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Plankton distribution during a coastal upwelling event off Hiiumaa, Baltic Sea: impact of short-term flow field variability

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Abstract—The evolution of an upwelling event and the associated plankton distribution off Hiiumaa island, northeastern Baltic Sea, is traced through continuous registration of wind and currents, consecutive CTD and chlorophyll fluorescence surveys and underway shipboard measurements of near-surface temperature and particle concentration over a 10-day period in June 1986. The earlier mesoscale pattern of warmer (13°C) near-shore waters containing higher chlorophyll concentration was drastically changed as the wind turned from SW to NNW and increased up to 12 m s^{-1}, which resulted in the offshore Ekman transport of the warmer coastal water and upwelling of cold (6–7°C) phytoplankton-poor deeper water along the coastal slope.

A relatively fast biological response to the upwelling resulted in the form of enhanced primary production and 4–7-fold increase of the standing crop of some phytoplankton populations (mainly dinoflagellates) within 4 days (at the upwelling frontal boundary). It is shown that a persistent, moderate wind is favourable to sustain a local phytoplankton bloom while keeping the vertical transport of the deeper nutrient-rich water still going but being not powerful enough to stir away the growing phytoplankton.

Our measurements confirm the importance of coastal upwellings for the productivity of the Baltic near-shore ecosystems in the summer stage.

INTRODUCTION

IN the marine near-shore environment many hydrodynamical processes have direct ecological consequences (see DENMAN and POWELL, 1984 for a recent review), and the spatio-temporal scales of the physical forcing determine the possible ecological responses that occur (HAURY *et al.*, 1978). However, it is often difficult to identify the pathways through which a particular physical event is transferred to a biological result because of the problems associated with following a water mass and the inability of single platform sampling strategies to provide the required synopticity of the measurements. For that reason an approach of quasi-continuous on-track and/or multiplatform measurements is more adequate to provide a comprehensive synoptic picture (PUGH, 1978; KAHRU *et al.*, 1986; SMITH *et al.*, 1987).

On smaller temporal scales, concentrating on the coupling between the physical and biological processes that operate on the same spatial and temporal scales, ecological responses can more readily be measured directly. For example, a generation within a few days of the phytoplankton spring bloom in high latitude shelf waters is usually directly

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attributed to the suppression of vertical turbulence by the onset of stratification (Sverdrup, 1953; Sambrotto *et al.*, 1986). The spatial scales of ecological importance are then basically the spatial scales of the important physical processes (Denman and Powell, 1984). Event scale processes of a few days duration are ideal for studies relating physical processes to biological processes because they are long enough for measurable biological responses to occur, but short enough to offer the possibility of small advective movements (Harris, 1980; Dagg, 1988).

The large-scale upwellings of cold and nutrient-rich water, characteristric of the eastern side of the oceans have been studied for a long time owing to their strong ecological consequences (Boje and Tomczak, 1978). Less is known about the wind-induced upwellings on smaller scales, which typically occur in a semi-enclosed sea like the Baltic. The ecology of the Baltic Sea as a whole cannot be treated without the understanding of the physical and biological fluxes from the coastal areas. For the large-scale (seasonal and annual) ecological models of the Baltic Sea, the boundary conditions and the parameterization of the coastal-offshore fluxes are of special importance. Therefore, besides the study of the frequency of coastal upwellings and their spatio-temporal development by means of satellite oceanography, the detailed *in situ* measurements of physical processes and the associated biological responses should be made.

Some observations of upwellings in the Baltic are given in Svansson (1975) and Shaffer (1979). Statistical analysis of upwellings based on satellite and *in situ* sea surface temperature measurements along the Swedish coastline gives evidence of the coastal upwellings as a common phenomenon along the Baltic coasts, occurring during one-quarter to one-third of the time for some coastal sections (Gidhagen, 1984). The dominant physical forcings are storms or strong wind events with the typical time scales ranging from a couple of days to a week.

In spite of the importance of such studies, still very little is known about the biological consequences of coastal upwellings in the Baltic Sea (Jansson *et al.*, 1984). Some possible pathways of vertical exchange processes with ecological consequences have been shown by Shaffer (1975) and Kahru *et al.* (1981).

In this paper we report a series of complex measurements made off the SW coast of the Hiiumaa island in the northeastern Baltic Sea in June 1986 following the evolution of an upwelling event. The aim of this study was to get an idea about the plankton response to the coastal marine dynamics and exchange processes associated with variable wind forcing.

OBSERVATIONS AND METHODS

The observations were conducted from R.V. *Arnold Veimer* at the Soela Strait inlet to the Moonsund area near the western coasts of the Hiiumaa and Saaremaa islands (Fig. 1) from 5 June to 1 July 1986. Shipboard data were collected in two sampling modes: along-track, where data were obtained rapidly and periodically as the ship was steaming along its course (Fig. 1, dotted lines); and on-station, where detailed vertical data were collected while the ship was stationary (Fig. 1, crosses).

The underway shipboard measurements of particles and temperature were obtained by pumping the seawater from a depth of 5 m to the sensors. The "flow-through" system also contained a bubble trap and a reservoir tank to maintain a relatively constant flow rate. The along-track particle concentration was determined using an on-line particle size

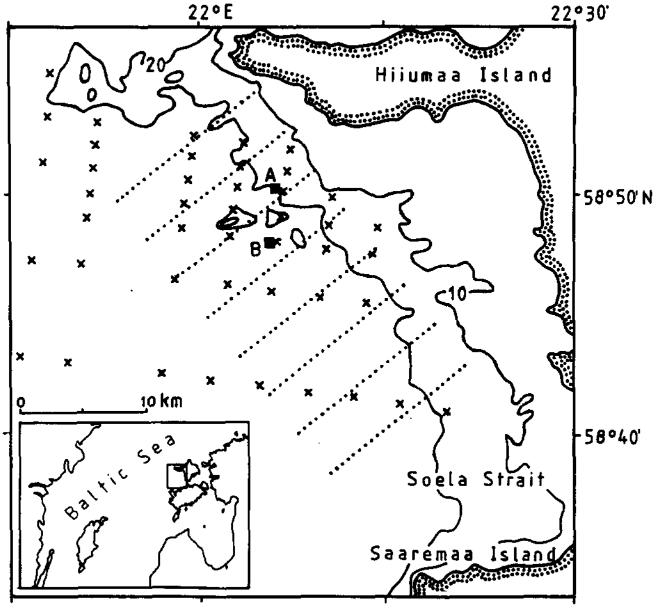

Fig. 1. Study area showing sections of underway shipboard measurements (dotted lines), locations of vertical casts (crosses), two mooring sites (A and B) and bottom topography (isobaths in metres).

analyzer Hiac-Royco PC-320 (see Pugh, 1978), which counted particles with the equivalent spherical diameter from 1 to 1000 μm in 12 size classes. The pumping system together with a minimal time interval needed to count a representative number of particles in each size group acted as a low-pass spatial filter, which when coupled with the ship's speed set a lower limit on the spatial scale of variability that could be sampled by the particle counter. The time interval between the registration of integrated particle counts by the computer/data logger was set at 1 min. The ship's speed was held at 8 knots ($\approx$4.1 m s^{-1}) during the on-track measurements that resulted in the corresponding sampling interval of about 250 m. Simultaneously the near-surface (5-m depth) temperature was recorded by the ship's automatic weather station.

Three consecutive underway surveys were undertaken after the onset of the upwelling-favourable winds at approximately 3-day intervals. During each survey six to eight regularly spaced (with 2 n. miles spacing) transects were made normal to the coast within a few (7–10) hours to provide a comprehensive synoptic picture. The high-resolution of the measurements in the coastal-offshore direction was required as abrupt changes could be expected.

Information on the vertical structure of the water column was obtained using a complex of a Neil Brown Mark III CTD, a submersible "EOS" fluorometer and a rosette sampler. The fluorescence data when calibrated against extracted chlorophyll from the discrete water samples from the rosette provided equispaced (z = 0.5 m) vertical profiles of chlorophyll a concentration. In most cases with a sufficient set of calibration samples ($N >$ 50), the regressions proved to be quite reliable (r = 0.87–0.93). Chlorophyll extraction and photometric analyses were made according to the recommendations by Edler (1979).

In most of the CTD stations water samples with the rosette sampler (General Oceanics) from the depth of 5 m (chosen according to the chlorophyll fluorescence profile) were collected for on-board productivity measurements and phytoplankton cell counts. Rates of ^{14}C fixation by phytoplankton were estimated in an on-board incubator at saturating light intensity. The irradiance in the temperature-controlled incubator bath was approximately 230 μE m^{-2} s^{-1}. Samples were incubated for 2 h. Millipore 0.45 μm membrane filters and liquid scintillation counting (LKB RackBeta 1217, DPM values) were used. The CO_2 content of the water was calculated from alkalinity titration. Assimilation numbers were calculated relative to the chlorophyll concentration obtained photometrically from the same discrete water sample. Samples for phytoplankton cell counts were preserved with Lugol's solution with acetic acid and analyzed with the inverted microscope according to Edler (1979).

Several on-station CTD/fluorescence surveys were undertaken prior to the onset of the upwelling-favourable winds, exactly during the upwelling-favourable storm event, and during the time lapse between the along-track surveys, to provide relative continuity of the observations of the upwelling event. The space interval between stations varied from 1 n. mile in the upwelling centre to 4 n. miles in the outer area.

During the upwelling-favourable wind period two Aanderaa RCM-4 current meters were deployed at separate mooring stations at two sites: Station A, almost in the upwelling centre, and B, close to the seaward edge of the upwelling zone (Fig. 1). The two current meters recorded instantaneous temperature, conductivity, pressure and current direction together with the averaged speed at 10 m depth with a recording interval of 10 min. The moorings were used to observe continuously the wind-driven currents and, together with the synoptic hydrographic surveys, to construct a coherent picture of the coastal flow field dynamics.

The real-time wind data were extracted at 30 min intervals from the ship's automatic weather recorder.

The current and wind observations were converted into along-shore–cross-shore components, with the positive directions chosen to be 135° and 45°, respectively.

Details of the observational programme prior to the upwelling regime of the coastal ecosystem are mostly beyond the scope of this paper and will be described elsewhere.

RESULTS

The distribution of the water properties and the associated biological activity in the study area were generally controlled by the dominating southern and western winds which influenced the water exchange between the open sea and the Moonsund area through the Soela Strait, and by the solar heating associated with a high pressure area over northern Europe and Scandinavia leading to a sharp thermocline at about 10 m depth and a faster warming of the shallower coastal waters. Prior to the onset of upwelling-favourable winds the situation was characterized by near-shore, warmer and less saline water with higher chlorophyll *a* concentration, clearly distinguished from the saline and colder water tongue, which penetrated to the area from the southwestern open part. A typical example of the horizontal distribution of water masses and chlorophyll *a* as observed on 11–12 June 1986 after a 10 m s^{-1} SW wind event (see Fig. 2) is shown in Fig. 3(A).

Abrupt changes occurred in the coastal ecosystem as the wind turned to NNW (favourable for upwelling) and increased up to 10–12 m s^{-1} for 2 days on 21 June (Fig. 2).

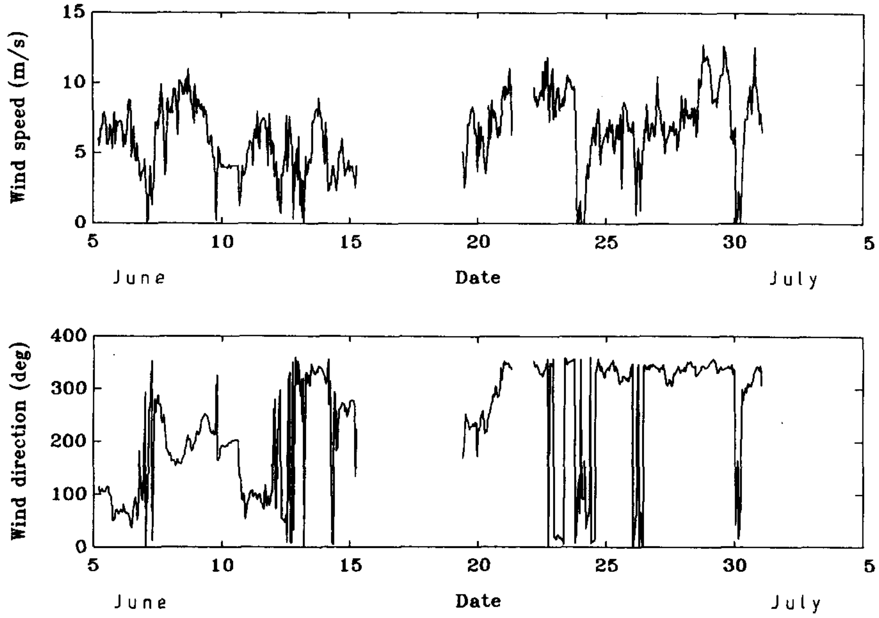

Fig. 2. Wind time series during the study period, June–July 1986.

This strong wind event was instrumental for an offshore Ekman transport of the warmer water and an upwelling of very cold (7°C) and phytoplankton-poor water near the southwestern coast of the Hiiumaa island (Fig. 3B). The band of the upwelling zone was attached to a certain properly oriented segment of a steeper coastal slope with the depth range of about 10–20 m. Off the western tip of Hiiumaa, the colder water protruded southwest, extending like a filament to some 30 km from the coast.

The wind time series (Fig. 2) confirm the persistence of upwelling-favourable northwestern winds sustaining the upwelling from 21 June to at least the end of the investigation period. After the onset of the upwelling the time sequence of the along-shore wind component can be divided into three phases (Fig. 4A): (1) 12 h of calm weather with almost no wind on 24 June; (2) a 4-day period of moderate wind (5–7 m s^{-1}) from 24 to 28 June; (3) a period of strong along-shore component onwards from 28 June with a short interruption on 30 June.

The sequence of underway surveys on 25, 28 and 30 June shows the development of the upwelling event due to wind forcing together with the plankton distribution in the area. A comparison of different upwelling phases based on the wind and current measurements and on-track temperature/plankton surveys is given in Table 1. The along-shore wind is chosen as the main forcing component of the offshore Ekman flux generation. The averages and standard deviations of wind and current components are calculated over the 48-h period before the beginning of each survey except the first survey on 25 June where a 12-h average is used. The minimum temperatures and maximum temperature gradients are given for the illustration of the upwelling intensity, and the maximum particle concentrations in the upwelling frontal zone as compared with the mean concentrations in the surrounding water (with temperature >12°C) during each survey depict clearly enough the evolution of phytoplankton bloom.

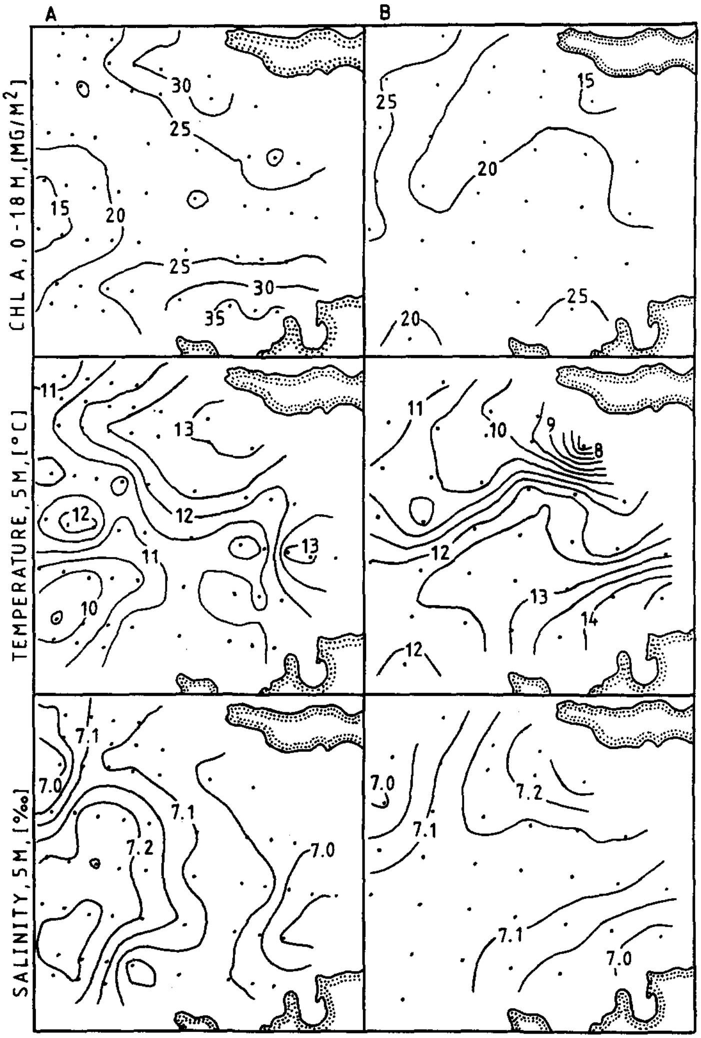

Fig. 3. Horizontal distribution of vertically integrated chlorophyll *a* concentration between 0 and 18 m, temperature and salinity at 5 m depth prior to the onset of upwelling on 11–12 June (A), and during the upwelling-favourable strong wind event on 21–22 June (B). Locations of vertical CTD/fluorescence casts are marked with dots.

The CTD/fluorescence surveys made in between the on-track surveys revealed a good correlation with the near-surface temperature and plankton distributions from the underway measurements, and give additional information on the physical processes in operation.

The first on-track survey revealed a striking cross-shore temperature structure. The isotherms at the 5-m depth level followed well the local bottom depth contours (Fig. 5A). Judging by the consecutive temperature maps (Figs 3B and 5A and B), the onset of calm weather caused the surface temperature front to sharpen and rapidly retreat towards the coast, to about 10 km from the shore. Both of the current meters also showed on-shore

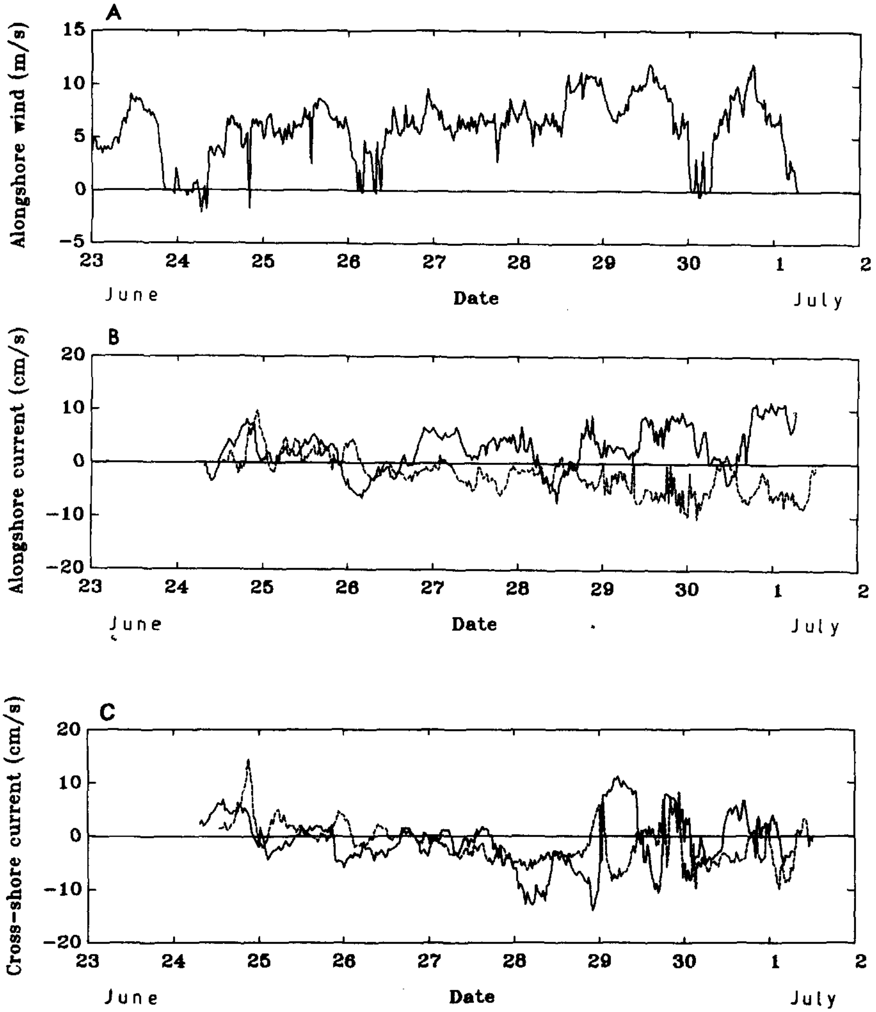

Fig. 4. Time series of along-shore wind component (A), along-shore (B) and cross-shore (C) current components from two moorings (site A—solid line, site B—dashed line) after the onset of upwelling.

current until 26 June, confirming the advection of the upper layer towards the coast (Fig. 4C). The calm conditions leading to reduced turbulence gave a boost to phytoplankton growth. A developing maximum of the phytoplankton concentration is already noticeable in the upwelling frontal boundary (Fig. 6A). As the phytoplankton ^{14}C fixation rate under unlimited light conditions was measured only at cross-shore CTD sections, the spatial resolution was, of course, many times lower compared to the particle data or near-surface temperature. Nevertheless, spectacular patterns were evident in the distribution of both the productivity and assimilation number (*AN*) (Fig. 7). The productivity and *AN* were uniformly low in the upper mixed layer of the "surrounding" water. A striking increase in *AN* [to 5.4 mgC (mg Chl *a*)$^{-1}$ h^{-1}] and potential primary production (to 4 mgC m^{-3} h^{-1}) occurred in the region of the sharp thermohaline gradient. While both the productivity and

Table 1. Comparison of the three consecutive upwelling phases

	Survey I	Survey II	Survey III
Date	25 June 1986	28 June 1986	30 June 1986
Start (GMT)	02.30	03.30	16.30
Days from beginning of upwelling	4	7	9
48-h average before survey	±SD	±SD	±SD
Along-shore wind (m s^{-1})	4.2 ± 3.0*	5.9 ±1.9	7.5 ± 3.3
Cross-shore current (cm s^{-1})			
Site A	3.2 ± 2.5*	−2.1 ± 2.8	0.5 ± 6.8
Site B	3.7 ± 4.5*	−1.8 ± 1.9	−2.5 ± 4.1
During survey			
Minimum temp. (°C)	8.1	7.7	5.8
Maximum temp. (°C)	14.1	13.9	13.2
Max. temp. gradient (°C km^{-1})	0.87	1.43	1.13† 0.42‡
Particles 10–20 μm (particles per ml)			
Max. concentration K_1	108	150	92
Surrounding mean K_2§	48 ± 10	34 ± 8	37 ± 8
Ratio K_1/K_2	2.3	4.4	2.5
Particles 28–73 μm (particles per ml)			
Max. concentration K_1	20	33	18
Surrounding mean K_2§	14 ± 2	13 ± 2	13 ± 2
Ratio K_1/K_2	1.4	2.5	1.4

*12-h average before survey.
†In northwestern part of the upwelling zone.
‡In southwestern part of the upwelling zone.
§Outside of 12°C isotherm at 5-m depth.

AN levelled down towards the upwelling centre due to very low chlorophyll content in the upwelling or recently upwelled water, the *AN* values stayed still considerably high indicating availability of nutrients.

The moderate wind prior and during survey 2 caused a cessation of the onshore flow and an onset of offshore flow at both mooring sites (Fig. 4C). However, the NW part of the front continued to advect further coastward about 1.5–2 km per day. The resulting meandering of the front was probably caused by a complicated interplay of the bottom topography, coastline and the wind (note also the split of the along-shore components of the current as site A and B in opposite directions beginning with 26 June, Fig. 4B).

By the time of survey 2 a band of high phytoplankton concentration with sharp boundaries had been formed along the intense frontal gradient (cf. Figs 5B and 6B). The maximum was obviously locally produced at the interface zone of the nutrient-rich upwelled water and the relatively chlorophyll-rich "old" water as evidenced by the curves of primary production and *AN* across the front. Microscopic counts of phytoplankton samples from the elongated patch showed 4–7-fold increase in the standing stock of several species (*Dinophysis* spp., *Exuviaella baltica*, *Botryococcus braunii*) compared to the surrounding water (Fig. 8). The number of particles in the size range from 10 to 20 μm

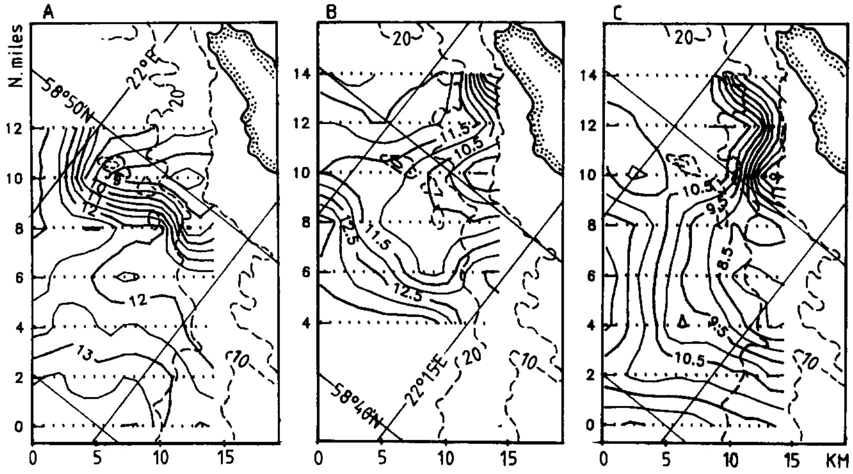

Fig. 5. Horizontal temperature (°C) distribution at 5 m depth during the three consecutive on-track surveys: A—25 June 1986, B—28 June 1986, C—30 June 1986. Isobaths (m) are shown with a dashed line.

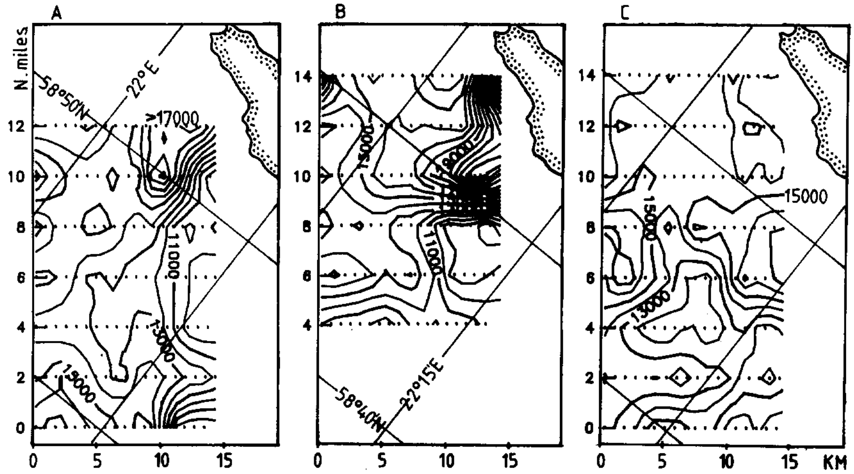

Fig. 6. Horizontal distribution of the 28–73 μm particle fraction (particles per litre) at 5 m depth during the three consecutive on-track surveys: A—25 June 1986, B—28 June 1986, C—30 June 1986.

increased up to 4.4-fold (mostly *Exuviaella baltica*) but in the size range 28–73 μm only by 2.5-fold due to missing some typical algal populations of that size (e.g. trichomes of cyanobacteria *Aphanizomenon flos-aquae*) in the cold upwelling centre. As a rule, the relatively low concentration of the particles in the size range 2–4 μm (detrite, small flagellates) seems to be a very good indicator of the newly upwelled waters (cf. Figs 5A–C and 9A–C).

The increase in the wind speed between surveys 2 and 3 brought along a reintensifying of the upwelling. The process was spatially inhomogeneous: in the northwestern part the front stayed stationary near the coast, whereas in the southeastern part the front was stirred over a larger area by an intense offshore transport and vertical mixing (Fig. 5C). The rapid disappearance of the well-defined phytoplankton patch (Fig. 6C) can be explained by the advective transport southward along the frontal isotherms and smoothing over a wide, mixed area.

The particle size group of 305–1000 μm, indicating the distribution of the copepod-fraction of zooplankton (*Acartia*, *Eurytemora*) showed quite a uniform distribution in the region during the first two surveys with very low abundances in the upper layer (Figs. 10A and B). By the time of survey 3, i.e. 9 days after the storm causing upwelling, the abundance in the zooplankton size range of particles had increased by 5–7-fold. The peak abundance coincided with the higher phytoplankton abundance (Fig. 10C).

DISCUSSION

Coastal upwellings which usually bring nutrient-rich water up into the euphotic zone are frequently associated with increased biological productivity (e.g. Walsh *et al.*, 1978; Paffenhöfer *et al.*, 1984) and in some cases the degree of upwelling can directly be linked to the amount of plankton produced (Peterson and Miller, 1975; Peterson *et al.*, 1979). It could be expected that in coastal areas of the Baltic Sea redistribution processes like upwellings do significantly affect the trophic processes during at least the summer season because of the strong vertical stratification restricting vertical mixing and the onshore–offshore gradients in the water properties.

During the coastal upwelling that was followed in this study, the consecutive surface temperature maps highlight the dramatic changes which the waters in the region can undergo in only a few days. Coupled with the current measurements they also serve as indicators of the main dynamical processes. Those processes define the circumstances

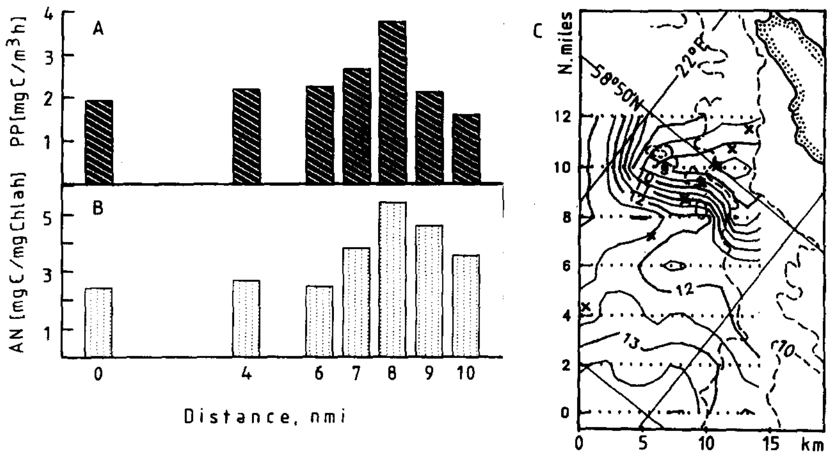

Fig. 7. Horizontal distribution of potential primary production (A) and assimilation number (B) at 5 m depths along the section of stations (crosses) shown on the reference map (C) of the near-surface (5 m depth) temperature (°C) distribution.

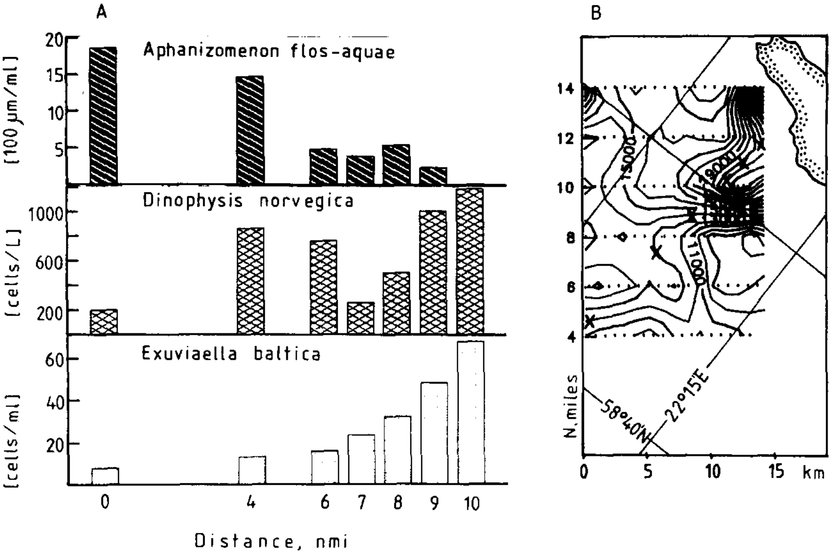

Fig. 8. Horizontal distribution of three phytoplankton species (A) at 5 m depth along the section of station (crosses) shown on the reference map (B) of the distribution of the 28–73 μm particle fraction (particles per litre) at 5 m depth.

permitting phytoplankton growth. The key question seems to be the time and space scales of the processes themselves. In general, the time scale of the Ekman flux should correspond to the turnover time of the algae to allow them to produce a significant response.

During the relaxation of wind the upwelling front shifted rapidly back towards the coast and sharpened. The four successive days of moderate wind resulted in a dynamic

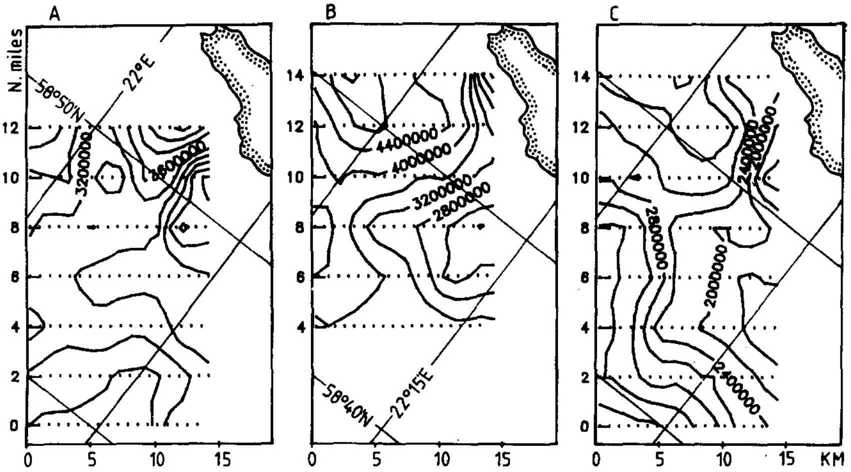

Fig. 9. Horizontal distribution of the 2–4 μm particle fraction (particles per litre) at 5 m depth during the three consecutive on-track surveys: A—25 June 1986, B—28 June 1986, C—30 June 1986.

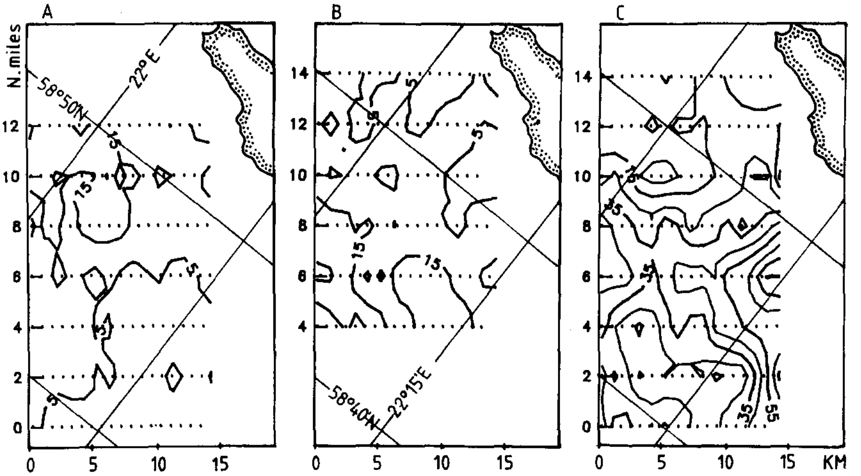

Fig. 10. Horizontal distribution of the 305–1000 μm particle fraction (particles per litre) at 5 m depth during the three consecutive on-track surveys: A—25 June 1986, B—28 June 1986, C—30 June 1986.

equilibrium of the upwelling front at the coastal slope with the vertical transport still effective at the coastal side but the horizontal velocities not large enough (≈ 2 cm s^{-1}) to redistribute the growing phytoplankton. Under these circumstances the 4-day period was sufficient for some algal populations (mostly dinoflagellates) to produce a 4–7-fold increase of the standing crop in the form of a 3–7 km wide elongated patch along the highest thermohaline gradient. The primary production measurements and the calculated assimilation numbers confirm the importance of a well-defined frontal boundary between the poorly seeded, nutrient-rich upwelled water and the relatively phytoplankton-rich "old" water for the upwelling productivity. A certain time-persistence of the equilibrium state between the sequence of upwelling intensification was necessary to allow the local phytoplankton bloom to occur. Sustained (or frequent) intense upwelling, on the other hand, would transport and mix algae and nutrients over a wide offshore area before the production cycle could be completed (Huntsman and Barber, 1977). As a result, the overall productivity of the nearshore coastal zone may even decrease due to the very low initial phytoplankton biomass in the upwelled water (see Brown and Field, 1986).

The 5–7-fold increase of the copepod-fraction of zooplankton after the 9-day period might be the result of diurnal vertical migration while the on-track survey 3, contrary to the two previous surveys, started in the evening and lasted over midnight (see Table 1). For instance, ovigerous *Eurytemora* females are shown to be concentrated in depths below 20 m during daytime, while non-ovigerous females are also commonly found in the surface layer (Vuorinen *et al.*, 1983). However, the young stages of copepods are usually non-migrant and live near the surface (Davis, 1984). On the other hand, as it is well known that a 9-day period is too short for the reproduction of copepods (e.g. Katona, 1970), the mechanism of migration or transport (either vertical or horizontal) should be responsible for the increase of zooplankton abundance as well as for the relatively good coherence between distributions of particles of phytoplankton and zooplankton size (cf. Figs 6C and 10C.

Our results have provided evidence that coastal upwellings in the Baltic Sea are of considerable biological importance. The formation of phytoplankton maximum in the upwelling frontal region is a matter of a fine balance between the biological and hydrodynamical processes. High resolution *in situ* measurements of the biological and physical parameters have been one of the best solutions to provide a comprehensive synoptic picture of the highly variable near-shore processes. The link between the primary producers and higher trophic levels as well as the contribution of coastal upwellings to the Baltic Sea productivity as a whole certainly requires further investigations.

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