Quantitative relationships between planktonic biomass and organic/inorganic resuspended particulate matter

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with 6 figures and 2 tables

Abstract: During a period of two years, organic and inorganic suspended particulate matter and phytoplankton biomass was frequently measured in Lake Erken, a moderately deep, eutrophic lake in south-eastern Sweden. Regression analyses of these data were used to differentiate and quantify newly produced planktonic particulate matter (zooplankton + phytoplankton + bacteria) and different types of resuspended particulate matter (organic, inorganic). Resuspended particulate matter was frequently dominant in the water column (yearly mean: 59% of suspended particulate matter), and resuspended particulate organic matter ranged from 11 to 99% of suspended particulate organic matter (yearly mean: 41%). The high amount of resuspended particulate matter originates from erosion/transportation bottoms which are located at water depths above 16 m and which cover 93% of the lake area.

Resuspended particulate matter was significantly related to diatom biomass but not to any other type of planktonic biomass. Consequently, the seasonal variations in the amount and distribution of diatoms can be explained by the hydrodynamic processes which affect the amount and distribution of resuspended particulate matter while seasonal variations in the amount and distribution of other planktonic biomass need further explanations, like active swimming, floating and grazing resistance.

Introduction

In many lakes, the increase of planktonic biomass has become a serious problem. It is well known that mainly shallow lakes are affected by eutrophication processes since frequent resuspension events, caused by direct wind/wave activities, delay the final burial of nutrients in the sediments (SANFORD 1992, VALEUR et al. 1995). However, also deeper lakes can be significantly influenced by sediment resuspension, especially during stratification when internal seiché activities are responsible for sediment resuspension (GLOOR et al. 1994, PIERSON & WEYHENMEYER 1994). As a result, it is explicable that in many lakes resuspended material frequently comprises the majority of the flux of particles to lake bottoms (EVANS 1994).

Mechanisms of sediment resuspension and sediment redistribution have been studied intensively (HILTON 1985, HILTON et al. 1986), as well as relations between sediment resuspension and nutrient concentrations (HAMILTON et al. 1988, DILLON et al. 1990, WAINRIGHT 1990, GÁLVEZ & NIELL 1992, CARRICK et al. 1993). Quite a few methods are available to identify resuspended particulate matter in sediment traps (GASTH 1975, BLOMQVIST & LARSSON 1994, CORNETT et al. 1994, VALEUR et al. 1995, WEYHENMEYER et al. 1995). The objective of this study is to apply one of the methods for sediment trap samples to water samples in which the composition of particles usually differs (WEYHENMEYER 1996a). For this application, the method of WEYHENMEYER et al. (1995) was chosen. The method allows to quantify the proportion of resuspended particulate matter in sediment traps and to differentiate organic resuspended particulate matter from inorganic one. It is attempted to apply this knowledge to water samples in order to establish quantitative relationships between newly produced and resuspended particulate organic matter in the water column. Furthermore, it is intended to determine seasonal variations in the amount of organic and inorganic resuspended particulate matter and
to relate them to those of different types of planktonic particulate matter. This relationship can give important insights into relationships between sediment resuspension and bioavailability of resuspended nutrients. In addition, dynamics of different types of planktonic particulate matter may be better understood.

Methods

In 1993 and 1994, water samples were taken in Lake Erken, a moderately deep (mean depth: 9 m, maximum depth: 21 m) dimictic lake, located in south-eastern Sweden close to the Baltic Sea. Lake Erken has a surface area of 24 km² and a calculated maximum effective wind fetch of 5.6 km in the east-west direction. The lake is regularly ice-covered during winter time and stratified during summer time. Measurements of epilimnetic lake water chemistry give yearly mean total phosphorus concentrations of 24 µg l⁻¹, mean chlorophyll a concentrations of 3.7 µg l⁻¹ and mean total nitrogen concentrations of 620 µg l⁻¹. The mean Secchi depth is 4.5 m.

During summer stratification, epilimnetic water samples (volume-proportional mixture of water from 0 m to the depth of the thermocline) were weekly taken with a tube-sampler at about 8 o'clock in the morning. Epilimnetic water samples were taken at 5 different stations and mixed together to obtain one representative lake water sample for each sampling occasion. During the rest of the year, water samples were taken biweekly as a volume-proportional mixture of water from 0 to 10 m at the same 5 stations, also at about 8 o'clock in the morning. Again the water samples from the 5 different stations were mixed together. In addition, water samples were taken biweekly from the main inflows of Lake Erken.

1 litre of each water sample was filtered through weighed, precombusted (3 h, 550°C) 47 mm GF/F Whatman glass-fibre filters. The filters were dried in the oven (105°C) overnight and reweighed to determine the total amount of suspended particulate matter. For the determination of the amount of inorganic suspended particulate matter the filters were combusted at 500°C for 3 hours and weighed again.

Some of the water which was not used for filtration was treated with Lugol's Iodine to identify and count phytoplankton in an inverted microscope. The organic dry weight of phytoplankton biomass was calculated at 20% of the biovolume divided by 10⁵ (PÁDÍSÁK & DOKULIL (1994). For a detailed description of phytoplankton determination and calculations see PÁDÍSÁK & DOKULIL (1994). Apart from measurements of phytoplankton biomass and suspended particulate matter, wind conditions were continuously monitored (10 minute time intervals) 10 m above the surface by an automatic sampling station, located on a small island 500 m from the southern shore.

Results and discussion

Seasonal variations in the amount and composition of suspended particulate matter

In 1993 and 1994 the amount of suspended particulate matter (SPM) ranged from 0.6 to 6.4 mg l⁻¹ in Lake Erken with a yearly mean of 2.5 mg l⁻¹ (mean of measurements in 1993). When the lake is ice-covered and during the period of stratification, the amount of SPM is quite low and relatively constant despite of significant wind speed peaks (wind speed = mean of the period 12 hours before sampling) (Fig. 1 A). Only during turnover when the whole water body is able to directly correspond to changes in wind speed, high wind speeds can lead to high SPM concentrations. However, from the available data it is quite difficult to find a convincing evidence for a causal relationship between wind speed and the amount of SPM, since the amount of SPM often increases while wind speed decreases.

Peaks in SPM are not obviously related to wind speed but they are related to peaks in the amount of phytoplankton biomass (dry weight) (Fig. 1 B). Talking about dry weight of phytoplankton biomass it is important to differentiate between organic and total phytoplankton biomass. The organic phytoplankton biomass can be calculated as described in the methods:

$$\text{POB} = 0.2 \cdot \text{biovolume} / 10^6$$ \hspace{1cm} (1)

where

$$\text{POB} = \text{amount of phytoplankton organic biomass (dry weight)}.$$
Fig. 1. A. Seasonal variations of suspended particulate matter (SPM) and mean wind speed. The mean wind speed is calculated as the mean of the last 12 hours before sampling. B. Seasonal variations of suspended particulate matter (SPM) and phytoplankton biomass (PB). C. Seasonal variations of suspended particulate inorganic matter (SPIM) and diatom inorganic biomass (DIB).

Provided that the volume of inorganic diatom shells is negligible the total phytoplankton biomass, i.e. the sum of organic and inorganic phytoplankton biomass, can be calculated as:

\[
PB = 0.2 \cdot \text{biovolume of phytoplankton without diatoms} / 10^6 + (0.2 \cdot \text{biovolume of diatoms}/10^6 + \text{dry weight of inorganic diatom shells})
\]
where

PB = amount of total phytoplankton biomass (dry weight).

The dry weight of inorganic diatom shells is assumed to be equal to the organic dry weight of diatom biomass (Weyhenmeyer et al. 1995)

\[
DIB = DOB = 0.2 \cdot \text{biovolume of diatoms} / 10^6
\]  
(3)

where

DIB = amount of diatom inorganic biomass (dry weight)
DOB = amount of diatom organic biomass (dry weight).

Therefore, equation 2 can be written as

\[
PB = 0.2 \cdot \text{biovolume of phytoplankton without diatoms} / 10^6
\]  
(4)

where

PB = amount of total phytoplankton biomass (dry weight).

In the following, any kind of suspended particulate matter, living and non-living, is expressed in dry weight, using the equations above.

In addition to the relationship between total phytoplankton biomass and total suspended particulate matter, there is a relationship between the inorganic phytoplankton biomass, i.e. diatom inorganic biomass (DIB), and suspended particulate inorganic matter (SPIM) (Fig. 1 C). During diatom blooms DIB can account for, as a maximum, 52% of SPIM (yearly minimum: 0.08%; yearly mean: 14%).

Even if the phytoplankton biomass is usually only a minor part of the total amount of SPM, suspended particulate organic matter (SPOM) is quite often dominant in the water column. During the years 1993 and 1994 the percentage of SPOM in the water column ranges
from 38 to 83% with a yearly mean of 56% in 1993. In general, the amount of SPOM in the water column is quite similar to the amount of SPIM. It is, therefore, possible to establish a relationship between SPOM and SPIM (Fig. 2).

Quantifying allochthonous, newly produced planktonic and resuspended particulate matter

Suspended particulate matter consists of allochthonous-, newly produced planktonic- and resuspended particulate matter. In Lake Erken, the input of allochthonous suspended particulate matter is, on average:

\[ \text{SPM}_{\text{alloch}} = Q \cdot \frac{\text{SPM}_{\text{in}}}{V} \]

\[ = 90,000 \text{ m}^3 \text{ day}^{-1} \cdot 12 \text{ mg} \text{ l}^{-1} / 213,500,000 \text{ m}^3 = 0.026 \text{ mg} \text{ l}^{-1} \text{ day}^{-1} \]

where

- \( \text{SPM}_{\text{alloch}} \) = mean amount of allochthonous suspended particulate matter in the lake
- \( Q \) = mean yearly water discharge
- \( \text{SPM}_{\text{in}} \) = measured maximum amount of suspended particulate matter in inflow waters
- \( V \) = lake volume.

This daily input of allochthonous particulate matter is about 1% of the mean amount of total suspended particulate matter. Assuming a sinking rate of 0.2–2 m d\(^{-1}\) and a lake water depth of 10 m yield a loss rate of 2–20% of allochthonous suspended particulate matter if the outflow is neglected. With an input of 1% per day, the contribution of \( \text{SPM}_{\text{alloch}} \) to the standing stock of total SPIM is 5–50%. The contribution of \( \text{SPM}_{\text{alloch}} \) can even be higher during periods of higher water discharge than the mean water discharge and due to shore erosion. Shore erosion should be most significant during rain storms, as well as water discharge should be highest during these times. As a result, \( \text{SPM}_{\text{alloch}} \) and thereby SPIM concentrations in the lake water should be increased during rainfall. However, in Lake Erken rainfall is not related to an increase in SPIM (Weyhenmeyer 1996b). This leads to the conclusion that \( \text{SPM}_{\text{alloch}} \) might not be as important for our water samples, taken in the main water basin, as calculated. It is likely that \( \text{SPM}_{\text{alloch}} \) from the main inflow settles to the sediments in the shallow (2–6 m), small water basin before it can reach the main basin. Also material from shore erosion is supposed to settle only a few meters away from the shores where it is still shallow. It can then be further transported to deeper areas but once it has reached the sediments it is defined as resuspended particulate matter. This explanation is supported by the observation that in sediment traps, exposed in the main water basin, new sedimentary allochthonous particulate matter accounted, on average, only for 1% of the total settling particulate matter (Weyhenmeyer et al. 1995). For this study, it is assumed that the amount of new sedimentary allochthonous suspended particulate matter in the main water basin can be neglected. As a consequence, mainly resuspended and newly produced planktonic particulate matter are responsible for the amount of suspended particulate matter in Lake Erken.

The amount of newly produced planktonic suspended particulate matter (total dry weight) can mainly be determined from living and non-living phytoplankton, zooplankton and bacteria biomass (total dry weight). The total dry weight of phytoplankton biomass is available. In Lake Erken, it is, on average, quite low compared to the total dry weight of suspended particulate matter. During a whole year, on average, only 17% of the total amount of SPIM is phytoplankton biomass. Even during phytoplankton blooms, phytoplankton biomass accounts for only, as a maximum, 60% of SPIM (minimum: 1%) (Fig. 3). Since the bloom of Gloeotrichia echinulata might be underrepresented in our water samples, their biomass was determined in another way. The maximum number of colonies was 116 in 1 litre water in mid July in 1993.
(FORSSELL & PETTERSSON 1995). During that time the carbon content in one colony is about 4 µg (FORSSELL & PETTERSSON 1995) which gives 116 * 4 µg C l⁻¹ = 464 µg C l⁻¹. To translate µgC into total dry weight, the result has to multiplied by 2 (HÅKANSON & JANSSON 1983). As a result, the maximum dry weight of Gloeotrichia echinulata is 0.93 mg l⁻¹. During the time when Gloeotrichia echinulata blooms the concentration of SPM is 3.5 mg l⁻¹. The bloom of Gloeotrichia echinulata accounts, therefore, for 27% of SPM.

Since phytoplankton biomass does not represent the total amount of newly produced planktonic suspended particulate matter (PSPM) a method was used to determine the total amount, i.e. the amount of phytoplankton, zooplankton, bacteria and detritus, and to differentiate it from resuspended particulate matter. The method was developed for sediment trap samples in Lake Erken, where the amount of allochthonous particulate matter is negligible. Here, the method is used for water samples in Lake Erken. For the method, a regression between organic and inorganic particulate matter is needed. The regression for the water samples

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**Fig. 3.** Seasonal variations of phytoplankton biomass (PB) and the percentage PB of suspended particulate matter (SPM).

**Fig. 4.** Seasonal variations of residuals of the regression suspended particulate organic matter (SPOM) on suspended particulate inorganic matter (SPIM) and phytoplankton biomass (PB) without diatoms.
is: \( y = 0.63x + 0.55 \) \( (r^2 = 0.57, p < 0.0001, n = 40) \) (Fig. 2). The intercept of the regression describes a condition where only organic particulate matter is suspended in the lake water. This condition is fulfilled when exclusively newly produced planktonic particulate matter is in the water because allochtonous and resuspended particulate matter always contain a certain fraction of inorganic particulate matter. The intercept can, therefore, be used as a measure for the amount of PSPM without diatoms. Diatoms are excluded because 50\% of their dry weight is inorganic particulate matter (WEYHENMEYER et al. 1995).

Provided that allochtonous particulate matter is negligible and the organic fraction of resuspended particulate matter remains similar to the organic fraction of lake sediments, the residuals of the regression SPOM versus SPIM can be interpreted as seasonal changes in the amount of PSPM (without diatoms). This interpretation seems to be reasonable for our water samples because positive residuals correspond to peaks in phytoplankton biomass (without diatoms) and negative residuals correspond to a low phytoplankton biomass (without diatoms) (Fig. 4).

The total amount of newly produced planktonic suspended particulate matter can now be calculated as:

\[
PSPM = I + R + DB
\]

where

- PSPM = amount of planktonic suspended particulate matter (dry weight)
- I = intercept of the regression SPOM vs. SPIM
- R = residual of the regression SPOM vs. SPIM
- DB = measured diatom biomass (dry weight).

The equation gives a mean amount of PSPM of 0.98 mg l\(^{-1}\), a minimum of 0.01 mg l\(^{-1}\) and a maximum of 2.83 mg l\(^{-1}\). From these values it can be calculated that the amount of PSPM is, on average, 4.6 (median: 2.3) times the phytoplankton biomass (minimum: 0.2, maximum: 15.6) (Fig. 5). Since PSPM is the sum of zooplankton, bacteria and phytoplankton biomass, the sum of bacteria and zooplankton biomass can be obtained by subtracting the phytoplankton biomass from PSPM. However, this calculation has to be used with care, since the measured phytoplankton biomass does not include all non-living phytoplankton. With this restriction in mind the sum of zooplankton and bacteria biomass is, on average, 3.8 (median: 1.4) times more than the phytoplankton biomass (minimum: 0.03; maximum: 14.6). Since bacteria bio-
mass in Lake Erken is, on average, 0.6 times the phytoplankton biomass during summer months (Bell et al. 1998), the zooplankton biomass is 3.2 times (summer mean) more than the phytoplankton biomass. This result correspond quite well with Nauwerck’s studies in Lake Erken which describe that zooplankton biomass was, on a yearly average, 5.5 times the phytoplankton biomass (Nauwerck 1963).

Apart from newly produced planktonic suspended particulate matter there is resuspended particulate matter in the water column. The amount of resuspended particulate matter can be calculated as:

\[ \text{RSPM} = \text{SPM} - \text{PSPM} \]  

(7)

where

- RSPM = amount of resuspended particulate matter (dry weight)
- SPM = measured amount of suspended particulate matter (dry weight)
- PSPM = calculated amount of planktonic suspended particulate matter (dry weight).

In Lake Erken resuspended particulate matter accounts, on average, for 59% of SPM (minimum: 25%; maximum: 99%) (Fig. 6).

Resuspended particulate organic matter

The amount of resuspended particulate organic matter can be calculated as:

\[ \text{RSPOM} = \text{SPOM} \ (\text{PSPM} - \text{DOB}) \]  

(8)

where

- RSPOM = amount of resuspended particulate organic matter (dry weight)
- SPOM = amount of suspended particulate organic matter (dry weight)
- PSPM = calculated amount of planktonic suspended particulate matter (dry weight)
- DOB = amount of diatom organic biomass (dry weight).

In Lake Erken, on average, 41% of SPOM was RSPOM (minimum: 11%; maximum: 99%). This percentage seems to be high. Consequently, a discussion about the origin of resuspended particulate matter in Lake Erken is required.
Table 1. Mean and range of the amount of different suspended particles in Lake Erken in 1993. For abbreviations see text.

<table>
<thead>
<tr>
<th>Type of suspended particulate matter</th>
<th>Mean mg l⁻¹</th>
<th>Minimum mg l⁻¹</th>
<th>Maximum mg l⁻¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPM</td>
<td>2.5</td>
<td>0.6</td>
<td>6.4</td>
</tr>
<tr>
<td>SPIM</td>
<td>1.2</td>
<td>0.2</td>
<td>3.3</td>
</tr>
<tr>
<td>SPOM</td>
<td>1.3</td>
<td>0.4</td>
<td>3.1</td>
</tr>
<tr>
<td>RSPM</td>
<td>1.5</td>
<td>0.3</td>
<td>4.4</td>
</tr>
<tr>
<td>RSPIM</td>
<td>1.0</td>
<td>0.2</td>
<td>2.8</td>
</tr>
<tr>
<td>RSPOM</td>
<td>0.5</td>
<td>0.1</td>
<td>1.6</td>
</tr>
<tr>
<td>PSPM</td>
<td>1.0</td>
<td>0.01</td>
<td>2.8</td>
</tr>
<tr>
<td>PSPM_{PB}</td>
<td>0.5</td>
<td>0.04</td>
<td>1.3</td>
</tr>
<tr>
<td>PB</td>
<td>0.5</td>
<td>0.01</td>
<td>1.6</td>
</tr>
<tr>
<td>DB</td>
<td>0.4</td>
<td>0.00</td>
<td>1.6</td>
</tr>
<tr>
<td>DIB</td>
<td>0.2</td>
<td>0.00</td>
<td>0.8</td>
</tr>
<tr>
<td>DOB</td>
<td>0.2</td>
<td>0.00</td>
<td>0.8</td>
</tr>
<tr>
<td>PB_{DB}</td>
<td>0.09</td>
<td>0.00</td>
<td>0.3</td>
</tr>
</tbody>
</table>

Origin of resuspended particulate matter

Sediments are resuspended on erosion and transportation bottoms and then transported to accumulation bottoms. Several methods are available to determine the boundary depths between the different lake bottoms (e.g., CARPER & BACHMANN 1984, HÄKANSON 1982, ROWAN et al. 1992). Some of these methods have earlier been applied to Lake Erken but due to internal seiche activities which frequently occur in Lake Erken during stratification and which are responsible for sediment resuspension in deeper areas, the methods underestimated the boundary depths (PIERSON & WEYHENMEYER 1994, WEYHENMEYER 1996b). According to a validated model, the boundary between transportation and accumulation bottoms in Lake Erken is at 16 m (WEYHENMEYER et al. 1997). Consequently, all bottoms from 0 to 16 m are subjected to sediment resuspension, an area which is 93 % of the whole lake area. This percentage is a rough estimation and it does not consider that Lake Erken has some small wind-protected bays where the boundary between transportation and accumulation bottoms is likely to be located at less than 16 m. Nevertheless, for most bottoms in Lake Erken the 16 m as a boundary between transportation and accumulation bottoms are suitable.

Relationships between different types of suspended particulate matter

In Lake Erken, the following types of suspended particulate matter (SPM) have been differentiated and quantified (Table 1):

1. suspended particulate inorganic matter (SPIM)
2. suspended particulate organic matter (SPOM)
3. resuspended particulate matter (RSPM)
4. resuspended particulate inorganic matter (RSPIM)
5. resuspended particulate organic matter (RSPOM)
6. planktonic suspended particulate matter (PSPM)
7. planktonic suspended particulate matter without phytoplankton biomass (PSPM_{PB})
8. phytoplankton biomass (PB)
9. diatom biomass (DB)
10. diatom inorganic biomass (DIB)
### Table 2. Relationships between different suspended particles in Lake Erken (n = 40). For abbreviations see text.

<table>
<thead>
<tr>
<th>Regression</th>
<th>$r^2$</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>SPM vs RSPM</td>
<td>0.76</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPM vs PSPM</td>
<td>0.40</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPM vs PSPM-PB</td>
<td>0.10</td>
<td>not significant (p &gt;0.05)</td>
</tr>
<tr>
<td>SPM vs PB</td>
<td>0.61</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPM vs DB</td>
<td>0.59</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPM vs PB-DB</td>
<td>0.03</td>
<td>not significant (p &gt;0.05)</td>
</tr>
<tr>
<td>SPIM vs RSPIM</td>
<td>0.93</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPIM vs DB</td>
<td>0.58</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPIM vs SPOM</td>
<td>0.57</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPOM vs RSPOM</td>
<td>0.37</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPOM vs PSPM</td>
<td>0.76</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPOM vs PSPM-PB</td>
<td>0.40</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPOM vs PB</td>
<td>0.50</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPOM vs DB</td>
<td>0.44</td>
<td>0.0001</td>
</tr>
<tr>
<td>SPOM vs PB-DB</td>
<td>0.12</td>
<td>0.0291</td>
</tr>
<tr>
<td>RSPM vs PSPM</td>
<td>0.10</td>
<td>0.0456</td>
</tr>
<tr>
<td>RSPM vs PSPM-PB</td>
<td>0.00</td>
<td>not significant (P &gt; 0.05)</td>
</tr>
<tr>
<td>RSPM vs PB</td>
<td>0.24</td>
<td>0.0012</td>
</tr>
<tr>
<td>RSPM vs DB</td>
<td>0.25</td>
<td>0.0010</td>
</tr>
<tr>
<td>RSPM vs PB-DB</td>
<td>0.00</td>
<td>not significant (p &gt; 0.05)</td>
</tr>
<tr>
<td>RSPIM vs DB</td>
<td>0.32</td>
<td>0.0001</td>
</tr>
<tr>
<td>RSPIM vs PSPM</td>
<td>0.04</td>
<td>not significant (p &gt; 0.05)</td>
</tr>
<tr>
<td>RSPIM vs PSPM-PB</td>
<td>0.00</td>
<td>not significant (p &gt; 0.05)</td>
</tr>
<tr>
<td>RSPOM vs PB</td>
<td>0.13</td>
<td>0.0200</td>
</tr>
<tr>
<td>RSPOM vs DB</td>
<td>0.14</td>
<td>0.0179</td>
</tr>
<tr>
<td>RSPOM vs PB-DB</td>
<td>0.00</td>
<td>not significant (p &gt; 0.05)</td>
</tr>
</tbody>
</table>

11. diatom organic biomass (DOB)
12. phytoplankton biomass without diatoms (PB-DB).

In order to identify relations between these different types of particulate matter, simple regression analyses were carried out (Table 2). The regression analyses show that most suspended particles are related to each other, no matter whether they are organic or inorganic. Many regressions suffer from auto-correlation, especially regressions like SPM versus RSPM, SPIM versus RSPIM and SPOM versus RSPOM since resuspended particulate matter is frequently dominant in the water column. Therefore, the regressions concerning newly produced planktonic- and resuspended particulate matter are of more interest. PSPM is mainly the sum of living and nonliving zooplankton, bacteria, diatom and other phytoplankton biomass. While planktonic biomass without phytoplankton and phytoplankton biomass without diatoms are not related to any other kind of particulate matter, diatom biomass is well correlated to SPM, SPIM, SPOM, RSPM, RSPIM and RSPOM. These observations demonstrate that zooplankton + bacteria and phytoplankton without diatoms have different sedimentation and distribution patterns than non-living particles due to their swimming activities or floating abilities. Only living diatoms behave like non-living particles. The significant relationship between diatom biomass and RSPM indicates that diatoms are resuspended from the sediments and then distributed in the water column in the same way as bottom sediments are. Resuspension of living diatoms from the sediments has also been observed in other aquatic systems (CARRICK et al. 1993, DE JONGE & VAN BEUSEKOM 1995). Another indicator that diatom biomass is directly
related to resuspension events is the slope of the regression between SPOM and SPIM (Fig. 2). As discussed earlier, the slope of the regression reflects the composition of resuspended particulate matter and of diatoms in Lake Erken. The slope of the regression would be 1 if only diatoms and no resuspended particulate matter are in the water, because diatoms (dry weight) contain 50% inorganic and 50% organic particulate matter. If only resuspended particulate matter is in the water and no diatoms the slope would be 0.2 because sediments in Lake Erken contain about 80% inorganic and 20% organic particulate matter (Weyhenmeyer et al. 1995). Since the slope of our regression is 0.6 we get a mass balance of 50% diatoms and 50% resuspended sediment. This means that the ratio between diatom biomass and the amount of resuspended particulate matter is, on average, constant in the lake water.

A direct, linear relationship between resuspension of nutrients and an increase in biomass could not be proven because phytoplankton without diatoms was not related to RSPM. Since in Lake Erken SRP concentrations in the hypolimnion increased during resuspension events (Persson & Weyhenmeyer 1994) the lacking relationship indicates that there is a time-delay between resuspension and bio-uptake of nutrients. It is likely that nutrients are kept in the hypolimnion during periods of stratification and only become bioavailable through metalimnetic entrainment or destratification. This statement corresponds to the observation that settling particulate matter was kept in the hypolimnion during periods of stratification (Weyhenmeyer 1996b).

**Conclusion**

The main source of suspended particulate matter in Lake Erken is sediment resuspension. Most inorganic particulate matter in the lake water is from sediment resuspension but also large amounts of organic particulate matter can be resuspended. The amount of resuspended particulate matter is related to phytoplankton biomass but it is important to differentiate between diatoms and other phytoplankton because the relation is only valid for diatoms and not for other phytoplankton. From this observation it can be concluded that phytoplankton without diatoms is differently affected by hydrodynamic processes than diatoms and resuspended particulate matter. To understand the seasonal variations in the amount and distribution of phytoplankton without diatoms and also those of zooplankton + bacteria, other phenomena than hydrodynamic processes have to be taken into consideration, like floating (= horizontal sedimentation), active swimming, grazing etc.

Direct relations between sediment resuspension and the biomass of phytoplankton without diatoms could not be observed in Lake Erken which indicates that resuspended nutrients are not directly bioavailable. It is likely that resuspended nutrients are kept in the hypolimnion during stratification, resulting in indirect relations between sediment resuspension and primary production. Further studies are needed where these indirect relations are quantitatively determined by separately relating diatom and other phytoplankton biomass to sediment resuspension events.

**References**


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