PLANKTON DISTRIBUTIONS AND PROCESSES IN THE BALTIC BOUNDARY ZONES

M. Kahru[1], S. Nômmann[1], M. Simm[1], and K. Vilbaste[2]

[1]Institute of Thermophysics and Electrophysics, Paldiski St. 1, Tallinn 200031 (USSR)

[2]Institute of Zoology and Botany, Vanemuise St. 21, Tartu 202400 (USSR)

ABSTRACT

Due to their estuarine origin, the brackish water masses of the Baltic Sea result from complicated mixing processes. As a result, boundary zones span the whole spectrum of space scales in both the vertical and horizontal directions. The ecological effects of these boundary zones are exemplified by the results of recent surveys. Evidence of a striking increase in primary productivity in an offshore front, elevated levels of chlorophyll and phytoplankton biomass in the thermocline, offshore and in coastal boundary areas, at the periphery of synoptic eddies, and of a higher standing stock of zooplankton in or adjacent to frontal boundaries has been obtained. Flow-through particle counting has revealed abrupt changes in the size distribution of phytoplankton populations indicating different stages of the vernal bloom. It is stressed that the frequency of the boundary effects is poorly known in both space and time, thus the assessment of their overall significance is not possible at present.

INTRODUCTION

The Baltic Sea may be regarded as a large "overmixed" estuary (Shaffer, 1979). Its brackish waters result from mixing between different water masses. A variety of mixing processes are involved on the whole spectrum of scales. As the mixing is not a smooth, Fickian diffusion, a whole spectrum of boundary zones, both in the horizontal and vertical, is being generated. Most persistent are those in the vertical, i.e. the seasonal thermocline and the permanent halocline. As both are strong pycnoclines and restrict the extent of vertical mixing (Kullenberg, 1982), they exercise a profound influence on the ecology of the Baltic (e.g. Jansson et al., 1984). In the horizontal, the boundary zones are as ubiquitous though not so persistent. Sharp boundaries in larger scales are commonly known as fronts. These transition zones between different water masses are often characterized by the accumulation of biomass and the increased biological activity (e.g. Holligan, 1981), and are supposed to be important for the feeding and survival of larval and juvenile fish (Iles and Sinclair, 1982).

The ecological significance of boundary zones in the Baltic, apart from the restrictions to the vertical mixing by the pycnoclines, is virtually unknown. Compared to better studied oceanic shelf analogs (Holligan, 1981; Marra et al., 1983; Fasham et al., 1985), the fronts in the Baltic are expected to be smaller in scales and less persistent in time. Their shorter life-time and intermittent occurence makes their investigation extremely difficult. From almost any good-quality satellite image of the Baltic (see Horstmann, 1983; Gidhagen, 1984) it is readily evident that the whole Baltic is tightly packed with eddy-like features and has more or less distinct boundaries in between (Fig.1). Taken singularly, each boundary zone may have little ecological impact. However, to assess the impact of the whole pattern of locally increased gradients and boundary zones is a challenging and important task. Up to now only single ecological studies of fronts have been made in the Baltic (Kahru et al., 1984). It is our general feeling that due to the diversity of hydrological/hydrobiological situations and the complexity of interactions, a statistically large number of cases must be analysed before any reliable assessment of the overall ecological significance of fronts and other boundaries in the Baltic can be made. Here we report some results of our biologically oriented studies from both the offshore and coastal areas of the Baltic.

METHODS

Vertical profiling

Vertical distributions of temperature, salinity, density, and chlorophyll a fluorescence were obtained by a complex of a Neil Brown Mark III CTD and a submersible fluorometer. As fluorometer first a "Variosens" (Früngel and Koch, 1976) and later a "EOS" manufactured by Elektro Optik Juan F. Suarez (Henstedt-Ulzburg, FRG) and described by Astheimer and Haardt (1984) were used. The signals were interfaced to a computer and processed on-line to equispaced (Δz = 50 cm) vertical profiles.

"Discrete" measurements

Water samples were drawn from Niskin samplers and used for on-

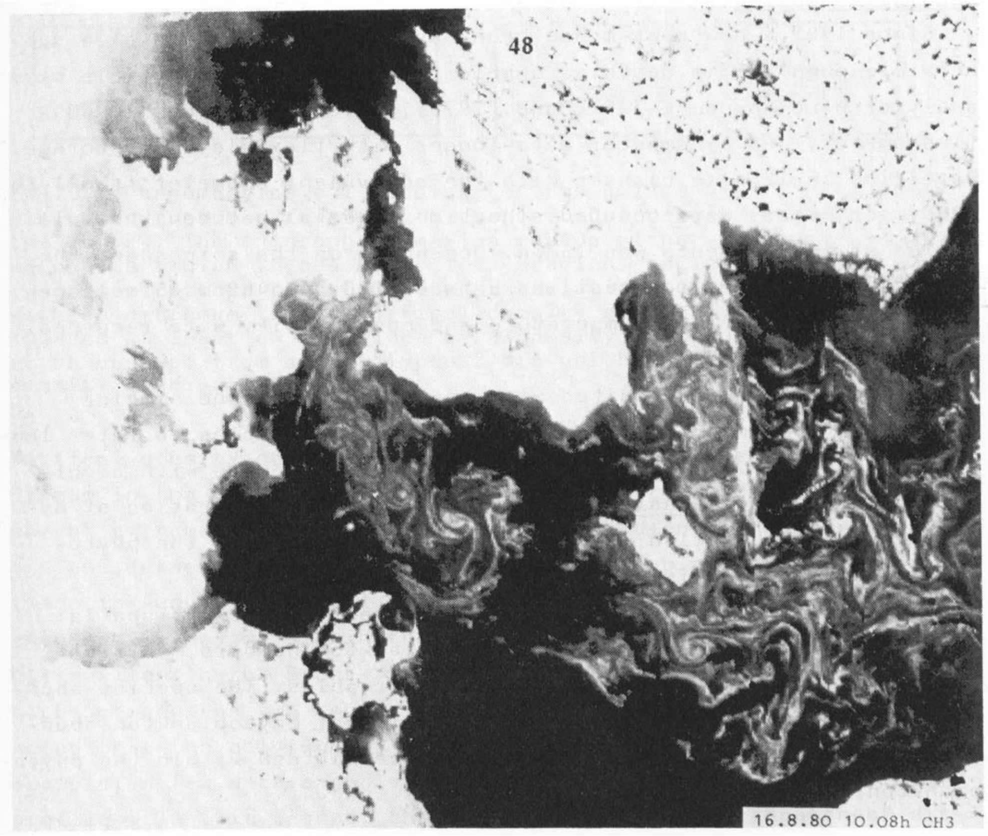


Fig. 1. CZCS image (channel 3) of the western Baltic Sea. Aggregations of the blue-green algae serve as tracers of the near-surface current field. Well-defined eddies are visible south and west of the Bornholm island.

board analyses of the extracted chlorophyll a, nitrate, nitrite, phosphate, silicate, primary production and for later phytoplankton counts. Not all the parameters were measured on every survey. Carbon fixation tests were made in a controlled temperature and light bath using the ^{14}C teqhnique. The potential primary production was measured by incubating vials with 120 ml of unfiltered seawater in duplicate at a saturating light intensity. Zooplankton samples were taken by vertical net (mesh size = 0.09 mm) hauls through the whole water column or through the upper 10-m layer. Phytoplankton samples were processed with the Utermöhl method (Utermöhl, 1958). More details on the methods are found in Kahru et al. (1984).

Underway sampling

Since 1985 a new system has been developed, consisting of a submersible pump at 5 m depth, a bubble trap, an on-line particle size analyzer Hiac/Royco PC-320 (Pugh, 1978), a Turner Designs 10-005R fluorometer, and a computer/data logger with flexible disk storage. Particles in 12 size classes with the equivalent diameter from 1 to 1000 micrometers were counted. The time interval between the full cycles of measurements was 1 min. Depending on the ship speed the corresponding space interval was between 180 and 400 m. Simultaneously the near-surface temperature and conductivity were recorded.

Near-shore surveys

Coastal areas were visited with smaller vessels and simpler equipment (Nômmann, 1985), leaving most of the samples to later laboratory analyses. In addition, algal assays were made with a culture of Scendesmus brasiliensis to assess the concentration of nutrients in the brackish water, directly utilizable by the phytoplankton (see Källqvist, 1973).

The principal component analysis was used to discover spatial patterns in multivariate data of phytoplankton numbers, nutrient concentrations and other environmental variables. The species-abundance curves were calculated for the empirical phytoplankton abundances to discover shifts in the dominance pattern within the phytoplankton assemblages (see Levich, 1980).

RESULTS

Vertical structure

The subsurface chlorophyll maximum is a conspicuous feature of many oceanic and shelf areas (Cullen, 1982). In the Baltic, a close association between the chlorophyll maximum layers and the depths of the local maxima in the Brunt-Väisälä frequency has been ascertained (Kahru, 1981). In relation to the vertical distribution of density (or, temperature) four phenomenological types of the chlorophyll maximum layers may be distinguished (Fig.2). In case of a well-mixed upper layer and bloom conditions the type H1 maximum may extend to the surface. However, type H1 may also be a subsurface maximum in an internal homogeneous layer. Type H2, i.e. a well-defined chlorophyll maximum without an adjacent vertical density gradient, is most probably caused by the active aggregation of vertically migrating phytoplankton. During the summer thermal stratification the chlorophyll maxima are most commonly associated with the

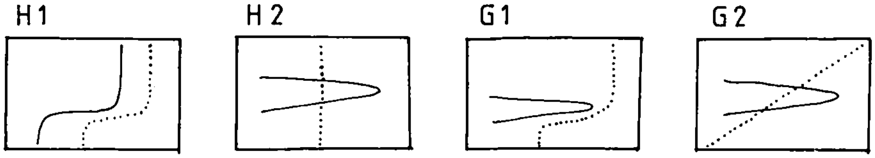


Fig. 2. Phenomenological typology of the chlorophyll maxima (continuous curves) in relation to the vertical density structure (dotted curve). The chlorophyll maxima reside either in a vertically homogeneous region (types H) or in a gradient region (types G). Both types are further differentiated in relation to the association with an extremum in the vertical density gradient. Types 1 are bounded at least on one side by a density extremum. Type H1 may also be bounded from above. Types 2 are not bounded by extrema in the density gradient.

vertical density gradient, belonging either to type G1 (with an extremum in the vertical density gradient) or type G2 (without an apparent extremum in the vertical density gradient). However, transitions between the types do occur. In the typical summer conditions in August, 1979 all the 62 vertical profiles observed had chlorophyll maxima within the interval of 4 m from the nearest local maximum in the Brunt-Väisälä frequency with the standard deviation between the two depths of 1.3 m (Kahru, 1981). It should be noted that the chlorophyll maxima considered here have the vertical scale of a few meters and are reproduced on consequtive vertical profiles. In this respect they differ from the "micropatches" discussed by Astheimer and Haardt (1984). As we have no rate measurements for the Baltic chlorophyll maxima, no firm connections between the phenomenological types and the functional types of Cullen (1982) can be established.

In or near horizontal fronts the vertical structure is much more complicated, showing various intrusions and interleavings (Fig. 3). The conversion of fluorescence to chlorophyll a concentrations in layers of different origin and with different phytoplankton populations may be problematical due to variations in the fluorescence yield. However, in most cases with sufficient range of data points, the calibration regressions (Fig. 4) are quite reliable (Kahru and Aitsam, 1985).

Another problem, related to the potentials of remote sensing to estimate the distributions of chlorophyll and primary production, is the correlation strength between the near-surface chlorophyll and the photic zone integral chlorophyll. On the basis of 570 vertical profiles from the Baltic (Kahru, 1985) it has been shown that

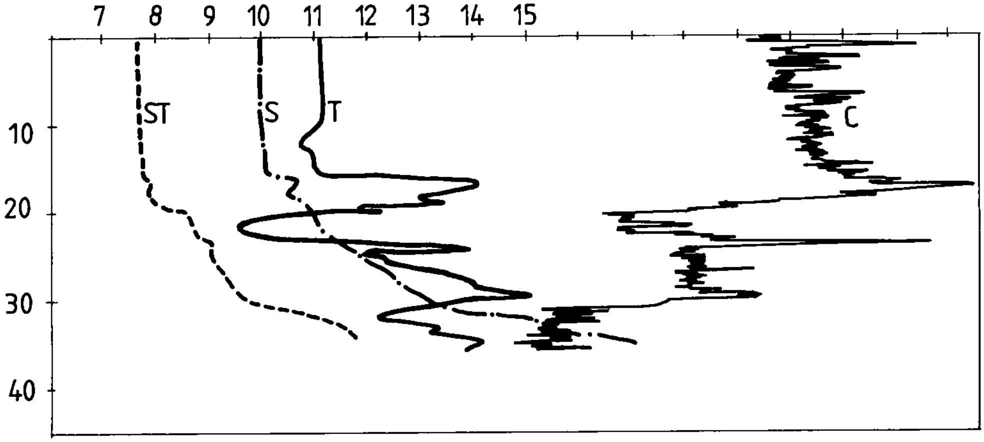


Fig. 3. Profiles of temperature (T, °C), salinity (S, °/₀₀), density (ST, sigma-t), and chlorophyll a fluorescence (C, rel. units) versus depth (m) near a front in the Arkona basin, 23 Sept 1979.

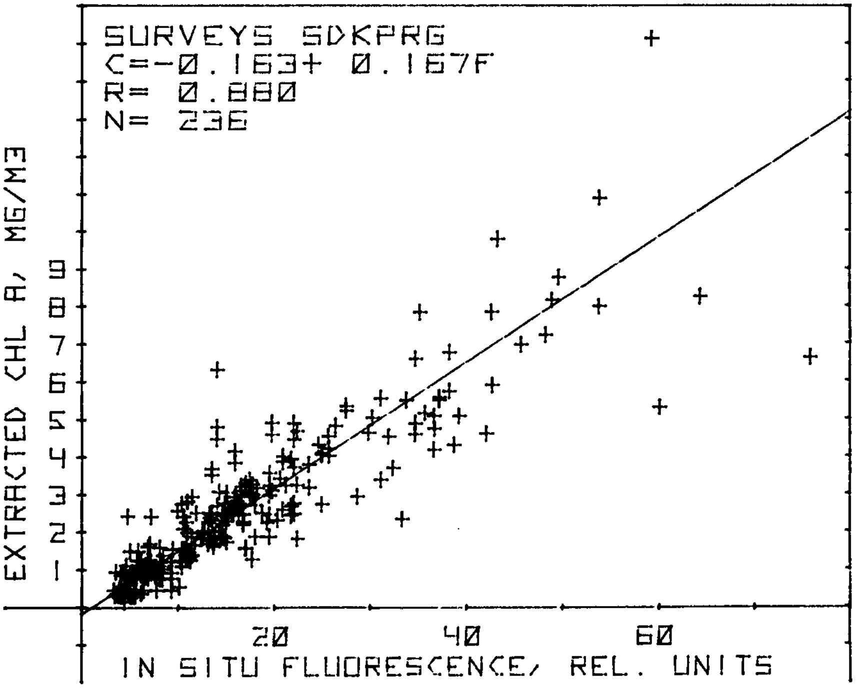


Fig. 4. Calibration regression of extracted chlorophyll a from discrete water samples versus in situ fluorescence for surveys in July-August, 1982.

only in case of a well-mixed upper layer serves the near-surface concentration as a good estimate of the photic zone chlorophyll. On the other hand, in case of a stratified photic layer the correlation between the near-surface and the photic zone chlorophyll is low. Moreover, it has been documented that if there are stations with a strong subsurface maximum and with a more or less uniform vertical distribution (Fig. 5), or if the photic zone depth changes primarily due to non-chlorophyllous material, the relation between the near-surface and the photic zone chlorophyll is inverse. This can be a source of error for the remote estimations of chlorophyll and primary productivity.

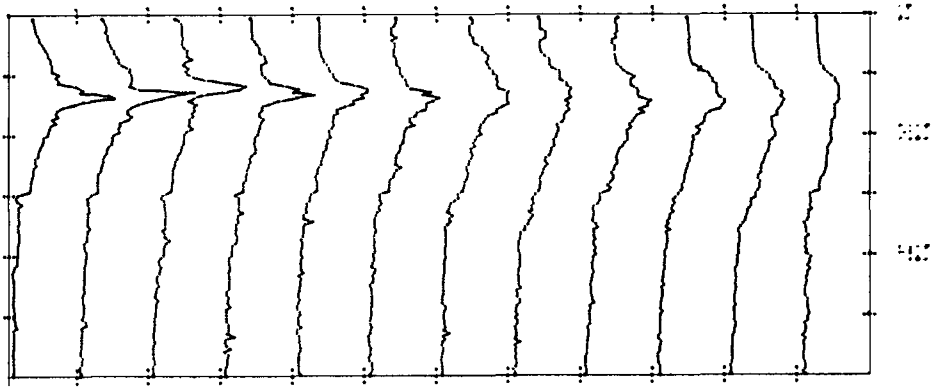


Fig. 5. Sequence of vertical chlorophyll a profiles along a transect line with a space step of 2.5 nautical miles (Gotland basin, 6 Aug 1982). Each ensuing profile is offset 3 mg m^{-3}. The shift in the vertical distribution from a strong subsurface maximum to a more or less uniform vertical distribution gave rise to an inverse relationship between the surface and the photic zone chlorophyll (only the central part of the transect is shown).

Offshore boundaries associated with fronts and eddies

Our first biological front study in the south-eastern Gotland basin in 1982 yielded rewarding results (Kahru et al., 1984). A 30-m thick water mass with anomalously low salinity extended vertically across the horizontally uniform thermocline (Fig. 6). The front was primarily a salinity front and not a density front (only the isopycnals in the top 10-14 m were inclined). In the top layer the higher salinity water had protruded onto the low-salinity water. It was hypothesized that after the initial convergence of the two water masses, a vertical stretching of the top layer was produced, the top isotherms being lifted up, and a cyclonic circulation es-

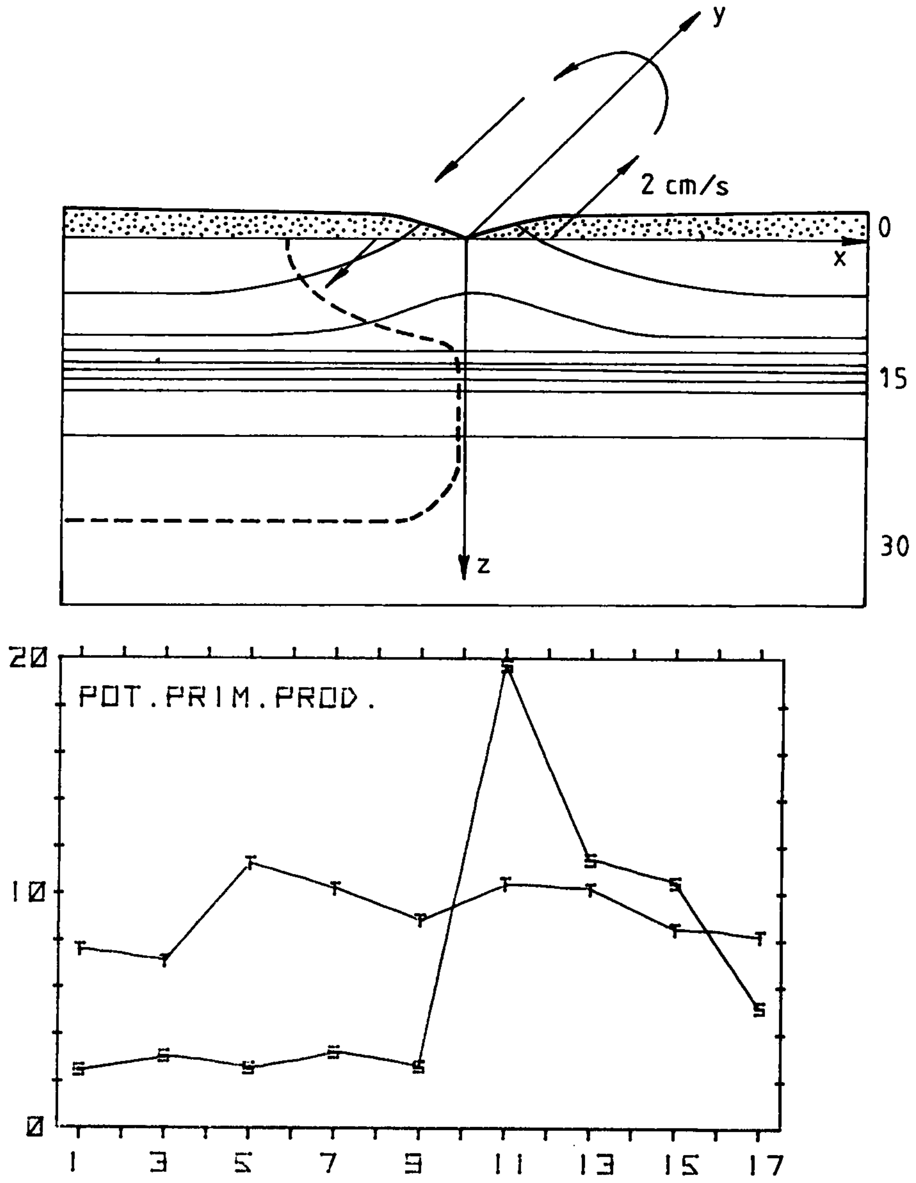


Fig. 6. (upper panel) Schematic description of the frontal structure and of the proposed mechanism for frontal upwelling (Gotland basin, 6 Aug 1982). Left from the dashed curve: the low-salinity anomaly; continuous curves: isopycnals (or isotherms); arrows: cyclonic circulation; stippled area: supposed deformation of the free surface.
(lower panel) Horizontal distribution of the potential primary production (mgC $m^{-3}h^{-1}$) near the surface (S) and in the thermocline (T).

tablished. The limited upwelling of the upper thermocline water was suggested to be responsible for the 7-fold increase in the potential primary productivity adjacent to the salinity interface. The productivity values were higher in the higher-salinity side of the front and levelled down further away from the front. The sharp thermocline where the upwelled waters could originate from obviously accumulated sinking organic matter which released nutrients. The changes in primary productivity were primarily caused by changes in the assimilation numbers and not in the biomass as the chlorophyll content had only a slight maximum adjacent to the frontal zone. However, the zooplankton biomass more than doubled in the higher-salinity side of the front.

Another type of fronts was under observation in the Bornholm basin in the summer of 1984. In a 4-day interval the transect was covered twice (2 and 6 August) and again after 4 days profilings were made on the rectangular grid of stations (Fig. 7). While both of

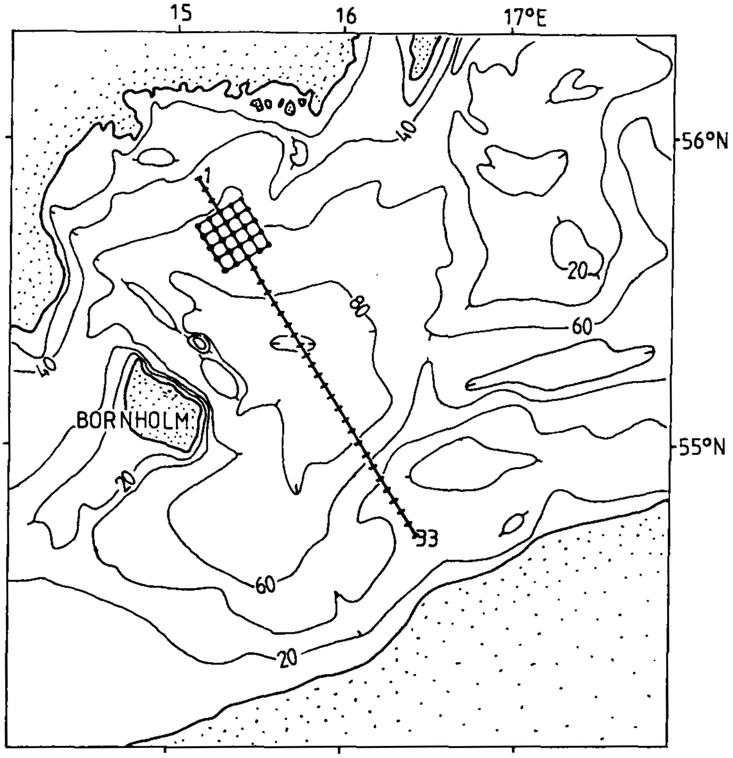


Fig. 7. Study area in the Bornholm basin in August, 1984. Station spacing along the transect and on the grid is 2.5 nautical miles.

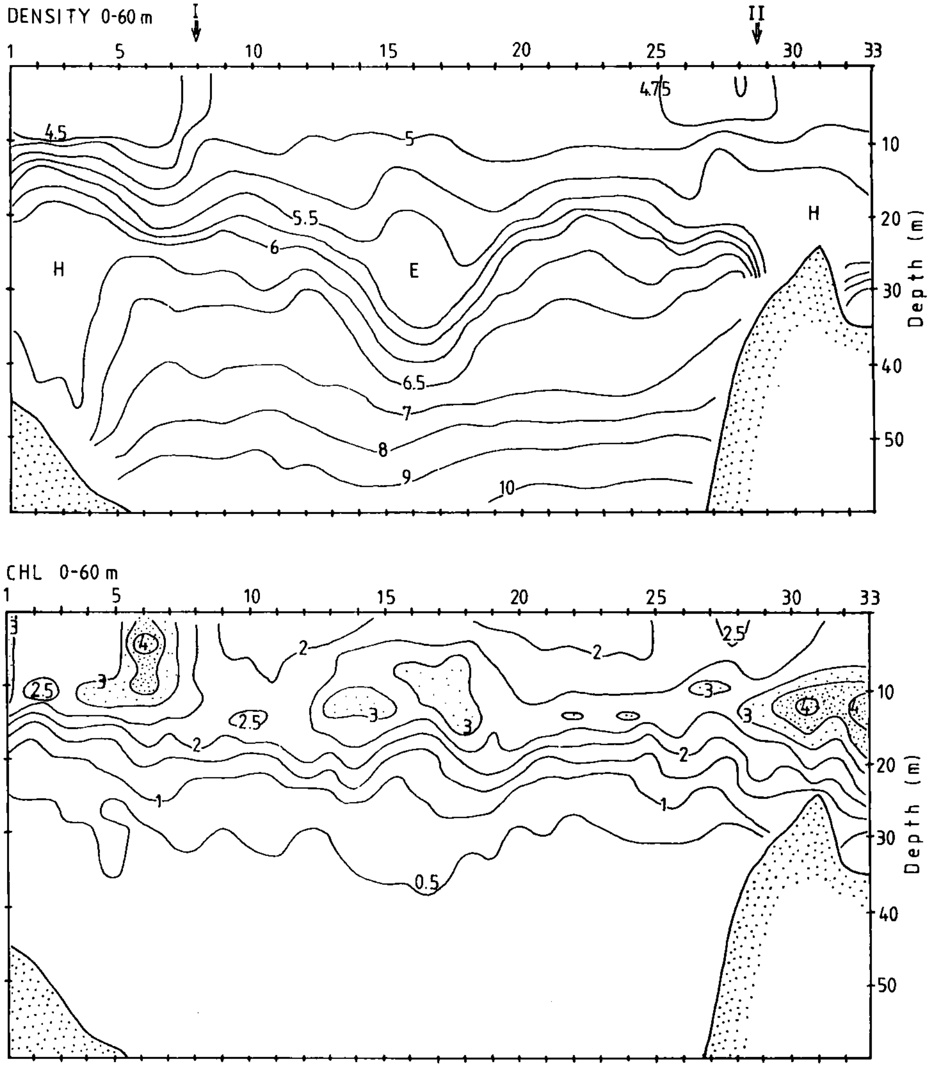


Fig. 8. Vertical distributions of density (sigma-t units) and chlorophyll a (mg m^{-3}) on the transect, 6 Aug 1984. Arrows point to the frontal structures labeled I and II. An eddy-like deformation of the thermocline (E) and two bottom-mixed homogeneous water masses (H) near shallow banks are labeled. Note the chlorophyll maximum in the low-salinity side of front I and another maximum above one of the bottom-mixing areas. The contour interval is 0.5 for chlorophyll, 0.25 for the sigma-t range 4.5-6.5 and 1.0 for the sigma-t range 7-10.

the frontal structures found (Fig. 8) were primarily caused by changes in salinity, they were also distinct density fronts. The frontal structures were not stationary in space but were advected (or meandered) in the NW direction (both fronts - 10 km in the 1st 4-day interval, front I - 5 km in the 2nd 4-day interval). The other distributions revealed several features related to the frontal structures. The chlorophyll maximum was bound to the low-salinity edge of front I on both of the transects. The two maxima in the distributions of the nonmigrating zooplankton most conspicuously responded to the both frontal structures (Fig. 9A). The distribution pattern of copepods could have been similar unless the upper layer samples were overmasked by their diel vertical migration. The dominant species in the frontal maxima were Bosmina coregoni maritima for the cladocerans and Synchaeta monopus for the rotifers. The nutrient concentrations were quite variable; however, the nitrate maximum between the stas. 6-10 may be associated with the frontal region (Fig. 9B). The phosphate maximum between the stas. 10-18 (not shown) seems to be characteristic of the water mass on the SE side of front I. Although the analytical error variance of the nutrient determinations might be considerable, the space resolution of 2.5 n. miles is obviously too big to resolve the intense smaller scale variability (see Hansen, 1985). The same was probably true of the primary productivity distributions. The productivity values were highly variable and did not show obvious connections with the other variables. This may partly be attributed to the dominance of the cyanobacteria (Aphanizomenon, Microcystis, Nodularia) forming large aggregates and increasing therethrough the sample variance.

Unfortunately, no current measurements in the fronts were available but in general fronts are known as sites of active convergence/divergence. The increased abundance of zooplankton in the frontal regions might have resulted from the flow convergence in the fronts. The organisms which can maintain their preferred depth can easily accumulate in convergence zones (Olson and Backus, 1985). The same mechanism, however, did not work for ichtioplankton which was more abundant in the region between the two fronts. Although fronts have increased gradients in the across-front direction, they are by no means merely 2-dimensional (vertical and across-front) phenomena. This was substantiated by mapping the temperature, salinity and chlorophyll distributions on the 2-dimensional grid (Fig. 10). Changes in the location of the frontal boundary, interpreted as the meandering or advection of the front, could easily be followed in

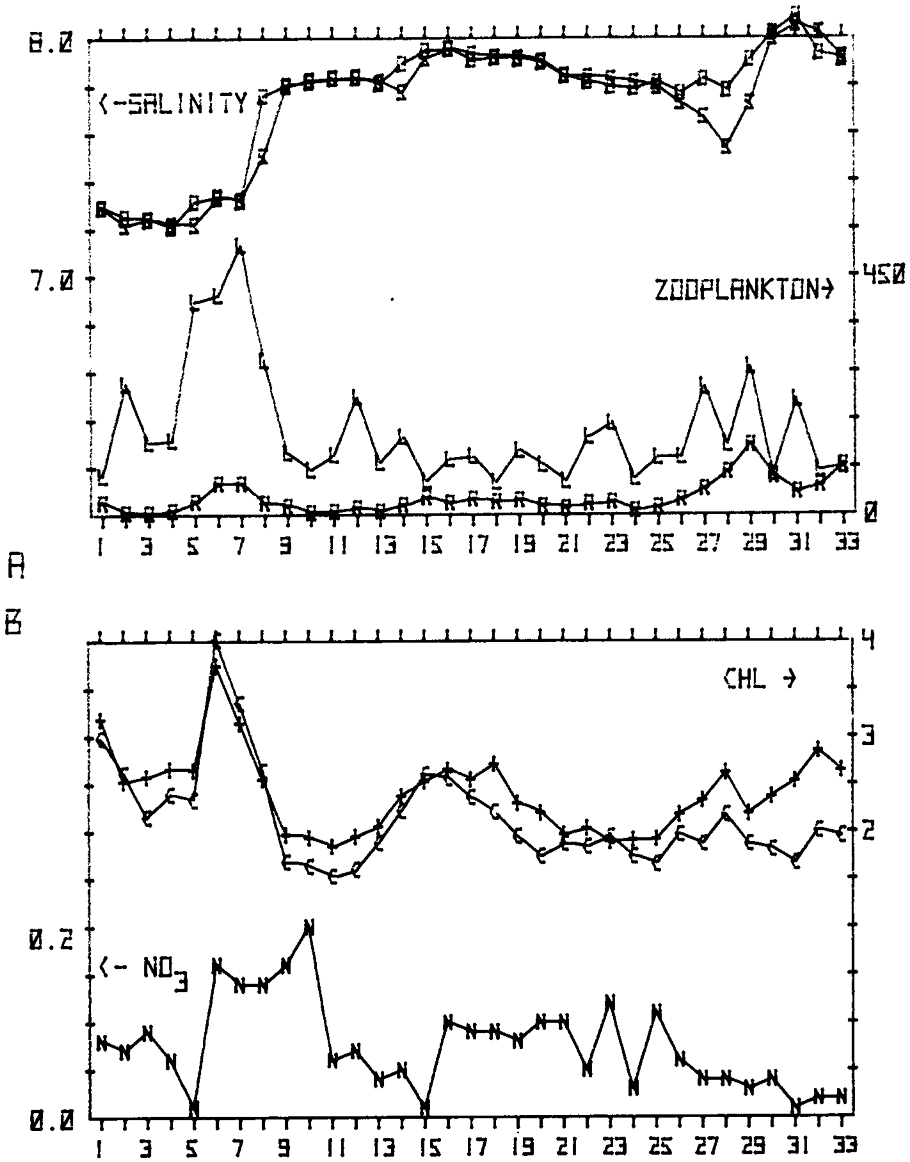


Fig. 9. Horizontal distributions along the transect through the Bornholm basin, 6 Aug 1984. (A) Salinity ($^{\circ}/_{oo}$) at the depths of 5 m (5) and 10 m (0), biomass (mg m^{-2}) of the cladocerans (L) and rotifers (R) in the upper 10-m layer.
(B) Surface (1m) concentrations of nitrate (N, µM), chlorophyll a as extracted from water samples (C), and the mean chlorophyll a concentration in the top 10-m layer as measured fluorometrically (+, mg m^{-3})

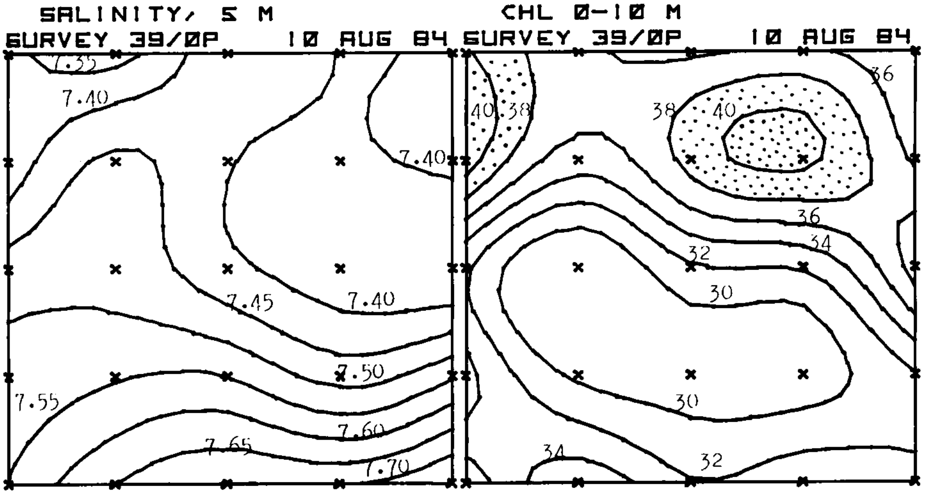


Fig. 10. Horizontal distributions on the 10 x 10 n. mile grid (for the position see Fig. 7): near-surface (5 m) salinity (‰) and the top 10-m chlorophyll concentration (mg m^{-2}).

the thermohaline structure. However, the biological and chemical distributions had undergone drastic changes between the surveys. As the dominant currents ought to be in the along-front directions, we suggest that the principal source of variations between the subsequent surveys was the advection of various scale patches across the station grid. This could account for the lack of resemblance between the consequent surveys for the chlorophyll (Figs. 8 and 10) and nutrient distributions.

We have presented evidence that the synoptic scale eddies contribute significantly to the distributions of biological and chemical variables in the Baltic (Kahru et al., 1981, 1982; Aitsam et al., 1984). Eddies may develop from frontal boundaries (Pingree et al., 1979) and can themselves produce smaller scale fronts by accentuating the existing gradients. The synoptic scale eddies contribute probably extensively to the vertical flux of nutrients in the interior of the Baltic (Kahru, 1982). However, the effect of an eddy field on the nutrient flux is highly dependent on the vertical thermohaline and nutrient stratification as well as on the energy available to overcome the buoyancy forces. Consequently, some eddies simply transport nutrient and chlorophyll anomalies over large distances (Aitsam et al., 1984). Apart from lifting or lowering the pycnoclines (and, possibly, nutricline) in eddy centers, the eddies influence the mixing in their periphery, probably owing to the intensified shear zones at the eddy boundaries. Fig. 11 is a result of a joint survey with the Institut für Meereskunde, Kiel (Dr. H.P. Hansen) showing coherent patch-like anomalies in the hydrochemical

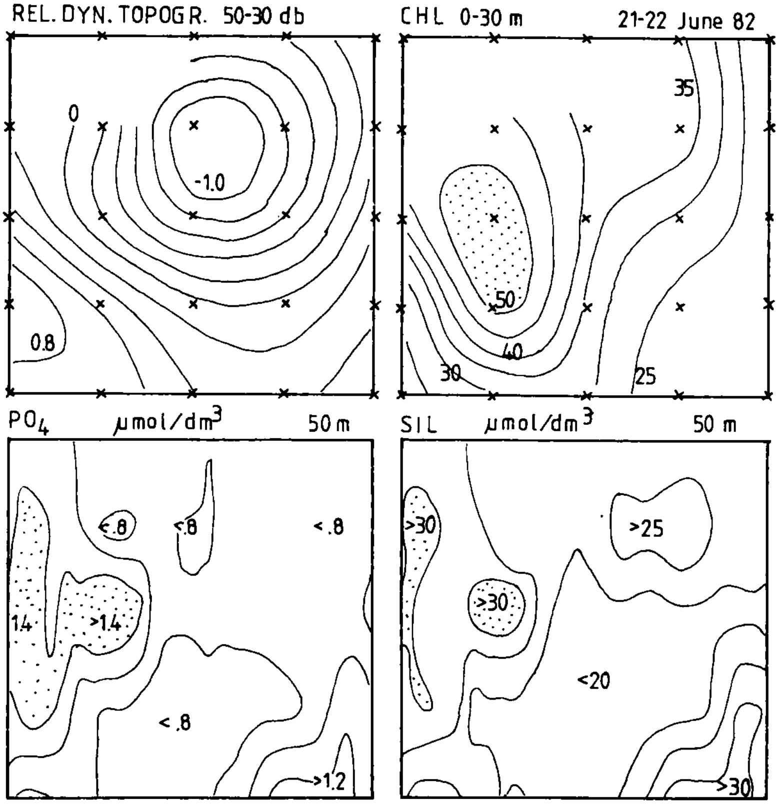


Fig. 11. Horizontal distributions on a 10 x 10 n. miles area in the Bornholm basin, 21-22 June 1982. The phosphate and silicale data were measured by Dr. H.P. Hansen (IfM, Kiel).

parameters and chlorophyll distribution. The anomaly with maxima in the nutrient concentrations and minima in pH and oxygen was located in the eddy periphery with maximal gradients in the geostrophic currents. The chlorophyll patch in the upper 30-m layer was located exactly above the nutrient patch at 40-60 m depths. Some of the differences between the corresponding contour maps are not due to different distributions but to different sampling schemes. Whereas the

CTD and chlorophyll profiles were taken at the grid points with a 2.5 n. miles step, the hydrochemical data were obtained by horizontal scanning along the parallel grid lines.

Offshore fronts also delimit different plankton communities or seasonal succession stages. This has been observed with the use of the flow-through measurement system. As most of the data are still under scrutiny, only one example will be presented. A sharp salinity front was observed during the spring bloom near the opening to the Gulf of Finland. Together with the drop in salinity an abrupt change in the particle size structure was observed (Fig. 12). While the channel 7 values remained on the same level, channels 8 and 9 as well as the fluorescence showed a sharp increase. It was proved later that the changes were due to the increased mean size of the diatom *Achnanthes taeniata* "chains". The longer chains of *A. taeniata* colonies were assigned by the counter into the higher size classes. Together with the other changes (Table 1), e.g. the increased chlorophyll, pheopigment and primary production levels, phytoplankton abundance and the increased numbers of the decaying cells of the cold water species *Melosira arctica* and *Nitzschia frigida* this indicates that the front marked a boundary between different successional stages of the vernal bloom. Whether there were some specific boundary effects, e.g. elevated values compared to the both sides, is not clear but the waters of the Gulf of Finland were certainly in a more advanced stage.

TABLE 1

Near-surface (5 m) hydrographic data and phytoplankton parameters for stations representative of the either side of the front and adjacent to the front (cf. Fig. 12).

	T5	F	T6
Salinity (°/$_{oo}$)	7.33	6.77	6.85
PO_4-P (µM)	0.42	0.48	0.40
Chlorophyll *a* (mg m^{-3})	5.47	14.28	12.68
Phaeopigment (- " -)	1.25	2.16	1.80
Light-saturated primary production (mg C $m^{-3}h^{-1}$)	21.0	48.1	48.5
Total phytoplankton abundance (solitary cells and colonies/ml)	490	808	596
Achnanthes taeniata (colonies/ml)	225	388	339
Mean equivalent diameter of (*A. taeniata* colonies (µm)	41.9	45.7	48.3

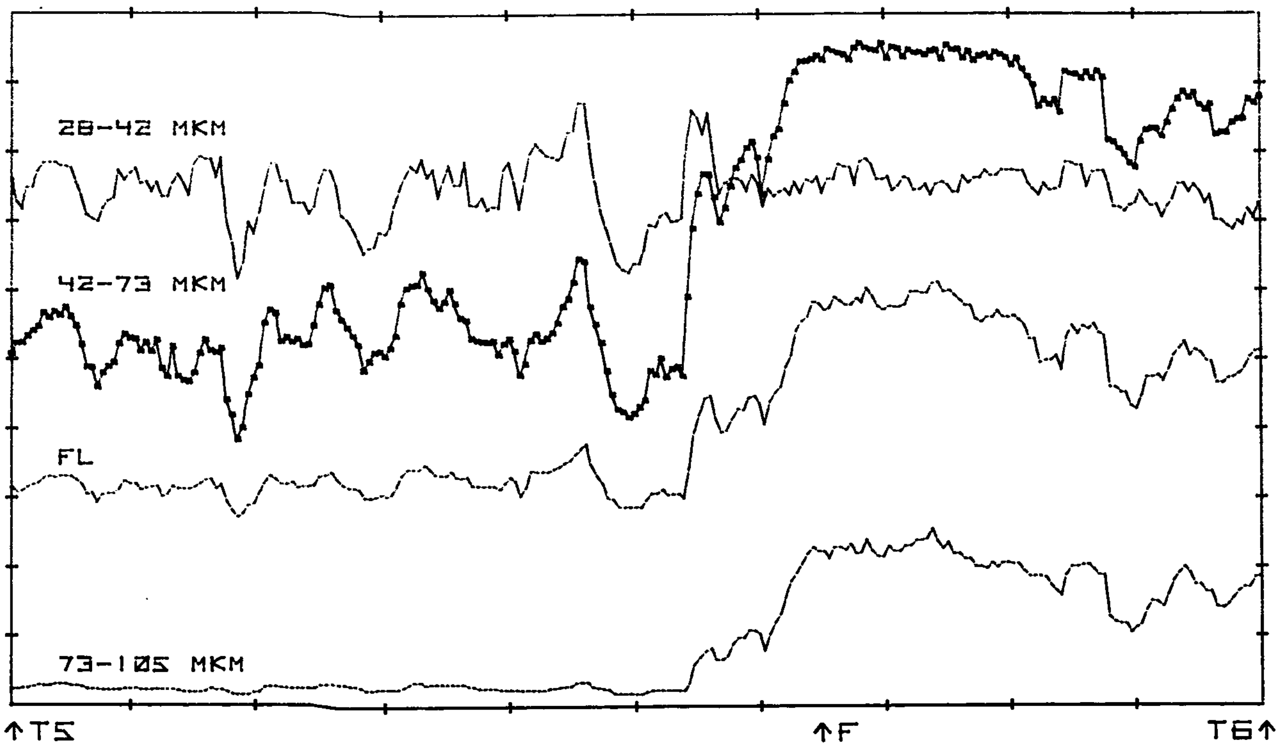


Fig. 12. Near-surface (5 m) horizontal distributions of chlorophyll fluorescence and particle concentrations in the equivalent diameter ranges 28-42, 42-73 and 73-105 μm The interval between points T5 and T6 is 50 n. miles. Water samples were taken from points T5, F, T6. The full scale is equivalent to 12o particles/ml.

Boundary effects in the Moonsund area

Altogether 6 surveys were made in the study area (Fig. 13) in May, July and October, 1982 and May, July and November, 1983 (Nõmman, 1985). In the space of the first two principal components a boundary area between the waters of the Matsalu Bay and the Soela Strait is distinguished (Figs. 13, 14). The boundary area is a site of strong vertical stirring due to a strong, fluctuating current over shallow areas, and of lateral exchange between different water masses. The boundary discussed here is not a front in its usual sense but rather an area of contact between different communities and water masses, and has a scale of about 10 km. While some parameters (the water transparency) decreased gradually from the west to the east (Fig. 15), several others showed pronounced maxima in the boundary zone, e.g. the nutrients, algal assay values, phytoplankton biomass and species richness. The species-abundance curves of the spring phytoplankton (Fig. 16) show that while the eutrophic Matsalu Bay community is strongly dominated by a single species (Diatoma elongatum v. tenuis), and the oligotrophic community has very long abundances with a low number of species, the boundary phytoplankton community has a rich variety of relatively uniformly distributed species. The results of the 6 surveys varied to some extent but at least some of the boundary effects mentioned were present on all the surveys.

DISCUSSION

Using results from our recent studies we have presented examples of various physical-biological couplings between the synoptic scale and the smaller scale distributions of variables in the Baltic Sea. We must admit that our abilities to interprete various details in these distributions in terms of the dynamics (i.e., their generation, transport and decay) are limited and ambiguous. Although the boundary zones described herein have often been characterised by elevated values of plankton concentrations and/or rates of related processes with respect to the surrounding waters, this is by no means always the case. As rightly noted by Richardson et al. (1985), there is a natural tendency to preferentially report those occasions with significant boundary effects, and to "forget" the cases with no apparent differences. We have demonstrated that the ecological system in the Baltic can actively respond to the physical forcings, such as the synoptic eddies, frontal dynamics, etc. We believe that much of the variability in the response stems from

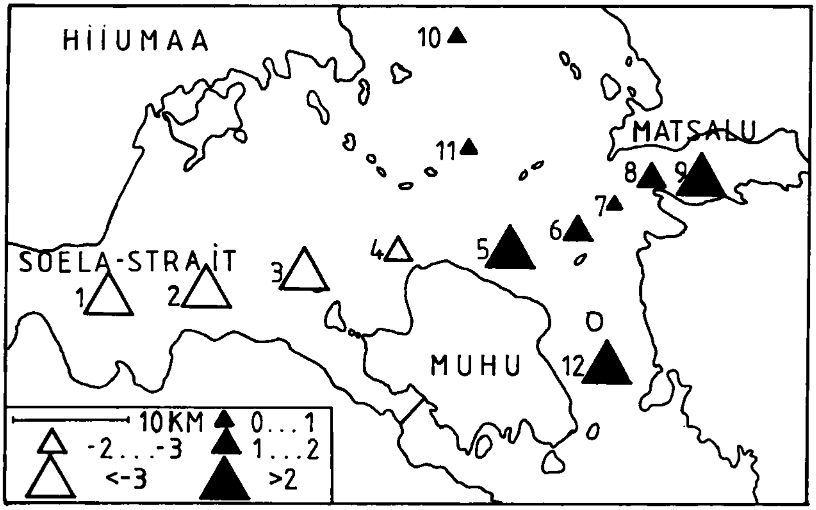
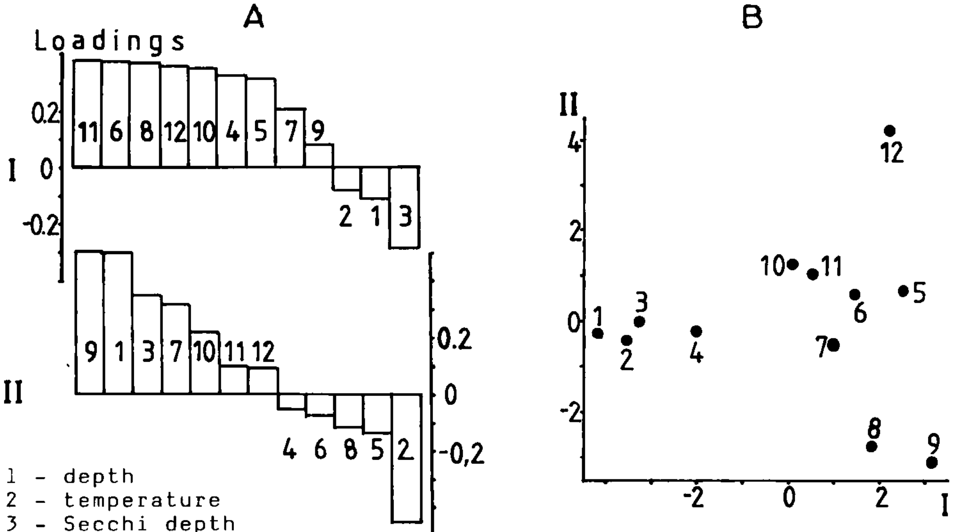


Fig. 13. Study area and horizontal pattern of scores of the first principal component in May, 1983.



1 - depth
2 - temperature
3 - Secchi depth
4 - nitrate concentration
5 - total phosphorus
6 - total number of phytoplankton
7 - number of Cyanophyta
8 - number of Diatomea
9 - number of Pyrrhophyta
10 - total phytoplankton biomass
11 - biomass of Diatomea
12 - number of species

Fig. 14. (A) Structure of the first two principal components with the ingredient variables listed below;
(B) Ordination of stations in the space of the first two components.

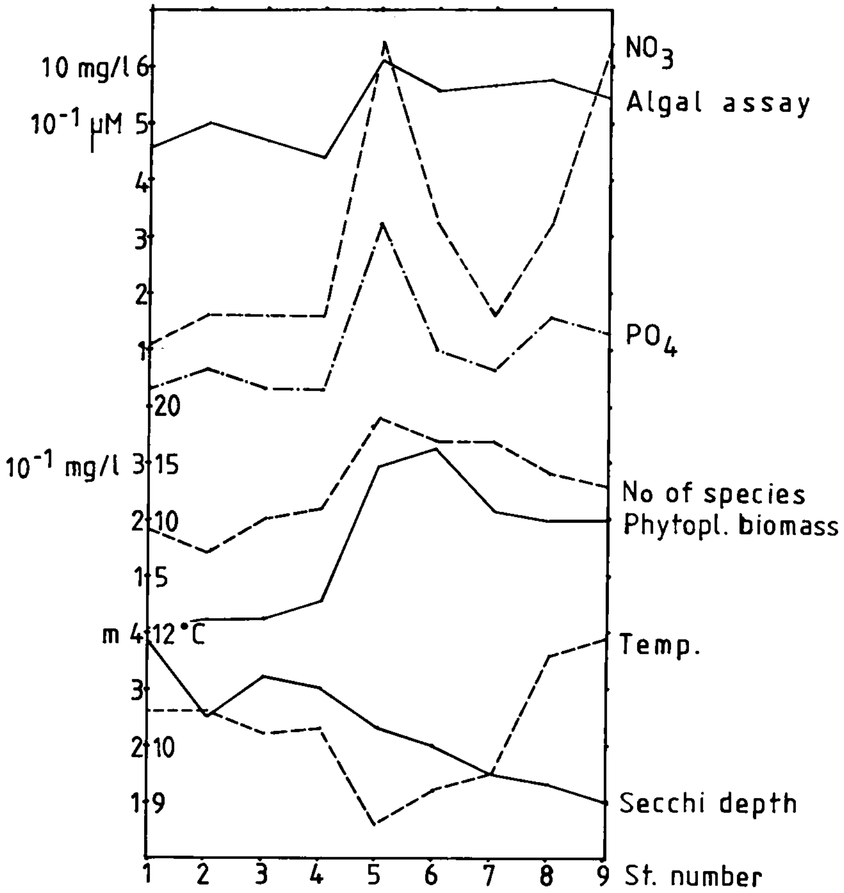
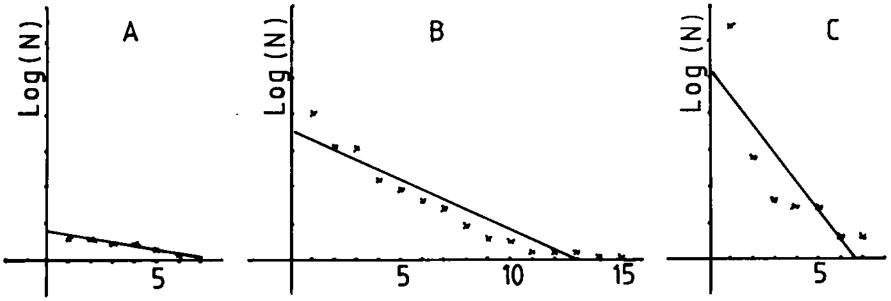


Fig. 15. Horizontal profiles of some biological, chemical and physical variables across the Moonsund boundary area in May, 1983.



N - number of individuals per species

Fig. 16. Species-abundance curves of three phytoplankton communities: A - Soela Strait, B - boundary area, and C - Matsalu Bay.

the intricate hydrodynamics of the forcings themselves. It seems that in the face of the ubiquitous occurrence of fronts and other boundary phenomena in the Baltic and in the face of the results from this and other areas, it is not the question any more _whether_ the boundaries have biological effects but what is the _density of occurrence_ in space and time of the boundaries with certain characteristics. The next task then should be the determination of the overall importance of the Baltic boundary zones to its ecology, to the local fisheries, etc. A major task for the coming years would be to accumulate representative statistics on biological effects of fronts and other boundary phenomena, and to reveal the mechanisms which govern the biological response to the physical forcing. To accomplish this task, a major improvement in the sampling strategy and techniques should take place. First, more extensive use of the remote sensing (see Campell and Esaias, 1985) and high resolution _in situ_ methods should be made. The temporal dynamics of the phenommena should be studied in their full dynamics, i.e. from their generation till their decay. In a system which is not at equilibrium, the temporal sequence of events is crucial (Harris, 1983). Therefore the correlations between planktonic and environmental variables as measured at a single instant need not yield much insight. It is also evident that the variability at the level of integral parameters such as biomass or _in vivo_ fluorescence obscures the inherent variability of a plankton community at the level of populations. It is at the level of populations or even their developmental stages that the significant interactions take place. We hope that the use of the high-resolution, flow-through particle counting system with the accompanying measurements will provide useful insights in the near future.

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