current shear, associated with a strong mesoscale eddy, probably dominated the chlorophyll pattern on three surveys. The upward velocities in the cyclonic eddy resulted in accumulation of phytoplankton in the aphotic zone. Intensive heat input from the surface caused a sudden sinking of the phytoplankton and the formation of a pronounced sub-surface chlorophyll maximum.

Introduction

Several investigations (Steele, 1978; Steele and Henderson, 1979; Pingree *et al.*, 1978, among others) have exemplified that the study of phytoplankton spatial heterogeneity can provide valuable information on the control and functioning of the whole pelagic ecosystem. Due to the plankton spatial variability and its interaction with a broad spectrum of motions in the sea, temporal sequences of point data are inherently difficult to interpret. Whilst it is generally acknowledged (e.g., Cushing, 1975) that factors controlling the temperate pelagic ecosystem are temporally different, there are only a few studies concerning the temporal succession of plankton spatial patterns (Horwood, 1978; Steele and Henderson, 1979). The *in vivo* fluorescence of chlorophyll *a*, in spite of some methodological problems, has widely been used as an index of phytoplankton biomass. Even using the method of *in vivo* fluorescence, it is inherently difficult to obtain sufficient areal coverage while retaining adequate resolution of the smaller horizontal and vertical scales. Hence, most investigations are restricted to mapping only the surface distribution of chlorophyll *a* along a transect. However, surface distributions need not be representative of the whole chlorophyll layer, since, as a common feature, a significant portion of the phytoplankton standing crop and its highest variability may be associated with the thermocline (Holligan and Harbour, 1977).

As part of an interdisciplinary study, spatial surveys of the chlorophyll and hydrographic fields were made on a stationary area in the Central Baltic Sea in 1979 and 1980. Vertical profiles on a rectangular grid with a spacing of 5 nautical miles sacrificed the horizontal fine structure but provided a three-dimensional picture of the coarse-scale (~ 10 km) distribution.

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Hydrographically, the Baltic Sea, with a permanent halocline between 50–70 m depths, can be considered as an "overmixed" estuary (Shaffer, 1979). The upward flux of nutrients across the halocline is of vital importance to the primary productivity, since the sedimentation of particulate organic matter is intensive, especially during the spring bloom (Smetacek *et al.*, 1978). Shaffer (1979) has recently presented evidence that intensive vertical mixing in the Baltic is highly localized, occurring mainly near the coast or in the regions of special topography. He was, however, unable to find data supporting the ecological significance of the heterogeneity of the nutrient fluxes, and concluded that the nutrients were probably spread out evenly before any biological interactions could take place.

Here an attempt is made to show that a significant portion of the pronounced coarse-scale variability in the phytoplankton standing crop (Kahru, 1981a; Kahru *et al.*, 1981) can be ascribed to the hydrographic pattern which affects the upward flux of nutrients. Recurrent nutrient injections in summer, in spite of the strong thermal stratification, must support the high chlorophyll levels. Whilst a quantitative evaluation of the enhanced summer production must await further studies, it certainly complements the general understanding of production cycles (Cushing, 1975) in this area.

Methods

Charts of the chlorophyll and hydrographic fields were made on several cruises of the RV *Ayu-Dag* in 1979 and 1980 near the BOSEX site in the Southern Central Basin of the Baltic Sea. The surveys comprised vertical profiles on a rectangular grid of 30 stations which covered an area of 20 x 25 nautical miles (37.0 x 46.3 km) with a 5-mile (9.3 km) spacing (Figure 1). Subsequent stations were oc-

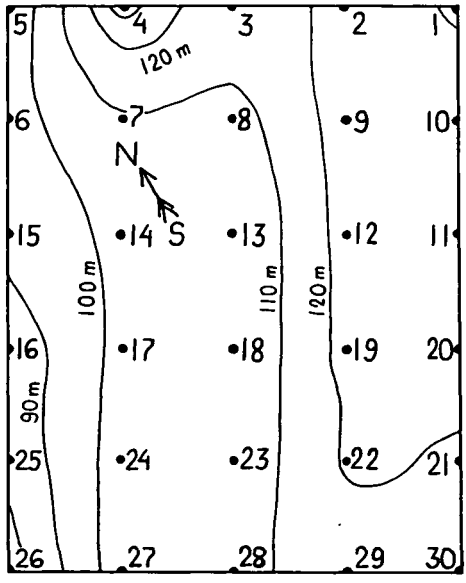

Fig. 1. Bathymetry and the station grid. Station spacing is 5 nautical miles. Station 17 has coordinates 56°09.7'N, 18°35.7'E.

cupied with ~1 h time intervals and the whole grid was covered in ~30 h. Analysis of the current measurements will be reported elsewhere. The surveys in 1979 are analyzed in Kahru (1981b). Here we describe the surveys in 1980: survey 1, 8–9 May; survey 2, 30–31 May; survey 3, 8–9 June; survey 4, 10–11 June, and survey 5, 1–3 July. Some details of survey 5 may be found in Kahru *et al.* (1981).

The profiler consisted of a Variosens *in situ* fluorometer (Impulsphysik GmbH, Hamburg, FRG) mounted on a Neil Brown Mark III conductivity-temperature-depth probe. The signals were interfaced to a HP 9825A computer used for data acquisition and processing. The vertical profiles were recorded down to at least 60 m depth with ~18 cm depth interval. The modified Variosens fluorometer (Herman and Denman, 1977), measuring *in vivo* fluorescence of phytoplankton chlorophyll *a*, was calibrated against the conventional trichromatic method (Jeffrey and Humphrey, 1975) for water samples taken from various depths at selected stations. Variability of the *in vivo* fluorescence yield of algal cells is well known (e.g., Heaney, 1978), but we found the mean standard errors of the estimates quite satisfactory (<0.5 mg m^{-3}) if separate calibrations were used for each survey. Details of the data processing and calibration procedures are reported in Kahru (1981a) and Kahru *et al.* (1981).

Due to the ship's drift, downtraces and uptraces had a spatial separation of the order of 100 m. Following the analysis of variance scheme of Therriault and Platt (1978), this was used to distinguish between the coarse-scale (~10 km) and the fine-scale (~100 m) components of density variability (Kahru *et al.*, 1981).

Results

General comments

The horizontal structure resolved by our station grid belongs to the coarse scale (Haury *et al.*, 1978), i.e., is of the order of 10 km. As horizontal, vertical, and temporal scales in a turbulent environment are not independent (Bowden, 1970), a consistent vertical scale must be selected. By analogy with the thermohaline fine structure (Fedorov, 1978), assuming the ratio of horizontal to vertical scales of the order of 10^3-10^4, the appropriate vertical scale is 10 m. As we are primarily concerned with the coarse-scale chlorophyll pattern, rather than the vertical fine structure (e.g., Derenbach *et al.*, 1979), the vertical profiles of chlorophyll *a* concentration were thus converted to integrated values over 10-m thick layers from 0 to 60 m depths. The integral concentrations were shown to be preferable to fixed depth values due to their less excessive fine-scale variance (Kahru *et al.*, 1981). The integral between 0–60 m depths is termed "total chlorophyll", although small and sometimes variable amounts of chlorophyll *a* existed even deeper.

Nutrient concentrations were measured on survey 5, but as the content of inorganic nitrogen was invariably very low in the upper and intermediate layers, no additional information was gained. McCarthy and Goldman (1979) have shown that under conditions of nitrogen limitation, almost immeasurable nitrogen pulses are rapidly removed by the phytoplankton. As both salt and nutrients are mixed upwards from the deep saline layer, a strong positive relationship exists

between them. Hence, we have used salinities at several depths as indicators of recent mixing and nutrient injections.

The means and estimates of variability of selected chlorophyll levels and salinities are summarized in Table I. The seasonal evolution of the chlorophyll *a* and sigma-t mean profiles is shown in Figure 2. Compared to the individual profiles, the mean profiles are, of course, over-smoothed. Variability in the physical structure is described by the vertical plots of the coarse-scale density variance (Figure 3). Maximal variances are clearly associated with the depth of the halocline. The formation of a strong thermocline (survey 5) has significantly reduced the density variance in the intermediate layer (depths 25–45 m), transferring it to the upper/intermediate layer interface.

Survey 1

The physical structure was characterized by a weak thermal stratification, intrusions and interleavings of different water masses. As the vertical density gradients above the halocline are low, this strong horizontal variability is not fully revealed by the sigma-t variance plot (Figure 3) which does not show the highest values at any depths.

The chlorophyll standing crop showed both maximal levels and maximal variability. Kaiser and Schultz (1978) have suggested that, in the central Baltic, the reduction of vertical mixing as a result of thermal stratification is the necessary condition for the phytoplankton spring outburst. Our data show no consistent linear influence of the upper 30 m stratification (measured as the sigma-t contrast between 5–30 m) on the chlorophyll levels. By contrast, the stratification is in-

Table I. Means and variabilities of some chlorophyll *a* integral levels (Chl) and salinities (Sal) on surveys 1–5.

	Depth (m)		1	2	3	4	5
Chl		Mean					
(mg m^{-2})	0–10		42.1	26.2	26.2	23.8	16.3
	0–60		120.3	72.1	66.3	73.4	61.5
		Max/Min					
	0–10		6.5	3.1	2.3	2.9	3.1
	0–60		3.2	3.2	1.8	1.5	2.4
		CV					
	0–10		41	39	23	21	25
	0–60		36	31	16	13	21
Sal		Mean					
(‰)	5		7.983	7.943	7.982	7.982	7.932
	60		8.379	8.609	8.628	8.485	8.385
		SD					
	5		0.060	0.106	0.038	0.033	0.043
	60		0.357	0.661	0.559	0.279	0.284

CV, coefficient of variation; SD, standard deviation.

hibitory to the 30–40 m chlorophyll ($r = -0.44$). On the other hand, there is strong evidence that the bloom was already nutrient limited. Highly significant correlations existed between the chlorophyll levels and the physical variables indicating vertical mixing: salinities at 5 m, 30 m, 60 m, and the deep layer depth (Table II). Shoaling of the depth of the deep saline layer is evidently an important condition for intensive vertical mixing. The correlation coefficient with the deep layer depth was −0.68 for the near-surface (0–10 m) chlorophyll and −0.58 for the total chlorophyll. The correlation coefficients with the salinities at 5 m and

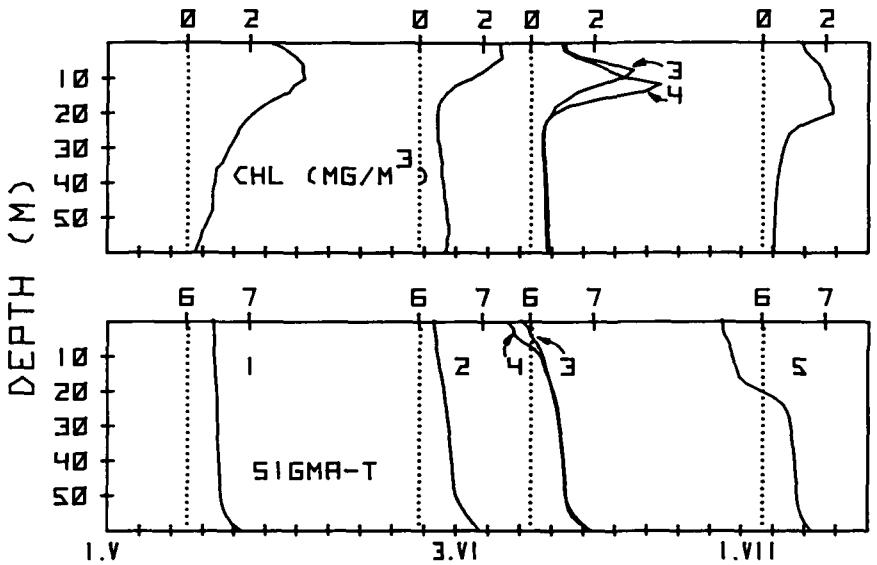

Fig. 2. Temporal changes in the mean profiles of chlorophyll *a* concentration and sigma-t on surveys 1–5. The vertical axes (dotted lines) are centered at the mid-times of each survey. For convenience, surveys 3 and 4, with a time interval of ~50 h, are plotted together.

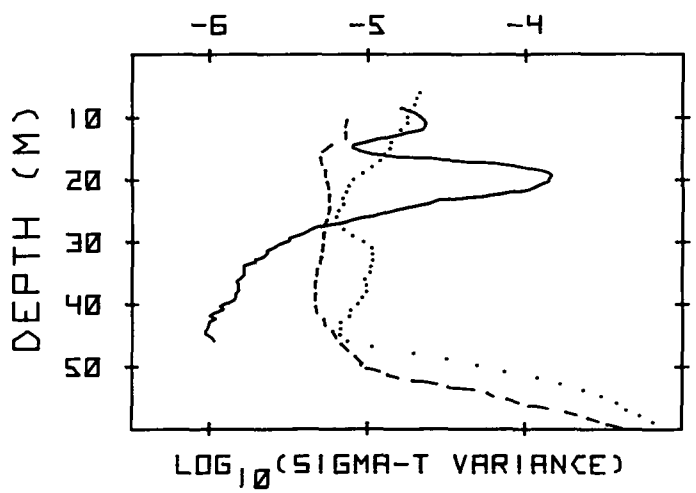

Fig. 3. Vertical plots of the sigma-t coarse-scale variance on surveys 1 (dashed), 2 (dotted), and 5 (solid line). Note the logarithmic scale. The data were treated by the log (x + 1) transformation.

60 m depths were of similar magnitude. Consequently, it is concluded that the phytoplankton bloom had generally reached the stage of nutrient limitation. High chlorophyll levels in layers well below the photic zone (~20 m) at many stations show a recent sedimentation or advection into the deeper layers, which is again indicative of the second half of the bloom (Smetacek *et al.*, 1978). The range of chlorophyll variability was striking. Contrasts in the total chlorophyll were 3.2-fold over a distance of 18.6 km, whereas for the 0–10 m chlorophyll they reached 6.5-fold over the area. The phytoplankton spring bloom, well understood in general terms, in fact, is extremely heterogeneous in space and most probably in time. Some weakly stratified stations might well have been yet in pre-bloom conditions. Steele (1978) gathered some evidence that, in the North Sea, the cycles of production differed along a 100 km line. Our data demonstrate striking variability on scales down to 10–20 km.

Survey 2

The hydrography was dominated by a strong baroclinic eddy, assumed to be cyclonic (Aitsam and Elken, 1980), near the NE corner of the area. Its spatial extent was ~40 km (the internal radius of deformation, R_{bc} ~10 km). Isopycnal elevations reached 22 m at the top of the deep layer. The geostrophic current shear, estimated at about 15–20 cm s^{-1} between 60 and 90 m depths, was probably responsible for the numerous interleaving layers at intermediate depths. Although the surface salinity was minimal (evidently a result of fresh water runoff), the strongest correlations between the salinities at 5 m/60 m and 30 m/60 m were suggestive of a strong vertical mixing.

The chlorophyll layer was mainly confined to the upper 15 m (Figure 2); the concentration increase between 30–55 m depths was a remnant of the past bloom. An obvious effect of the eddy was the accumulation of chlorophyll below the photic depths (between 30–50 m) in the active eddy zone. This was caused by

Table II. Correlation coefficients between some pairs of variables on surveys 1–5.

	1	2	3	4	5
S_5/S_{60}	0.57	0.72	(0.28)	0	0.33
S_{30}/S_{60}	0.60	0.70	0.70	0	0.55
C_{0-10}/S_5	0.49	0	0	0	0.62
C_T/S_5	0.51	0	0	0	0.53
C_{0-10}/S_{60}	0.58	0	0	(0.22)	0.31
C_T/S_{60}	0.63	0	0	0.42	(0.16)
C_{0-10}/DLD	−0.68	0	0	0	−0.58
C_T/DLD	−0.58	0	0	0	−0.54
C_{30-40}/DLD	−0.54	−0.45	0	0	(−0.23)
C_{40-50}/DLD	(−0.19)	−0.54	0	0	(−0.24)
$C_T/\Delta\sigma_t$	0	0	0	−0.52	0

0 stands for $|r| < 0.15$; values not significantly different from zero at 90% probability level ($|r| < 0.306$) are in brackets. S_5, S_{30}, S_{60} – salinities at 5, 30, 60 m depths; C_{0-10}, C_{30-40}, C_{40-50}, C_T – chlorophyll *a* levels between 0–10, 30–40, 40–50, and 0–60 m depths; DLD – deep layer depth, taken as the depth of the 6.75 sigma-t contour; $\Delta\sigma_t$ – sigma-t contrast between 5–30 m.

the upward directed vertical velocity component which tended to reduce or even override the sinking tendency of phytoplankton cells. A local reduction in the speed of a particle flow in its term brings about an accumulation of the particles in that layer. The negative relationship between the deep layer depth (minimal in the eddy) and the chlorophyll levels between 30 – 50 m (Table II) shows the accumulation effect. We could not extract other significant relationships between the physical variables studied and the chlorophyll. A possible explanation might be that the nutrient limitation was not acute, but seems more likely that, due to vigorous advection, stirring and vertical shears associated with the eddy, the chlorophyll pattern was thoroughly distorted during the reproductive time (1 – 3 days) for the phytoplankton.

Survey 3

Nine days later the eddy had weakened and drifted ~ 15 km to the south. The salinities were high, but, probably as a result of the vertical current shears, the surface/deep correlation had decreased. Heat input from the surface was associated with the formation of a shallow sub-surface chlorophyll maximum. The correlation with the 5-m salinity was positive for the sub-surface (10 – 20) chlorophyll ($r = 0.37$) but absent for the total chlorophyll.

Survey 4

The survey area was enlarged and shifted to NE by one gridpoint but, due to an instrumentation failure, the survey had to be interrupted. The final number of stations was almost the same but with some gaps and non-overlappings. As the mapping track had been changed, the time intervals between surveys 3 and 4 for different stations were from 36 to 82 h. By that time, the eddy had split into two smaller perturbations (Aitsam and Elken, 1980). Compared to other "snapshots" of eddy evolution in the study area, the splitting was very fast, resembling a collapse, and seems to be non-geostrophic.

Intense solar radiation and weak wind action had resulted in a rapid increase in the surface temperature. This was accompanied by striking and almost simultaneous changes in the chlorophyll pattern uniformly over the area (Figure 4). The sub-surface chlorophyll maximum had deepened by 5 – 9 m and become highly pronounced. A net increase in the total chlorophyll, from 66.3 to 73.4 mg m^{-2}, had occurred. The estimated apparent sinking speed was 10 – 20 cm h^{-1}. There is little doubt about the connection between the simultaneous phytoplankton sinking and the surface heat input, but the actual mechanisms, however, are not clear. The increased sinking might be a direct response to a decreased viscosity in accordance with Stokes Law but the weakened turbulence, a result of the increased stratification, was evidently more important. Quite likely, the sinking response included the physiological mechanisms which changed the buoyancy of the phytoplankton cells as a response to high illumination, increased temperature, nutrient stress, or a combination of them. The blue-green algae, among others, are known to regulate their buoyancy (Reynolds and Walsby, 1975). Unfortunately, no data is available on the species composition of the algae. The correlation between the 5-m temperature and the near-surface

(0 – 10 m) chlorophyll was −0.53, hence, besides the uniform sinking over the area, even the minimal coarse-scale variations confirmed the role of surface temperature instigating the phytoplankton sinking. Furthermore, this was the only survey with a significant (negative) linear effect of the upper layer density gradient on the total chlorophyll.

Survey 5

Typically of the Baltic Sea in summer, the water column was partitioned into three layers: upper, intermediate and deep, separated by two distinct peaks of the Brunt-Väisälä frequency. We have suggested (Kahru *et al.*, 1981) that mixing in these conditions, through the interaction of increased current shears and breaking internal waves, is effective at a thin intermediate layer.

The chlorophyll levels in all the 10-m layers were positively correlated between one another, therefore, it suffices to consider only the near-surface (0 – 10 m) chlorophyll. Highly significant correlations between the near-surface chlorophyll and both the intermediate layer thicknesses ($r = -0.63$) and the 5-m salinity ($r = 0.62$) show the effect of nutrient injections from the deep layer. Light limitation by mixing the cells into the aphotic zone was not crucial as there was a positive influence of the upper layer thickness on the chlorophyll levels. The total chlorophyll, ranging from 39.0 to 93.6 mg m^{-2}, was, on the average, lower than on the former surveys. Nevertheless, this comparatively high phytoplankton standing crop during the summer months could not be supported without recurrent

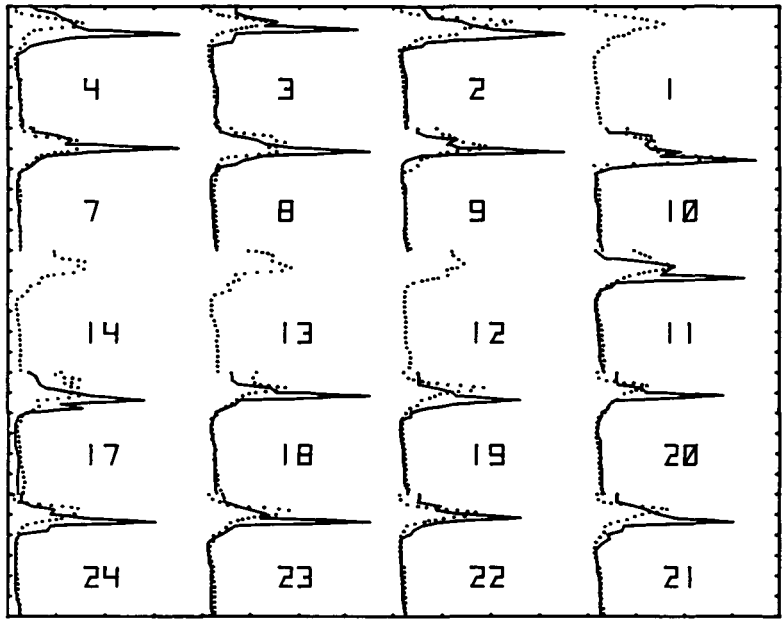

Fig. 4. Rapid changes in the vertical profiles of chlorophyll *a* on a portion of the study area during ~ 50 h between survey 3 (dotted line) and survey 4 (solid line). Units on the axes are: 10 m in the vertical and 2 mg Chl *a* m^{-3} in the horizontal. Profiles are shifted according to the location of the station on the grid (Figure 1). Profiles for stations 1, 12 – 14 on survey 4 are lacking.

nutrient injections from the deep layer.

Spatial scales

Since the number of stations is inadequate for applying spectral analysis, a first order approximation to the spatial scales of variability may be assessed from the autocorrelation function for the minimal space lag. Although anisotropy of the fields under study is evident, we have averaged the spatial correlations for the 5-mile lag in both orthogonal directions (Table III). Values for higher lags are not given since their confidence limits are too wide. Again surveys 1 and 5 exhibit more similarity: the chlorophyll field has bigger spatial scales. Survey 2, in spite of the "coarse-grained" physical structure (Figure 5), a consequence of the strong eddy, shows a "fine-grained" chlorophyll structure (i.e., no significant correlations over 9.3 km). Surveys 3 and 4, made during the decaying eddy, are outstanding for a low surface salinity variance and its extremely "fine-grained" pattern. This confirms our conjecture that strong advection, stirring and current shears are responsible for the weak coarse-scale coupling between the phytoplankton standing crop and the physical structure on surveys 2-4.

Discussion

The Baltic Sea, due to its shallow depths and irregular bottom topography, is characterized by smaller spatial scales of variability when compared to the oceanic scales (Aitsam *et al.*, 1981). The current pattern, strongly determined by the bottom topography, through geostrophic balance, results in tilted isopycnals, e.g., in coarse-scale variations in the deep layer depth or intermediate layer thickness. This, in turn, has a direct influence on the intensity of vertical mixing. We have hypothesized (Kahru *et al.*, 1981) that on a thin intermediate layer, as a result of increased current shears and their interaction with internal waves, instabilities arise, leading to localized and intermittent vertical mixing. Here we have suggested that high surface salinities and the shoaling of the depth of the deep layer, connected between each other, are both associated with increased vertical mixing. We have frequently observed density inversions (overturnings) with $\geqslant 0.5$ m vertical extent on many sigma-t profiles but their number is highly variable even between up- and down-traces. The absence of data on the spatial and temporal frequency and extent of the overturnings is an important gap in our

Table III. Spatial correlations over 5 nautical miles (9.3 km) on surveys 1 – 5.

	1	2	3	4	5
C_{0-10}	0.46	0	0.30	0.23	0.42
C_T	0.23	(0.11)	(0.20)	0.36	0.39
S_5	0.55	0.54	0	0	0.44
S_{60}	0.46	0.80	0.74	0.59	0.57
$\Delta\sigma_t$	0.23	(0.12)	0	0.26	(0.18)
DLD	0.70	0.77	0.70	0	0.58

See Table II for definition of symbols. 0 stands for $|r| < 0.10$; values not significantly different from zero at 90% probability level ($|r| < 0.23$) are in brackets.

knowledge. The coarse-scale chlorophyll pattern of two of the five surveys was clearly related to the respective hydrographic pattern, hence, to the transfer of nutrients into the surface layer. The surveys showing weak coupling between chlorophyll and hydrography are characterized by decaying of a strong mesoscale eddy. With the weakening of the eddy, the chlorophyll/hydrography coupling tended to increase. We conjecture that vigorous advection, stirring, and vertical current shears had distorted the chlorophyll pattern during the phytoplankton growth response delay. The "fine-grained" structure of the surface salinity and the reduction in the surface/deep correlation in salinity on surveys 3 – 4 may be

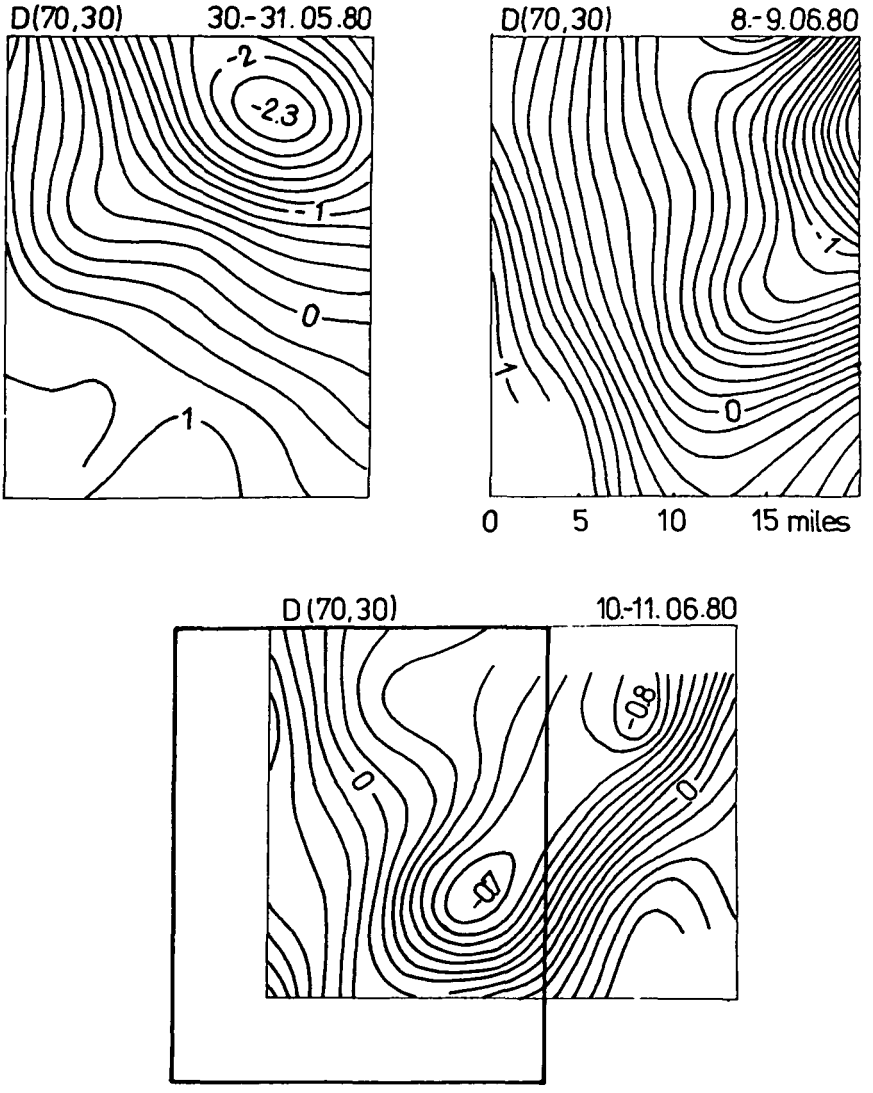

Fig. 5. Evolution of the synoptic eddy on maps of relative dynamic topography between the 70 and 30-dbar levels on surveys 2 – 4. The numerical values are in 0.01 dynamic meters. The eddy is weakening and finally splits into two smaller eddies.

ascribed to the stirring and the vertical current shears, respectively. The importance of advection in relation to the turnover time of the phytoplankton may be assessed from the non-dimensional number of O'Brien and Wroblewski (1973) for a geostrophic flow,

$$S = \frac{U}{V_m}\left(\frac{f}{A_H}\right)^{1/2},$$

where U is the characteristic speed of organized flow, V_m is the maximum growth rate of the phytoplankton, f is the Coriolis parameter, and A_H is the eddy diffusivity. For typical parameter values ($V_m = 2 \times 10^{-5}\,s^{-1}$, $f = 10^{-4}\,s^{-1}$, $A_H = 10^6\,cm^2\,s^{-1}$) it appears that advection becomes increasingly important (S equals and exceeds 1) for $U \geq 2$ cm s^{-1}. This was the translational velocity of the eddy, whereas its rotational velocity was bigger by an order of magnitude. Hence, the importance of advection on surveys 2–4 is evident.

Grazing by zooplankton may also control the phytoplankton distribution pattern. Zooplankton counts on survey 5 (M. Simm, unpublished data) showed agreement with Lindahl (1977) who has estimated the zooplankton production during that time of the year at ~60–70 mgC $m^{-2}\,d^{-1}$. This corresonds to ~5 mg $m^{-2}\,d^{-1}$ of ingested phytoplankton chlorophyll *a* which is rather small, compared to the average standing crop. However, due to the pronounced zooplankton patchiness (Cushing and Tungate, 1963; Mackas and Boyd, 1979), grazing may still dominate the phytoplankton dynamics locally.

Mesoscale eddies with spatial extent of 20–40 km which persist for at least 10–20 days have frequently dominated the hydrographic structure on the study area (Aitsam *et al.*, 1981; Aitsam and Elken, 1980). These eddies have probably an important influence on the phytoplankton growth (cf., Pingree *et al.*, 1979) but further studies are needed to evaluate this. So far we have demonstrated the accumulation of phytoplankton in the aphotic depths in cyclonic eddies, and, in 1979, we were able to show (Kahru, 1981a) that a cyclonic eddy transformed the chlorophyll horizontal isopleths as of a passive scalar.

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References

Aitsam,A. and Elken,J.: 1980, 'Results of CTD surveys on the BOSEX area in the Baltic Sea (in Russian)', in *Fine Structure and Synoptic Variability of the Sea*, Proc. All-Union Symp., Eesti NSV Teaduste Akadeemia, Tallinn, pp. 19-23.

Aitsam,A., Elken,J., Pavelson,J. and Talpsepp,L.: 1981, 'Preliminary results of the investigation of spatial-temporal characteristics of the Baltic Sea synoptic variability', in *The Investigation and Modelling of Processes in the Baltic*, Tallinn, pp. 70-97.

Bowden,K.F.: 1970, 'Turbulence II', *Oceanogr. Mar. Biol. Annu. Rev.*, **8**, 11-32.

Cushing,D.H.: 1975, '*Marine Ecology and Fisheries*', Cambridge University Press, Cambridge, 246 p.

Cushing,D.H. and Tungate,D.S.: 1963, 'Studies on a *Calanus* patch. I. The identification of a *Calanus* patch', *J. Mar. Biol. Assoc. U.K.*, **43**, 327-337.

Derenbach,J.B., Astheimer,H., Hansen,H.P. and Leach,H.: 1979, 'Vertical microscale distribution of phytoplankton in relation to the thermocline, *Mar. Ecol. Prog. Ser.*, **1**, 187-193.

Fedorov,K.N.: 1978, '*The Thermohaline Fine Structure of the Ocean*', Pergamon Press, Oxford, 179 p.

Haury,L.R., McGowan,J.A. and Wiebe,P.H.: 1978, 'Patterns and processes in the time-space scales of plankton distributions', in *Spatial Pattern in Plankton Communities,* J.H.Steele (ed.), Plenum Press, New York, pp. 277-327.

Heaney,S.I.: 1978, 'Some observations on the use of the *in vivo* fluorescence technique to determine chlorophyll-*a* in natural populations and cultures of freshwater phytoplankton', *Freshwater Biol.*, **8**, 115-126.

Herman,A.W. and Denman,K.L.: 1977, 'Rapid underwater profiling of chlorophyll with an *in situ* fluorometer mounted on a 'Batfish' vehicle', *Deep Sea Res.*, **24**, 385-397.

Holligan,P.M. and Harbour,D.S.: 1977, 'The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976', *J. Mar. Biol. Assoc. U.K.*, **57**, 1075-1093.

Horwood,J.W.: 1978, 'Observations in spatial heterogeneity of surface chlorophyll in one and two dimensions', *J. Mar. Biol. Assoc. U.K.*, **58**, 487-502.

Jeffrey,S.W. and Humphrey,G.F.: 1975, 'New spectrophotometric equations for determining chlorophylls a, b, c_1 and c_2 in higher plants, algae and natural phytoplankton', *Biochem. Physiol. Pflanzen,* **167**, 191-194.

Kahru,M.: 1981a, 'Variability of the chlorophyll field in the Baltic Sea', in *The Investigation and Modelling of Processes in the Baltic*, Tallinn, pp. 165-171.

Kahru,M.: 1981a, 'Variability in the three-dimensional structure of the chlorophyll field in the open Baltic Sea', *Oceanology,* **21**, 685-690.

Kahru,M., Aitsam,A. and Elken,J.: 1981, 'Coarse-scale spatial structure of phytoplankton standing crop in relation to hydrography in the open Baltic Sea', *Mar. Ecol. Prog. Ser.*, **5**, 311-318.

Kaiser,W. and Schultz,S.: 1978, 'On the causes for the differences in space and time of the commencement of the phytoplankton bloom in the Baltic', *Kieler Meeresforsch. Sonderh.*, **4**, 161-170.

Lindahl,O.: 1977, 'Studies on the production of phytoplankton and zooplankton in the Baltic in 1976, and a summary of results from 1973–1976', *Medd. Havsfiskelab. Lysekil,* **220**, 30 p.

Mackas,D.L. and Boyd,C.M.: 1979, 'Spectral analysis of zooplankton spatial heterogeneity', *Science (Wash.).*, **204**, 62-64.

McCarthy,J.J. and Goldman,J.C.: 1979, 'Nitrogeneous nutrition of marine phytoplankton in nutrient-depleted waters', *Science (Wash.),* **203** , 670-672.

O'Brien,J.J. and Wroblewski,J.S.: 1973, 'On advection in phytoplankton models', *J. Theor. Biol.*, **38**, 197-202.

Pingree,R.D., Holligan,P.M. and Mardell,G.T.: 1978, 'The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf', *Deep Sea Res.*, **25**, 1011-1028.

Pingree,R.D., Holligan,P.M. and Mardell,G.T.: 1979, 'Phytoplankton growth and cyclonic eddies, *Nature,* **278**, 245-247.

Reynolds,C.S. and Walsby,A.E.: 1975, 'Water-blooms', *Biol. Rev.*, **50**, 437-481.

Shaffer,G.: 1979, 'On the phosphorus and oxygen dynamics of the Baltic Sea', Contrib. *Askö Lab. Univ. Stockholm,* **26**, 90 p.

Smetacek,V., Bröckel,K.v., Zeitzschel,B. and Zenk.W.: 1978, 'Sedimentation of particulate matter during a phytoplankton spring bloom in relation to the hydrographic regime', *Mar. Biol.*, **47**, 211-226.

Steele,J.H.: 1978, 'Some comments on plankton patches', in *Spatial Pattern in Plankton Communities,* J.H. Steele (ed.), Plenum Press, New York, pp. 1-20.

Steele,J.H. and Henderson,E.W.: 1979, 'Spatial patterns in North Sea plankton', *Deep Sea Res.*, **26A**, 955-963.

Therriault,J.-C. and Platt,T.: 1978, 'Spatial heterogeneity of phytoplankton biomass and related factors in the near-surface waters of an exposed coastal embayment', *Limnol. Oceanogr.*, **23**, 888-899.