

Annual cycle of particle size fractions and phytoplankton biomass in the northern Baltic proper

Mati Kahru, Ellen Kaasik, Aina Leeben

Institute of Ecology and Marine Research, Paldiski Rd. 1, Tallinn 200031, Estonia, USSR

ABSTRACT: A large data set of particle concentrations in the range 1 to 1000 μm , chlorophyll *a*, and associated measurements from the surface waters of the northern Baltic proper during 1985 to 1989 was analyzed to construct spatially and temporally averaged annual time curves of particle size fractions and phytoplankton biomass. Chlorophyll *a* concentration was well correlated with the 28–73 μm size fraction and had 2 seasonal peaks: in April–May, corresponding to the diatom spring bloom, and in August, corresponding to the late-summer bloom of blue-green algae. The 2 maxima were separated by the early summer minimum when the 1–10 μm particle fractions corresponding to a mixed assemblage of small phytoplankton and microheterotrophs reached their maxima. The largest particles (163–1000 μm), corresponding to smaller mesozooplankton, reached their maximum in July–August before the blue-green maximum. Automated particle counting is well suited for routine monitoring of pelagic systems as it reveals all major shifts in the planktonic community.

INTRODUCTION

Due to the dramatically increased nutrient loadings during recent decades (Larsson et al. 1985), the ecosystems of the Baltic Sea are under pressure to adjust in response to the changing environment. However, in contrast to benthic and near-shore ecosystems, where such changes have been clearly documented (Elmgren 1989), analogous effects in the pelagic systems have been difficult to demonstrate. One reason is that data from off-shore areas are scarce compared to coastal areas. Another obstacle to unequivocally detecting trends is the high inherent temporal and spatial variability of the Baltic pelagic ecosystem. It has been estimated that temporal variability in chlorophyll concentration during the productive season causes average errors of over 100 % in a monitoring point sample whereas the mesoscale spatial variability (e.g. eddies and fronts) adds another 100 % error (Kahru & Aitsam 1985, Kahru et al. 1987). Reliable time curves of the annual development of the pelagic communities in the Baltic are needed, e.g. for modeling of the long-term development of the ecosystem (see Wulff 1988), as well as for detecting trends.

In this paper we try to establish averaged annual

time curves for some characteristics of the pelagic system in the northern Baltic proper based on a large set of automated measurements of particle size fractions, chlorophyll *a* concentration (chl *a*), and associated measurements. Statistical analysis of the variability structure of these parameters will be reported elsewhere.

In offshore areas the influence of resuspension and land-based runoff are expected to be minimal, hence most of the particles measured are of biological origin. The size of a planktonic particle is itself an ecologically important parameter, as it often determines its specific growth rate (Fenchel 1974), its fate in the food chain (Platt & Denman 1978), and its ability to remain suspended (Malone 1980). Hence seasonal time curves of the particle size fractions may give some insight into the functioning of the pelagic ecosystem.

MATERIALS AND METHODS

Data collection. Measurements were made from RV 'Arnold Veimer' cruises 6, 8, 10, 11, 13, 14, 18, 19, 20, 23, 30, 31, 32 between 1985 and 1989 in the 'on-track' mode while the ship was steaming along a straight

course at a constant speed. Underway shipboard measurements of particle concentrations, chlorophyll in vivo fluorescence, temperature and salinity were obtained from 5 m depth (Kahru et al. 1989, Kahru & Nömmann 1990). The sampling system consisted of an on-line Hiac-Royco PC-320 particle counter, a Turner Designs 10-005R flow-through fluorometer, and a thermosalinograph measuring water temperature and conductivity.

The time interval between the registration of integrated particle counts and other parameters was set at 1 min and corresponded to a space interval of 200 to 400 m.

The Hiac-Royco particle counter (Pugh 1978) with 2 sensors registered particles with equivalent spherical diameter from 1 to 1000 μm in 12 channels (Table 1). The sensors operate on the principle of light blockage. The counting time was 10 s during which 1 and 170 cm^3 of seawater, respectively, passed through the 2 sensors. Concentrations in the channels (size classes) are designated as Ch1 to Ch12. Ch6 was discarded from the analysis as it was mostly covered by Ch7 and Ch8 of the other sensor, but because of the very small flow rate through the small sensor, the number of counts in it was too low to be reliable.

The on-track measurements were supplemented with quantitative samples of phyto- and zooplankton abundance to establish links between the particle size fractions and plankton species as well as measurements of the extracted chl (Edler 1979). The fluorescence was converted to chlorophyll *a* by calibration against extracted chl separately for each cruise (correlation coefficients, $r = 0.73$ to 0.99).

Data analysis. The usual way of representing particle data is to express them as volume concentrations (Sheldon et al. 1972), but as particles can seldom be considered spherical, the conversion of surface area measured by the Hiac-Royco sensors to volume was not

pursued. Moreover, the activity of organisms is roughly proportional to their surface area and not to their volume (Fenchel 1974, Platt & Denman 1978, Kiørboe et al. 1990). Hence, as a measure of the integral particle concentration, we use the total particulate surface area (PSA) in the range 1 to 1000 μm . Total PSA is calculated by multiplying the channel concentrations by the respective average surface area, and summing over all channels. As a measure of the relative importance of a size fraction, the percent contribution of the fraction to the total PSA is used.

The on-track data with 200 to 400 m interval were averaged over 10 km segments of track. Hence, each sample considered here is an average over 10 km, i.e., depending on the ship's speed, 25 to 50 individual measurements. This was found to be a suitable averaging scale to represent the mesoscale structure (Kahru et al. 1987).

From the on-track measurements covering the whole Baltic (with the exception of the Gulf of Bothnia), data from the most frequently visited northern Baltic proper (north of 58°N) and the western Gulf of Finland (west of 24°E) were extracted (Fig. 1). Data from all cruises between 1985 and 1989 were pooled. The combined study period covered most of the year with the exception of the winter period (January to March). Samples over several years were combined according to their corresponding Julian day. These samples were further pooled into 10 d periods from the beginning of the year (e.g. 1 to 10 January is period 1, etc.). The total number of 10 km averaged samples was 790 and most of the 10 d periods had between 40 and 60 samples (Fig. 2). Because of occasional malfunctioning of the small particle sensor, the actual number of samples is somewhat smaller for the small size fractions (Ch1 to Ch5) with resulting gaps in the coverage of the annual cycle.

Table 1. Channel settings for the Hiac-Royco Model PC-320 particle counter in equivalent spherical diameters

Sensor	Channel	Diameter (μm)	Dominant particles
CMH-60	1	1–2	Bacteria, picoplankton
	2	2–4	Picoplankton
	3	4–6	Nanoplankton
	4	6–10	Nanoplankton
	5	10–20	Nanoplankton
	6	20–60	Not used
E-1000	7	28–42	Diatoms, blue-greens
	8	42–73	Diatoms, dinoflagellates
	9	73–105	Diatom chains, dinoflagellates
	10	105–163	Large protozooplankton
	11	163–305	Copepodites, nauplii
	12	305–1000	Copepods

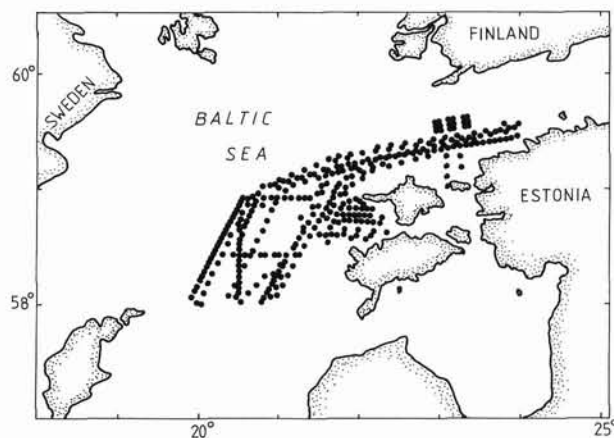


Fig. 1. Spatial distribution of samples in the northern Baltic proper. Each sample (dot) is an average over a 10 km transect (25 to 50 measurements) at 5 m depth

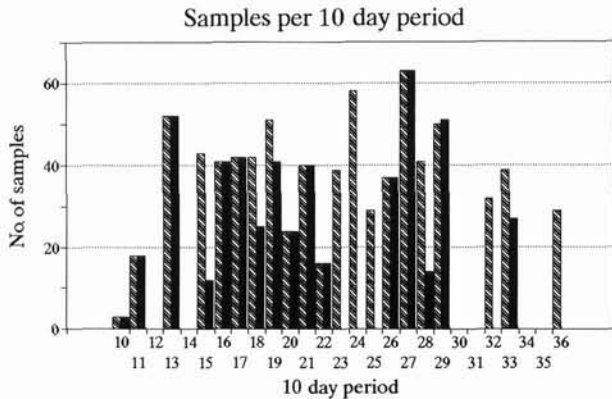


Fig. 2. Temporal distribution of the pooled particle samples from 1985 to 1989 in 10 d periods. The total number of samples is 790 for Ch7 to Ch12 (28–1000 μm , left bar) and 506 for Ch1 to Ch5 (1–20 μm , right bar)

RESULTS

The annual course in sea-surface temperature (Fig. 3) gives at the same time a qualitative time curve of changes in water column stratification: high surface temperature indicates a shallow upper layer and vice versa. Only during the commencement of the spring bloom (up to 10 d period 13 in Fig. 3) did slight salinity stratification provide vertical stability of the water column, when the water temperature was still below the point (about 2.4 $^{\circ}\text{C}$) at which maximum density is attained.

The time curves of the 2 integral parameters – chl *a* concentration and the total particulate surface area (PSA) in the diameter range 1 to 1000 μm – both show 2 maxima (Fig. 4) corresponding respectively to the diatom spring bloom (10 d periods 11 to 13, April–May) and to the late-summer bloom of blue-green algae (10 d periods 23 to 28, August–September). Chl increased faster in the beginning phase of the spring bloom while total PSA accumulated slower. The early-summer minimum (10 d periods 17 to 20, June–July) was more pronounced in chl than in total PSA. Chl values decreased almost to pre-spring-bloom values. The vigorous increase in the small particle fractions (Fig. 5A,B) and the more gradual increase in the largest particle fractions (Fig. 5E) to some extent compensate for the drastic loss of the 28 to 105 μm size range (Fig. 5C,D). However, the compensation is only partial as a considerable fraction of the particulate matter sediments out of the surface layer with the decline of the diatom bloom (Leppänen 1988).

It must be noted that due to averaging over several years, some features may appear prolonged compared to the time that they actually last in a particular year. For example, the spring bloom on each of the 2 years included (1985, 1986) was shorter than the averaged

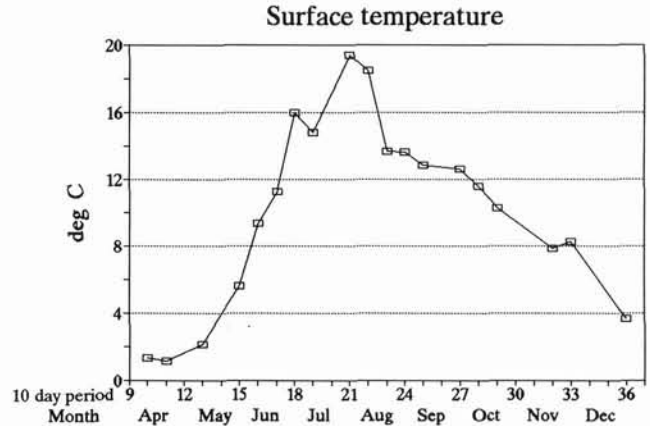


Fig. 3. Annual time curve of temperature versus 10 d periods and months

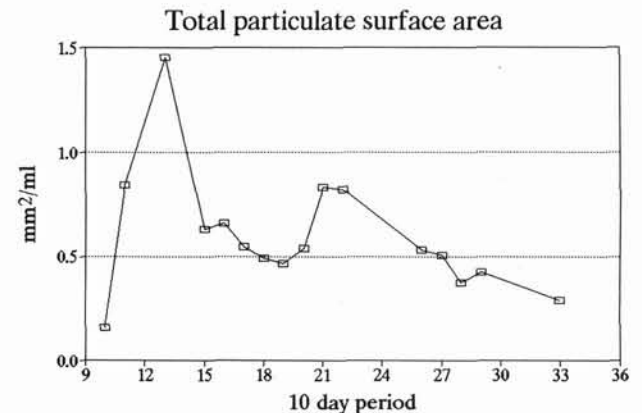
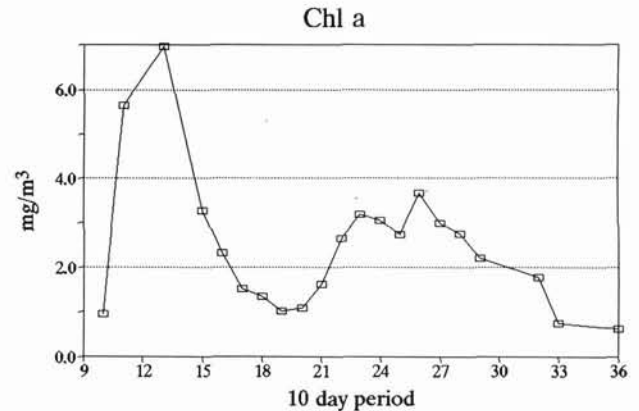


Fig. 4. Annual time curves of chlorophyll *a* and total particulate surface area in the 1–1000 μm size range

curve. Another result of the 10 d and yearly averaging is that the maxima become lower and the minima higher.

Apart from the general increase-decrease of the integral phytoplankton biomass or particle concentration, the contribution of a size fraction to the total PSA should give an estimate of the changing share of that size fraction in the community metabolism.

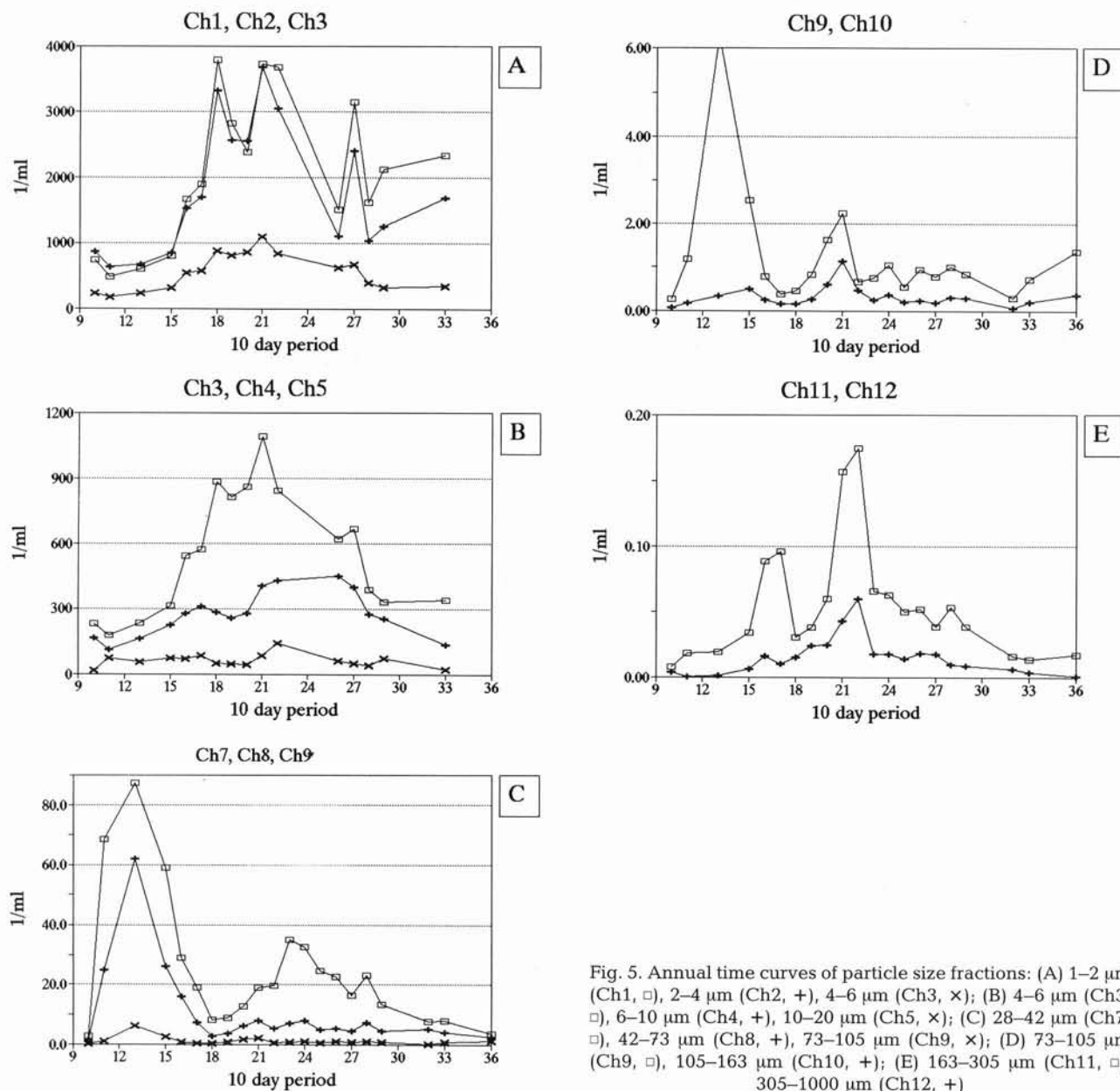


Fig. 5. Annual time curves of particle size fractions: (A) 1–2 μm (Ch1, \square), 2–4 μm (Ch2, +), 4–6 μm (Ch3, \times); (B) 4–6 μm (Ch3, \square), 6–10 μm (Ch4, +), 10–20 μm (Ch5, \times); (C) 28–42 μm (Ch7, \square), 42–73 μm (Ch8, +), 73–105 μm (Ch9, \times); (D) 73–105 μm (Ch9, \square), 105–163 μm (Ch10, +); (E) 163–305 μm (Ch11, \square), 305–1000 μm (Ch12, +)

The smallest size fractions (Fig. 6A,B) represented a high percentage of the total PSA before the start of the massive diatom bloom, and increased again during the decline of the diatom bloom. For example, in 10 d periods 10 (April) and 18 (June) the 1–10 μm size fraction made up respectively 52 and 50.5 % of total PSA in the range 1 to 1000 μm (Fig. 7), and its percentage dropped to 5 % during the peak of the spring bloom (beginning of May). The concentration of the largest particle size fractions (Fig. 5E) as well as their contribution to the total PSA (Fig. 6D) showed a general maximum in August (163–1000 μm) or another maximum after the diatom spring bloom (163–305 μm). The major seasonal changes in the plankton community are

shown by the time curves of the combined covarying size fractions (Fig. 7). The 28–105 μm size fraction (Ch7 to Ch9) made up 83 % of the total PSA during the diatom spring bloom. In strong diatom blooms its share may locally reach 95 %.

In the medium to large size fractions (Ch7 to Ch12), the first concentration maximum is attained later, the bigger the mean size of the particles is (Fig. 8). Because of the coarse resolution in time (10 d period), the difference in the Ch7 to Ch9 size fractions is not resolved in this figure. A more detailed examination shows that even within Ch7 to Ch9 the maximal values in the bigger size classes occurred definitely later. This is also true for the percent contributions where

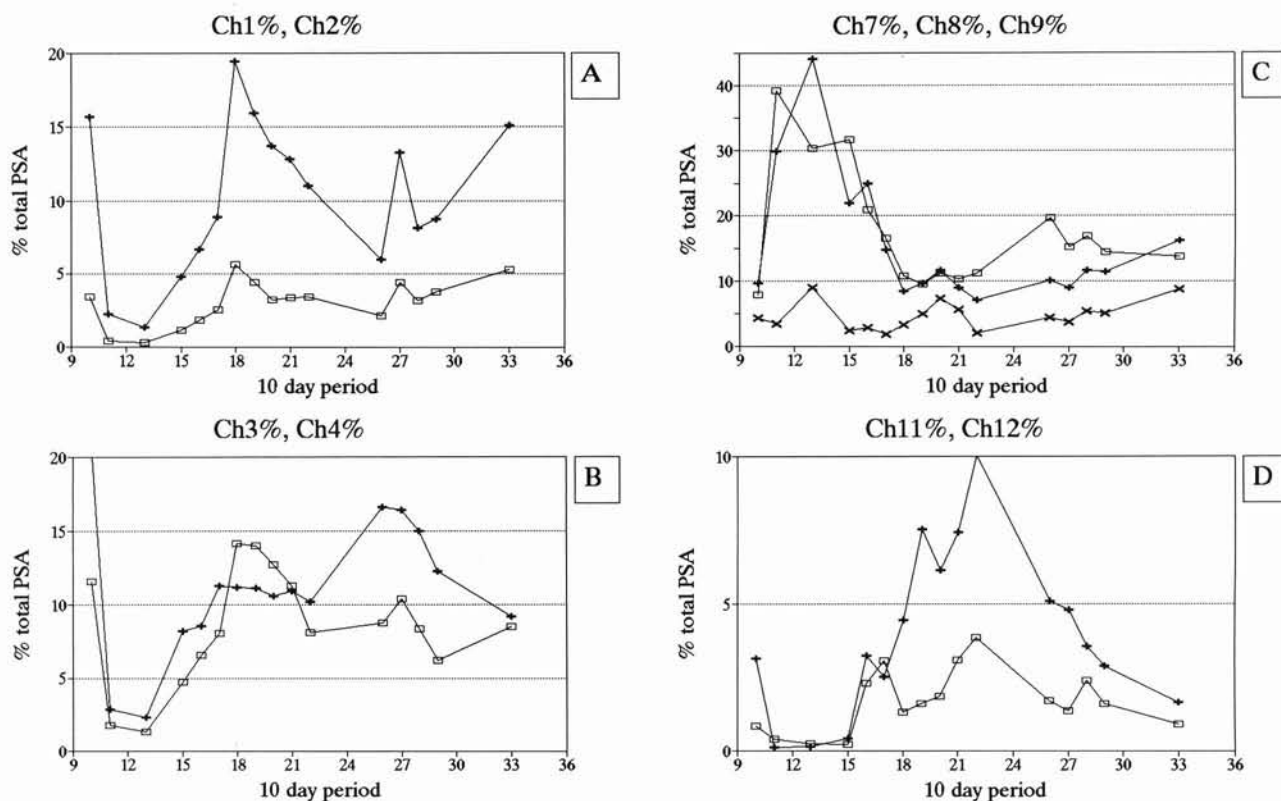


Fig. 6. Annual time curves of the percent contribution of a size fraction to the total particulate surface area: (A) 1–2 μm (Ch1 %, \square), 2–4 μm (Ch2 %, +); (B) 4–6 μm (Ch3 %, \square), 6–10 μm (Ch4 %, +); (C) 28–42 μm (Ch7 %, \square), 42–73 μm (Ch8 %, +), 73–105 μm (Ch9 %, \times); (D) 163–305 μm (Ch11 %, \square), 305–1000 μm (Ch12 %, +)

the maximum of Ch7 preceded the maxima of Ch8 and Ch9 (Fig. 6C).

In order to find covarying groups of variables, the 10 d averaged data set was submitted to principal component analysis (see e.g. Mayzaud et al. 1984). The first set of data included all the size fractions and chl (Table 2).

Nearly half of the variance was described by the first component with positive input from Ch1 to Ch3, and negative input from Ch7 to Ch9 and chl. The second component represented mostly the positive contributions from chl and Ch7 to Ch9. In the second data set with only Ch7 to Ch12 and chl, the first principal component (48 % of variance) had positive contributions from chl and Ch7 to Ch9, and the second component was associated with the large particles (Table 3).

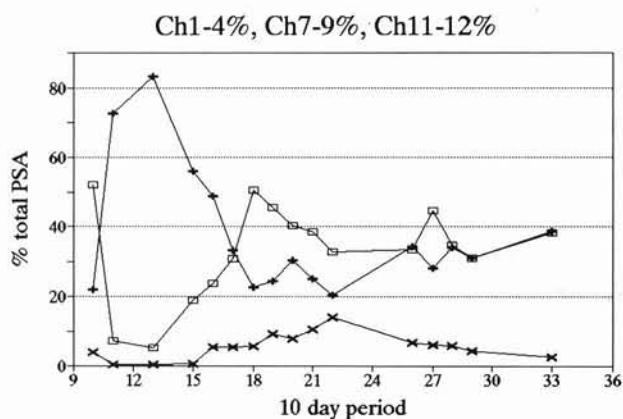


Fig. 7. Annual time curves of the combined contributions to the total particulate surface area: 1–10 μm (Ch1 to Ch4 %, \square); 28–105 μm (Ch7 to Ch9 %, +); 163–1000 μm (Ch11 to Ch12 %, \times)

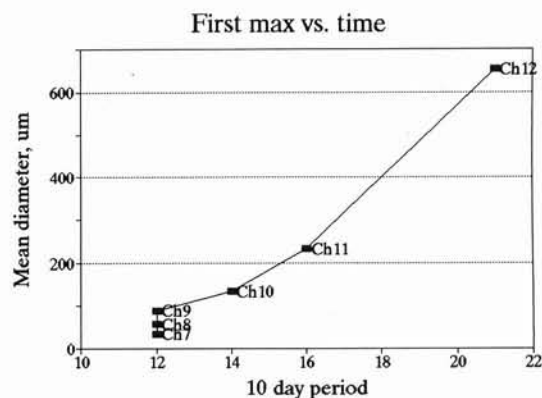


Fig. 8. Relationship between time of first concentration maximum and mean particle size (from Ch7 to Ch12)

Table 2. First 3 principal components of the particle size fractions Ch1 and Ch12, and chl. Constituents with positive and negative contributions are listed in the order of importance

Component no.	% of variance	Cumulative variance	Major constituents
1	43.3	43.3	+ Ch1, + Ch2, + Ch3 – Ch8, – Ch7, – Ch1, – Ch9
2	23.8	67.1	+ chl, + Ch9, + Ch7, + Ch8
3	13.6	80.6	– Ch5, – Ch4, + Ch10

Table 3. First 3 principal components of the particle size fractions Ch7 to Ch12 and chl. Constituents with positive and negative contributions are listed in the order of importance

Component no.	% of variance	Cumulative percentage	Major constituents
1	47.6	47.6	+ Ch8, + Ch7, + chl, + Ch9
2	30.4	78.0	+ Ch11, + Ch12, + Ch10
3	13.6	91.6	– Ch10

DISCUSSION

One of the major problems in dealing with particle size data is the interpretation of the particles in terms of ecologically more meaningful components. As shown by Lahdes & Leppänen (1988) in the same area, the particulate matter in the surface water is predominantly autochthonous, originating from plankton organisms. Although detritus particles may be significant, especially during the declining phase of a phytoplankton bloom, due to sedimentation and other processes removing detritus from the near-surface layer, the majority of particles presumably represent plankton organisms. Indirect proof for that is provided by the frequently high correlations between certain particle size fractions and chl fluorescence while direct proof has been provided by microscopic analyses.

The dominant types of particles in each size fraction were included in Table 1. Although the majority of plankto-bacteria are smaller than 1 μm (Lahdes et al. 1988), according to other results (Larsson & Hagström 1982) 40 % of the bacteria are retained by a 1 μm filter. We believe that the 1 to 2 μm fraction (Ch1) consisted mostly of large free-living bacteria and small autotrophic cells. The general dynamics of the small fraction corresponds well with the known seasonal development of bacterial biomass from the northern Baltic (Larsson & Hagström 1982, Kuparinen et al. 1984, Lahdes et al. 1988). The time curves of the other < 10 μm fractions showed quite similar changes. The shift towards the dominance of nanoplankton during

summer is well known (Hobro 1979). From the results of Huttunen & Kuparinen (1986) we may guess that among the dominant organisms in our size fractions are the following: Ch1 (1–2 μm) – *Nannochloropsis* sp. (mean diameter 1.5 μm); Ch2 (2–4 μm) – *Nannochloropsis* sp., *Chrysochromulina* spp., flagellates; Ch3 to Ch4 (4–10 μm) – *Chrysochromulina* spp., *Cryptomonadales*, flagellates. The dominance of *Pyramimonas* sp. and *Cryptomonas* spp. in the Ch4 to Ch5 fraction during the spring bloom has been confirmed (Kahru & Nömmann 1990). 'Flagellates' combine both autotrophic and heterotrophic plankters.

The easiest to interpret are the Ch7 and Ch8 (28–73 μm) fractions which during the diatom spring bloom predominantly represent the dominant diatom species (e.g. *Achnanthes taeniata*, *Chaetoceros* spp.) (Kahru & Nömmann 1990), and during the late-summer blue-greens maximum represent the dominant blue-green algae (e.g. *Aphanizomenon flos-aquae*) (Kahru et al. 1989). The shift towards bigger particles (from Ch7 to Ch9) during the vernal phytoplankton succession is sometimes caused by the increasing size of *A. taeniata* chains (Kahru et al. 1986). During the late-summer blue-green bloom, Ch9 (73–105 μm) has been found to be well correlated with the abundance of the dinoflagellate *Dinophysis norvegica* (Kahru et al. 1989). Ch10 (105 to 163 μm) may be correlated with larger protozooplankton or small metazooplankton but no evidence has been acquired. Ch11 and Ch12 represent smaller zooplankton (Kahru et al. 1989); Ch11 (165–305 μm) is correlated with copepodites, copepod nauplii and eggs, and large protozoans; Ch12 (305–1000 μm) with copepods and smaller cladocerans.

The annual cycle of the Baltic pelagic community has been extensively studied in several coastal areas of the Baltic Sea, i.e. the Kiel Bight (Smetacek et al. 1984), the Askö-Landsort (Hobro 1979, Larsson & Hagström 1982, Jansson et al. 1984), and the Tvärminne areas (Niemi 1975, Forsskahl et al. 1982, Kuparinen et al. 1984, Huttunen & Kuparinen 1986, Kononen & Niemi 1986). The last area borders with that under study in this paper.

The general features of the annual dynamics as revealed here are similar to results obtained in the studies mentioned above. These results together support the emerging general concept that in a stratified, oligotrophic water column small phytoplankton cells and the 'microbial loop' (Azam et al. 1983) type of food chain dominate whereas in case of stronger vertical turbulence large phytoplankton cells (diatoms) and the 'classical' (Steele 1974) type of food chain prevail (Cushing 1989, Kiørboe et al. 1990).

However, in contradiction to that concept is the observation by Kahru & Nömmann (1990) that the well-known, massive diatom bloom is preceded by a short period with initial growth of unidentified small-sized

(1–4 µm) phytoplankton which are then outgrown by diatoms.

The coincidence in the peaks of summer nanoplankton dominance and bacterial production supports the concept of their trophic relationship (Larsson & Hagström 1982).

The seasonal shift in the maximum of Ch7 to Ch12 resembles the cascade of organic matter from smaller to larger particles along the 'classical' foodchain (Platt & Denman 1978).

The 2 maxima in the annual curve of Ch11 (Fig. 5E) seem to be related to the biology of zooplankton and not artifacts. The first maximum (10 d periods 16 and 17, 31 May to 19 June) occurred after the decline of the spring bloom, and the second (10 d periods 21 and 22, 20 July to 9 August) preceded the peak in the blue-greens. The second maximum is also prominent in Ch12 and corresponds well to the known zooplankton maximum in this area (Kuparinen et al. 1984).

Because of the low overwintering zooplankton population in the Baltic Sea, the 'classical' food chain is not effective and the bulk of the organic matter produced by the diatom spring bloom sediments out of the upper layer (Forsskahl et al. 1982, Jansson et al. 1984, Leppänen 1988). Another characteristic feature of the Baltic ecosystem is the late-summer bloom of the nitrogen-fixing blue-green algae (e.g. Jansson et al. 1984), also evident in the particle data.

The averaged time curves of the particle concentrations, showing quite different behavior depending on the size fraction, clearly reveal the major shifts in the structure and functioning of the planktonic system. As data from offshore areas are difficult and expensive to obtain with the required time and space resolution, automated particle and fluorescence measurements that can be obtained semi-automatically with a high resolution present an attractive compliment to more elaborate biological analyses.

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