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Allochthonous contribution to seasonal and spatial variability of organic matter sedimentation in a deep oligotrophic lake (Lake Constance)

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Previous studies analysing the chemical composition of profundal sediments of Lake Constance suggest a overall large contribution of allochthonous material to total sedimentation but also a large spatial variability in the relative importance of allochthonous versus autochthonous sedimentation. Here we analyse sedimenting particulate organic matter (POM_{sed}) during an annual cycle at two sites differing in their position relative to the major inflow and thus in their proposed contribution of allochthonous matter to the sedimentary flux, i.e., site [AL] characterised by a more allochthonous contribution und the site [AU] characterised by a more autochthonous contribution.

Chemical and mineralogical composition (chlorite contents) of sedimenting matter were used for discrimination of autochthonous and allochthonous sources in addition to stable isotope signatures ($\delta^{13}C$, $\delta^{15}N$) of POM_{sed}. Generally, $\delta^{13}C$ values were "heavier" at site AL (−26.5 to −30.9‰) than at site AU (−33.10 to −29.30‰), especially during the main sedimentation period from April to September. In contrast differences between sites AL und AU in respect to $\delta^{15}N$-values were small (averages: +5.10‰ and +5.80‰, respectively). $\delta^{13}C$ values were shown to be inversely correlated to contents of chlorophyll a of POM_{sed} (i.e. lighter values with higher concentration), whereas they were positively correlated to chlorite contents and the C:N ratio of sedimenting material. The contribution of autochthonous and allochthonous POM_{sed} changed also seasonally at both sampling sites. These differences resulted on the one hand from the seasonal succession of plankton, and on the other hand from the discharge characteristics of the inflowing rivers with regular (snow melting) and irregular maxima (flood events). A mixing model suggests that on average the allochthonous POM_{sed} from river loads contributes at site AL 73.40% of total organic matter sedimentation and at the site AU 33.80%.

Introduction

Generally, autochthonously produced organic carbon is considered to be a major source of sedimenting particulate organic matter (POM_{sed}) in many lakes (Wetzel, 2001), especially in lakes with long residence time (Caraco and Cole, 2004; Kumar et al., 2011; Moschen et al., 2009). On the other hand, a contribution of allochthonous matter to POM_{sed} had since long been recognised to be important for small unproductive or most boreal dystrophic lakes (del Giorgio et al., 1997) and for reservoirs (Filstrup et al., 2009). Moreover, even in large, deep and non-boreal lakes the supply of allochthonous organic carbon may be more important than hitherto assumed (Carpenter et al., 2005; Cole et al., 2006, 2010; Pace et al., 2004), especially so, when their residence times are relatively short and there is considerable terrestrial erosion in the catchment. Depending on lake type and position of sampling site within a lake, the seasonal pattern of organic matter sedimentation may therefore not only reflect its respective plankton succession (Bunn and Boon, 1993; Matthews and Mazumder, 2005; Taipale et al., 2007) but may additionally be more or less modified by loads of riverine organic matter. As a consequence, a more or less pronounced spatial variability of organic matter sedimentation can be expected in addition to the well known seasonal variability.

Within a recent comprehensive survey on the state of sediments of the large and deep oligotrophic Lake Constance, it was shown that large parts (more than a third of the sediment surface (*i.e.*, roughly 150 km^2) of its profundal sediments are characterised by deposition of matter from riverine origin, most pronouncedly in the northeastern part of the lake where most of the inflowing water is entering the lake (IGKB, 2009). Although sediments in this area have a lower concentration of organic matter (due to high dilution by mineral sedimentation) a significantly higher total sedimentation of organic matter was calculated for these areas compared to sites with low riverine influence contribution (Sobek et al., 2009).

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Table 1
Comparsion of TOC and POC annual river loads to Lake Constance-upper lake basin (source IGKB, 2001) and planktonic primary production estimates (sources: Tilzer et al., 1991; Güde et al., 1998) derived from measurements of ^{14}C-carbonate assimilation by plankton.

Year	1985/1986	1995/1996	1996/1997
TOC load ($\times 10^3$ t)	44.5	40.1	49.1
POC load ($\times 10^3$ t)	24.9	21.5	39.2
Primary production ($\times 10^3$ t)	58. 9	–	34.7

The potential importance of allochthonous carbon supply for the lake is further underlined by existing carbon budgets (Güde et al., 1998; IGKB, 2000; Tilzer et al., 1991). Especially after its successful reoligotrophication, loads of allochthonous organic carbon from rivers exceed estimates of primary production (Table 1).

In order to obtain more direct information on the contribution of autochthonous and allochthonous sedimentation of organic matter in a deep oligotrophic lake, we analysed sedimenting particulate organic matter (POM_{sed}) during a vegetation period at two contrasting sites. These two sites differ in their allochthonous contribution to sedimentation and were selected from a total of 50 sampling sites which sediments have been characterised chemically, physically and biologically (IGKB, 2009). Although located more than four kilometres away from the major riverine inflow of the Rhine (Fig. 1), the sediments from the site AL in the northeast basin are dominated by allochthonous matter, while the sediments of site AU at the south shore of the central basin, are dominated by autochthonous material (Wessels, 1998; IGKB, 2009).

At these sites, quantity and quality of sedimenting matter collected by sediment traps was analysed during an annual cycle. In addition to mineralogical indicators, i.e., chlorite contents (Wessels, 1995; IGKB, 2009; Müller, 1966), $\delta^{13}C$, $\delta^{15}N$, and C:N ratios (Meyers and Ishiwatari, 1993; Bernasconi et al., 1997) were used to estimate the relative importance of allochthonous matter to total organic sedimentation at the two sites.

For this aim, the following working hypotheses were examined:

a. POM_{sed} sedimentation at site AL will exceed considerably that of site AU due to a much higher contribution of allochthonous POM_{sed}.
b. These quantitative differences will also be reflected by qualitative differences of sedimenting matter (isotope signatures, elementary analysis of POM_{sed}, contents of Chl a, and mineralogical composition) which will allow an estimate of the allochthonous and autochthonous POM_{sed} contribution at the respective study sites.
c. The allochthonous contribution will show pronounced seasonal patterns related to variability in water inflow at both sites.

Materials and methods

Lake Constance is a deep monomictic lake (surface: 539 km^2, maximum depth: 254 m, mean depth: 100 m) which is situated north of the Alps at the border of Austria, Germany and Switzerland. The river Rhine is the largest inflow of the lake. Its mostly alpine catchment (6.119 km^2) comprises 56.1% of the area of the total catchment of the lake, and its annual discharge amounts to 66% of the total annual water inflow. The river discharges on average annually 2–3 Mio m^3 of solid matter to the lake, which consists to 98% of minerals, while the organic fraction is less than 2% (IGKB, 2000; Wessels, 1998). The remaining part of the hydraulic and nutrient loads a provided by small rivers, which enter the lake predominantly in its northeastern part (Fig. 1). Discharge of the river Rhine and total organic carbon (TOC) loads were downloaded from the website of the

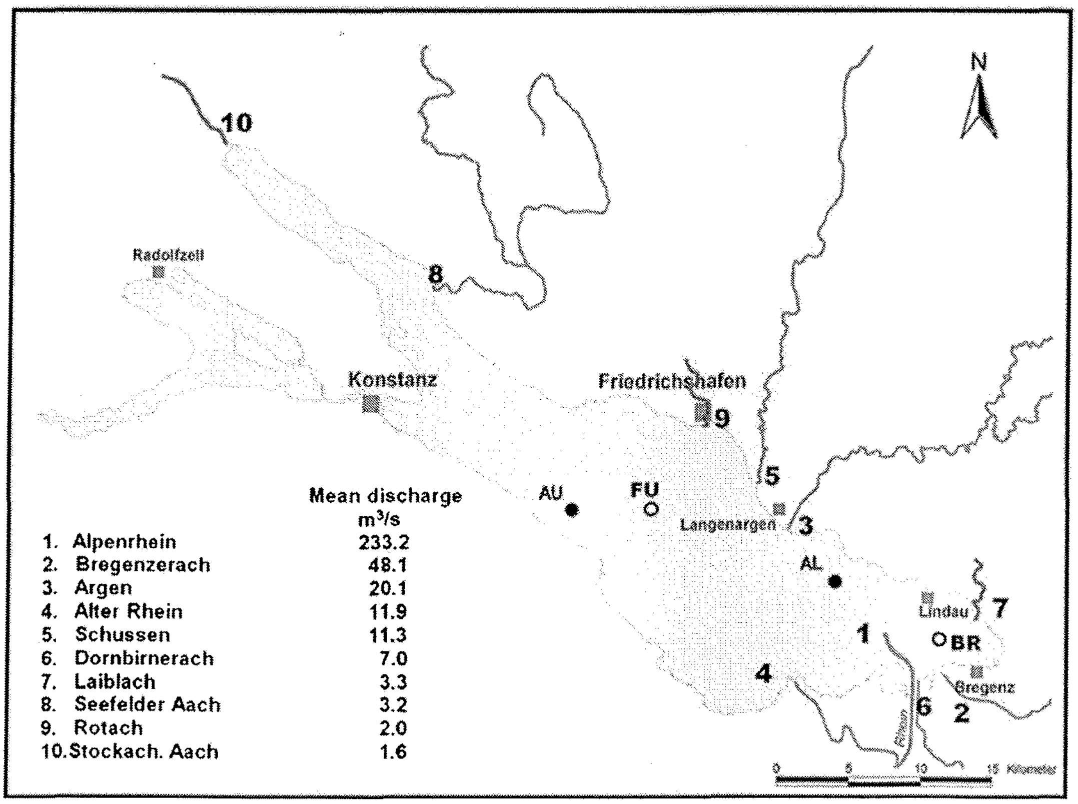

Fig. 1. Map of Lake Constance with main inflows, their annual mean discharge and sampling sites.

Swiss National River Monitoring and Survey Programme (NADUF, http://www.bafu.admin.ch/hydrologie/01831/01840/index.html).

The sampling sites chosen for the present study were in the central and north-eastern part of the main lake basin (Obersee, Fig. 1). Sampling site AL (latitude: 47°.5558N, longitude: 9°.6007E, depth 143 m) is situated close to the northeastern shore. Although this site is situated in considerable distance (more than 4 km) from the mouths of the main contributing rivers (Fig. 1), the sediments of this area are under strong riverine influence. Therefore, it is representative for the allochthonously dominated northeastern part of the lake (IGKB, 2009). Sampling site AU (Latitude: 47°.5996N, longitude: 9°.3579E, depth 102 m) is situated close to the central basin south shore. It is representative for the southern part of the lake which receives less matter from riverine origin. It was therefore considered to mirror more pronouncedly patterns caused by autochthonous processes (IGKB, 2009).

In addition to these two main sampling sites, water samples were also taken at the sampling site FU (latitude: 47°37.44N, longitude: 9°22.5287E depth 254 m), which is situated at the site of maximum depth in the central basin and which serves as main sampling site for long-term monitoring of the lake. For comparison of horizontal patterns of phytoplankton biomass distribution also station BR was included which was situated in the most eastern part of the lake (latitude: 47°37.1802, longitude: 9°28.2314, depth 65 m). Generally, all stations were sampled fortnightly, but not simultaneously because sampling at sites FU and BR was alternating weekly with sampling at sites AU and AL.

Water samples

Samples were taken from the euphotic zone (0–20 m) at sizes AU, AL, BR and FU with an integrating sampler. For analysis of chlorophyll contents, samples were filtered through glassfibre filters (Whatman GF/F). Chlorophyll retained on the filters was extracted as described below.

Sediment traps

Sedimenting matter was collected by sediment traps at both sampling sites. The traps consisted of six tubes of acrylic glass (height: 60 cm, diameter: 10.5 cm) per sampling site which were exposed 5 m above ground. The sedimenting matter deposited in the traps was sampled in 14 days intervals. An exposure time of 14 days is unlikely to significantly alter the quality of sedimenting material, e.g. its isotope signature (Lehmann et al., 2002). After decanting the overlying water the sedimented particulate material was freeze dried and thereafter weighed in the laboratory. Daily sedimentation rates S_r (g dry matter m^{-2} day^{-1}) were calculated using the formula:

$$S_r = \frac{W \times 1/f \times 1}{d}$$

where W is the measured total weight (g), f is the surface of tube (m^2) and d is the number of days of exposition.

Sediment analysis

Total carbon (TC) of the freeze-dried material obtained from sediment traps was determined with an infrared analyser (Leco CS 125). Total organic carbon (TOC) was determined as difference between total carbon (TC) and total inorganic carbon (TIC). The latter was determined by measuring CO_2 liberated after acidification of the sample with 16% HCL.

Bulk mineralogy of the sediment samples was determined with a X-ray diffractometer (Siemens D500) which was operated in steps of 0.05° 2θ/s. As relative units of concentrations the results were expressed in counts per second (cps).

Chlorophyll a

Chlorophyll a contents of water samples and of POM_{sed} were used as proxy for algal standing crop and sedimenting algal biomass, respectively. For that 500 ml of sample water were filtered trough Whatman GF/F glassfibre (filters 25 mm diameter). The filters were extracted in 4 ml 90% acetone for 5 min at 55 °C under light exclusion. For POM_{sed}, 1 g of sediment (dry weight) was extracted in 4 ml 90% acetone for 5 min at 55 °C under light exclusion. A specific "ion-pair reagent" was added to each sample, followed by sonication of the samples for 5 min. Finally, Chl a contents of the extracts were measured by HPLC analysis as described by Schmid and Stich (1995).

Isotope and elementary analysis

For measurements of $\delta^{13}C$ in POM_{sed}, the dried material was treated in an exsiccator for eight hours by HCL-fumigation of the sample above an open beaker containing 100 ml of 12 mol/L HCl after the method of Harris et al. (2001). This will remove all inorganic carbon from the sample as long as carbonate contents are below 50% (Harris et al., 2001) as is the case for Lake Constance. For $\delta^{15}N$ measurements untreated samples were analysed because $\delta^{15}N$ would have become enriched by the acid treatment (Harris et al., 2001; Lohse et al., 2000).

Isotope contents were measured by a mass spectrometer interfaced with Carlo Erba elemental analyser. The mean standard deviation amounted to <0.2 sd and <0.15‰ sd for N and C, respect. The relative isotope ($\delta^{13}C$ or $\delta^{15}N$) content is expressed by relating the isotope ratio measured for the sample to that of standard substances according to the equation $\delta^{13}C$ or $\delta^{15}N$:

$$(‰) = \left[\left(\frac{R_{sample}}{R_{standard}}\right) - 1\right] \times 1000$$

where R is the $^{15}N/^{14}N$ or $^{13}C/^{12}C$. The reference materials used were secondary standards (meal) of known relation to the international standards, PeeDee Belemnite for carbon and atmospheric nitrogen for nitrogen (Fry, 2006).

Mixing model

A simple mixing model approach was adopted for estimates of quantify the fraction of the allochthonous and authocthonous POM_{sed} at site AL and AU. Source 1 = terrestrial plants, source 2 = phytoplankton of Lake Constance. In this model, the fraction of allochthonous and authocthonous POM_{sed} was calculated according to the formula (Fry, 2006):

$$f_{sample} = \frac{\delta^{13}C_{sample} - \delta^{13}C_{Phytoplankton}}{\delta^{13}C_{allochthonous\,material} - \delta^{13}C_{Phytoplankton}}$$

For this approach, it was assumed that differences observed between signatures of POM_{sed} were exclusively due to supply of allochthonous organic carbon at the sampling sites.

Statistical analyses

The relationship between the stable isotope signatures ($\delta^{13}C$, $\delta^{15}N$) and chlorite [cps], C:N ratio and chlorophyll a concentrations at the two sites was analysed with linear regression models. Prior to statistical analyses chlorite counts and Chlorophyll a concentrations were log-transformed to achieve normality and constant

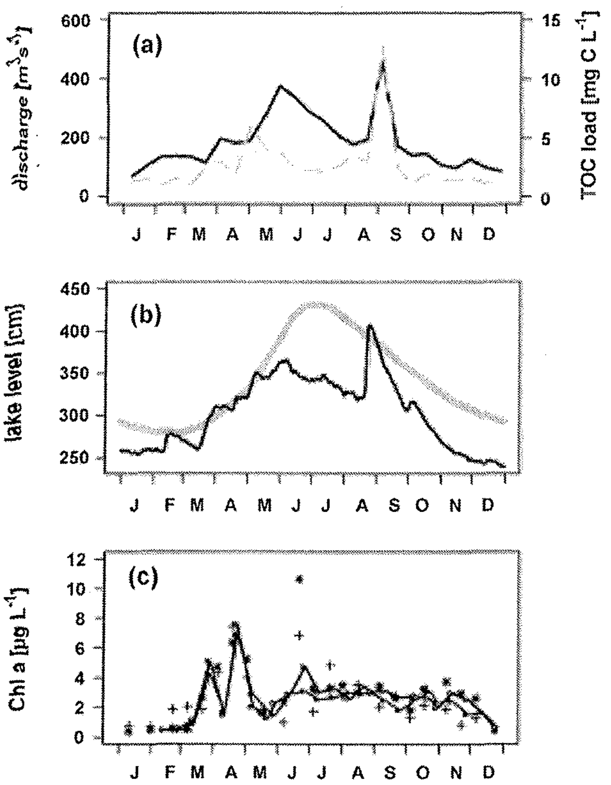

Fig. 2. (a) Discharge (solid line) and TOC (dashed line) loads of the river Rhine into Lake Constance during 2005, (b) water level dynamic of Lake Constance (related to gauge Constance) observed in 2005 (black line) and on average during 1850–2010 (grey line), (c) chlorophyll a concentrations in the upper 20 m water layers observed in 2005 at sampling sites AU (open circles), AL (filled circles), FU (*) and BR (+) in the central and eastern basin of Lake Constance (see Fig. 1). Symbols without connecting lines are from sampling sites FU and BR for which the sampling date differed by one week to that of the sites AL and AU, respectively.

variance. For analysing the relationship between Chlorophyll a concentrations and stable isotope signatures one outlier, i.e. the observation resulting from the extreme flooding event at site AL (see below), was excluded.

Results

Discharge of the river Rhine into Lake Constance showed two maxima, one at the end of May and a second one at the end of August during a major flood event. Discharge maxima were associated with maxima of TOC loads (Fig. 2a). Water levels of Lake Constance mirrored to a large extent the water discharge from the river Rhine. Compared to its long-term average seasonal dynamics, the water level during 2005 was low (Fig. 2b), with the exception of the end of August (Fig. 2b).

Chlorophyll a dynamics were similar at the 4 selected sampling sites (Figs. 1 and 2b) and were characterised by a short spring peak followed by a clear-water phase and a smaller but extended summer bloom. The similarity was most pronounced for the sites AU and AL which were sampled simultaneously. The other two sites for which the sampling date differed by one week to that of the sites AL and AU showed a similar seasonal course, albeit with a somewhat higher variability.

The dynamics of sedimentation and of sedimentary characteristics differed strongly between sampling sites. Fluxes of total sedimenting matter (Fig. 3a), total carbon (Fig. 3b) inorganic (Fig. 3c) and organic carbon (Fig. 3d) and of nitrogen (Fig. 3e), were on average two- to three-fold higher at site AL than those at AU and their dynamics were more immediately and strongly affected by the two periods of water level increase. These fluxes increased also at AU in response to the August flooding, however with a 2-week delay and with much less pronounced peaks. Overall, the differences of sedimentary fluxes between the two sampling sites were large during periods of increased inflow, while they were rather small during periods of low inflow and consequently reduced sedimentation as in winter, early spring and autumn. A similar seasonal pattern was observed for concentrations of the mineral chlorite which serves as allochthonous marker (Fig. 3g).

In contrast to most other fluxes, Chl a sedimentation (Fig. 3f) was remarkably similar at the two sites. Only a moderate increase of rates of chlorophyll a sedimentation was observed after the algal spring bloom in April/May. In contrast, the early epilimnetic summer peak resulted in a pronounced maximum of Chl a sedimentation in mid July with a delay of roughly two weeks after the peak in the euphotic water layers (Fig. 2b). During the following months rates of chlorophyll a sedimentation dropped more or less continuously until the end of the observation period. The C:N ratio (Fig. 3j) differed also considerably between both sites during end of April/May and during the flooding event.

Also the seasonal course of sedimentation of inorganic carbon deviated from July onwards from the pattern observed for TPM (total particulate matter) and TC, because it remained at an elevated level at both sites, although total sedimentation decreased during July and August until the onset of the flooding event (Fig. 3a–c). This period of deviation between TPM, TC and inorganic carbon fluxes corresponds to a maximum of autochthonous calcite precipitation (Fig. 3h). Simultaneously up to 90% of total carbon sedimentation at site AU was contributed by inorganic carbon (Fig. 3i). The highest percentage (90%) was observed at site AU in July, presumably due to increased biogenic calcite precipitation at this site. At site AL the peak of the calcite signal was less pronounced. However, at this site the percentages were already elevated during the preceding period coinciding with the increasing inflow in April and May. Overall, inorganic carbon contributed at least 40% to total carbon sedimentation but the majority of percentages were higher than 60%, at site AL throughout the whole sampling period and at site AU from July to September. Lowest percentages were observed in April and May at site AU which means that during this period the major part of carbon sedimentation was contributed by organic carbon at this site.

$\delta^{13}C$ values from site AU were significantly more negative, i.e. "lighter" (−31.31 ± 1.18‰, range: −33.10 to −29.30‰) than at the site AL (−29.33 ± 1.13‰, range: −26.51 to −30.92‰) (ANOVA, $F_{1,32} = 24.9$, $p < 0.05$). However, also for this parameter, remarkable seasonal differences were observed (Fig. 3k). While the values were similar at both sites until April, they deviated strongly from May to July, after which they approached each other again. A stronger deviation was again observed after the flooding event at the end of August. At this time, the "heaviest" signature (−26.51‰) was found at site AL. At site AU the flood event became visible only with delay and less pronounced. Similarly, the values show – although with some delay and less pronounced – a tendency toward heavier values after snow melting. Results from a carbon isotope mixing model reveals large differences between the two sites in respect to the importance of allochthonous matter for overall carbon sedimentation fluxes (Table 3), with absolute contribution of allochthonous matter depending on the assumed isotope signal of autochthonous primary production.

Differences between both sampling sites were less pronounced for $\delta^{15}N$ (AU = +5.80 ± 0.87‰; AL = +5.10 ± 1.03‰; Fig. 3l). Largest differences in $\delta^{15}N$ between sites (maximum +2.57‰ at the beginning of May) were observed during the period of alpine snow

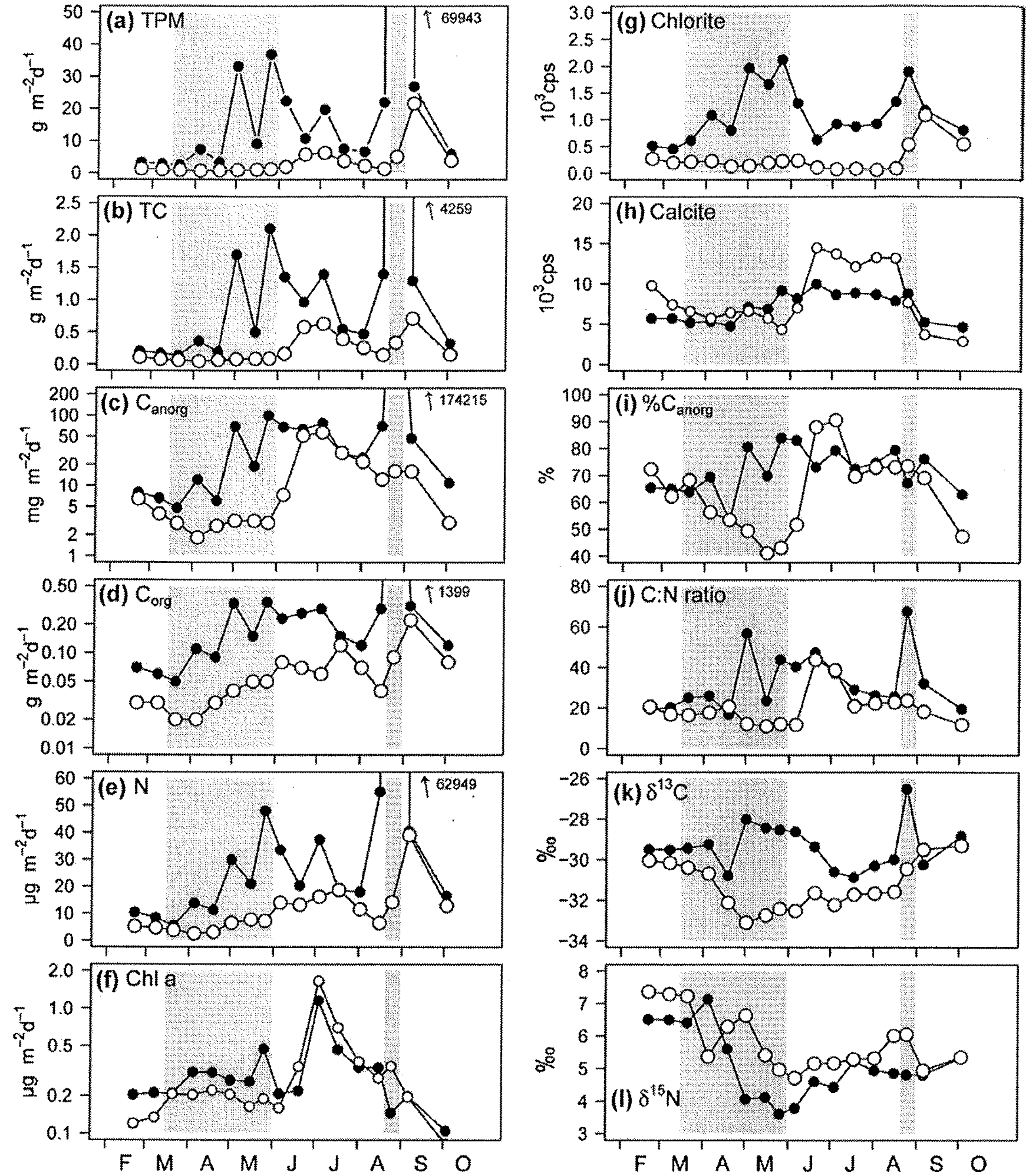

Fig. 3. Seasonality of the characteristics of sedimented material. The two periods of water level increase are shaded: Left row (rates). (a) TPM = total particulate organic matter; (b) TC = total carbon; (c) C_{anorg} = inorganic carbon (note the logarithmic scaling); (d) C_{org} = organic carbon (note the logarithmic scaling); (e) N = nitrogen; (f) Chl a = chlorophyll a (note the logarithmic scaling). Right row (concentrations); (g) chlorite; (h) calcite; (i) % C_{anorg} = inorganic carbon of total C; (j) ratio C_{org}/Chl a; (k) $\delta^{13}C$; (l) $\delta^{15}N$. Open circles show values from site AU, filled circles values from site AL. Numbers in panels (a)–(e) indicate fluxes during the flood event. Please note that fluxes observed during the this event may represent overestimates as due to strong turbulences near the bottom, resuspended matter from sediments presumably contributed strongly to overall observed sedimentary fluxes (IGKB, 2009).

melting and after the flood event (Fig. 3l). Both sites exhibited also a trend from heavier (+7.29‰ at AU and +6.47‰ at AL) values in winter towards lighter values in spring and summer (Fig. 3f). The lighter values were thus closer to the values measured as average for epilimnetic seston (+4.16 ± 0.43‰).

$\delta^{13}C$ signals were strongly related to other markers of allochthony, i.e., chlorite (Fig. 4a, $R^2 = 0.63$, $p < 0.001$), C:N ratio (Fig. 4b, $R^2 = 0.31$, $p < 0.001$) and Chl a concentrations (Fig. 4c, $R^2 = 0.54$, $p < 0.001$) in sedimentary material. In contrast, the relationship of $\delta^{15}N$ to these markers of allochthony was less tight (chlorite: $R^2 = 0.19$, $p < 0.01$, Fig. 4d, C:N ratio: $R^2 = 0.25$, $p < 0.01$ (Fig. 4e), Chl a concentration, $R^2 = 0.15$, $p < 0.05$ (Fig. 4f).

Discussion

Our results document a large variability in respect to quantity and composition of sedimentary fluxes at two pelagic sites within a large oligotrophic lake and suggest that also in non-humic lakes allochthonous material can contribute substantially to sedimentation.

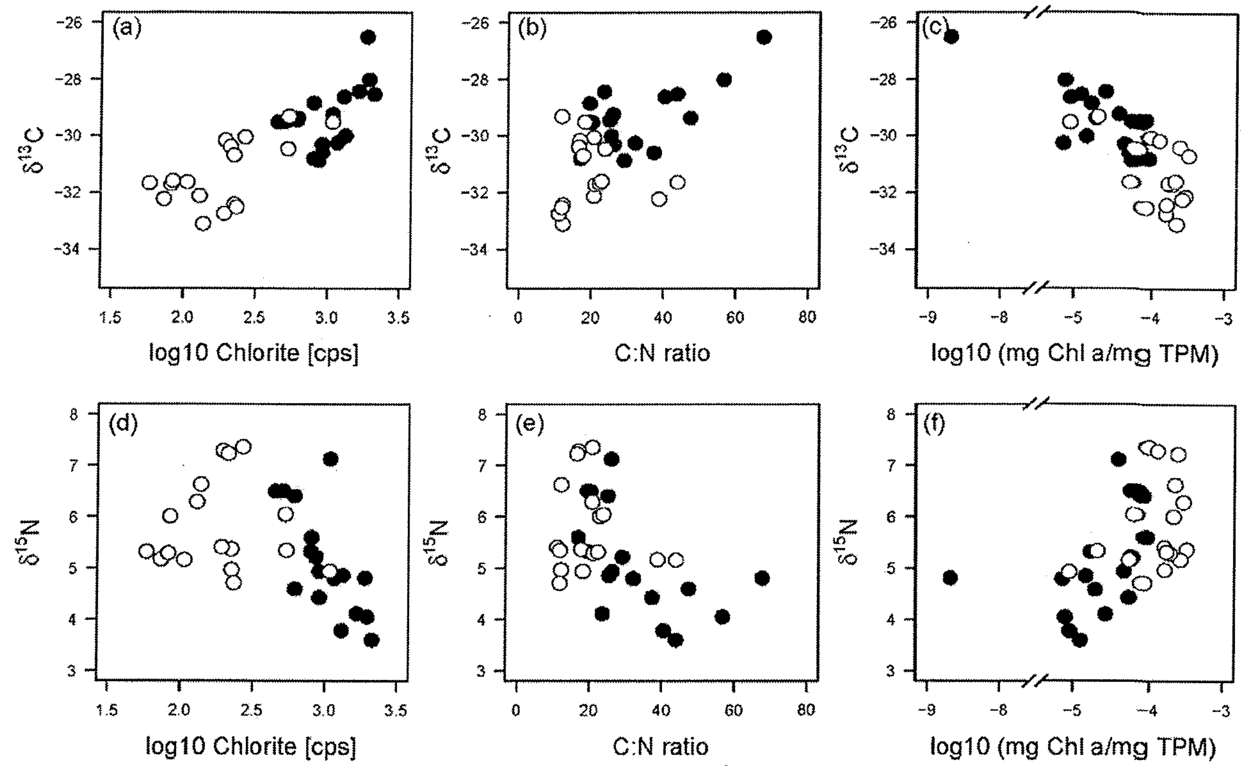

Fig. 4. Plots of stable isotope signatures against: (a) and (d) log-transformed chlorite counts, (b) and (e) C:N ratios and (c) and (f) log-transformed chl a concentrations of sedimenting material. Open circles show values from site AU, filled circles values from site AL. Main discharge is provided by the river Rhine "Alpenrhein".

Differences in sedimentation patterns between sites

The site AL experienced much higher sedimentation loads as compared to site AU in terms of TPM, POM, TC, and of C_{org} sedimentation. In contrast to POM sedimentation fluxes, chlorophyll a sedimentation fluxes did not differ strongly between the two sites, which is in agreement with the rather uniform horizontal distribution of Chl a concentrations in the euphotic water layers (Fig. 2b). This indicates that the sedimentation flux originating from autochthonous algal production was horizontally rather homogenously distributed (Fig. 3f) and suggests that the differences in POM sedimentation between sites are due to differences in allochthonous input. This is strongly supported by differences between sites in respect to chlorite concentrations, C:N ratios and stable isotope signatures.

The $\delta^{13}C$ values observed at the site AL (range −26.50 to −30.90‰) were much closer to the range reported for terrestrial plants and emersed macrophytes in other studies (France, 1995; Gu et al., 1994; Leventhal, 2004; Peterson and Fry, 1987) and for Lake Constance (Table 2; Fuentes 2010). Theoretically, such values could have also been caused by sedimentation of littoral epilithic algae (Table 2) which could have been transported to the pelagic water after events of wind resuspension (Moschen et al., 2009). However, because only negligible percentages of benthic algae were detected by microscopic examination of the sediments (IGKB, 2009) their impact in pelagic sedimentation appears to be negligible in our lake. Consequently, the mixing model suggests a dominance of allochthonous sedimentation fluxes at size AL of 66.75–73.5% depending on the assumption of the $\delta^{13}C$ signal of autochtonously produced material (Table 3). Such a dominance is also supported when estimating the contribution of allochthonous material by assuming that (1) all Chl a sedimentation is of autochthonous origin, there is on average (2) a Chl a/POC ratio of 50 (Riemann et al., 1989) and (3) a ratio of heterotrophic and detrital carbon to autotrophic carbon of 2.5 (Hessen et al., 2003). According to these assumptions roughly 75% of the sedimentation fluxes at site AL would be of allochthonous origin.

In contrast, $\delta^{13}C$ values (range −33.10 to −29.30‰) at AU were much closer to those observed for seston in Lake Constance (Table 2; Fuentes, 2010), which, how usually cannot be considered as pure phytoplankton because it is frequently masked by allochthonous and/or littoral detritus (del Giorgio and France, 1996). As a consequence seston tends to have "heavier" $\delta^{13}C$ values than those reported for pure phytoplankton (del Giorgio and France, 1996; Gu et al., 1994), but is still significantly lighter than allochthonous plant material (Table 2). Consequently, the $\delta^{13}C$ mixing models suggest that sedimentation at site AU was dominated by autochthonous sedimentation with estimates of allochthonous contribution ranging from 17.25% to 33.80% (Table 3) and 35% based on chlorophyll a sedimentation rates (see above). Hence, all calculations revealed large differences between the two sites in respect to the contribution of allochthonous material to sedimentation fluxes.

Table 2
Range of isotopic signatures ($\delta^{13}C$, $\delta^{15}N$) observed for different autochthonous and allochthonous sources in Lake Constance and its catchment.

Source	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Epilimnetic pelagic lake seston (Sampled in spring and summer 2004)	−32 to −33	4–5
Submersed macrophytes (*Chara* spp. and *Potamogeton* spp.)	−14 to −18	1–5
Littoral epilithic algae (mainly blue-greens and diatoms)	− 27 to −29	6–7
Terrestrial plants (leafs from various riparian plants)	−27 to −29	−2 to 6
River seston (Schussen)	−25 to −28	4–6

Data from Fuentes (2010).

Table 3
Calculation of the fraction of the autochthonous and allochthonous carbon of the organic matter sedimentation in the site characterised by a more allochthonous contribution [AL] und at the autochthonous characterised site [AU] on the basis of a simple two-source mixing model according to FRY 2006.

Site	Mean $\delta^{13}C_{sedimenary\ material}$	Assumed $\delta^{13}C_{T.Plant}$	Assumed $\delta^{13}C_{aurochthonous\ production}$	Contribution of allochthonous carbon
AU	−31.31‰	−28‰	−32 to −33‰	17. 25–33.8%
AL	−29.33‰	−28‰	−32 to −33‰	66.75–73.4%

However, according to our calculations up to 30% sedimentary fluxes is possibly of allochthonous origin also at AU despite its location apart from significant riverine inputs. This suggests transport of TPM to this site, which is consistent with knowledge on dominant currents in the lake (Auerbach and Ritzi, 1938; Bäuerle et al., 1998; Wasmund, 1928), satellite documentations (Odermatt et al., 2008) and studies on the spatiotemporal distribution of river water in the lake (Rossknecht, 2003). A contribution of allochthonous material for sedimentary flux at AU is also suggested by the significant correlation of $\delta^{13}C$ values with chlorite (Fig. 4). Furthermore, the seasonal course of sedimentary fluxes also suggests an influence of allochthonous matter as the flooding event caused enhanced sedimentation rates also at AU albeit less pronounced and with a 2-week delay compared to site AL.

Differences between both sites were much less pronounced for $\delta^{15}N$ values compared to $\delta^{13}C$ values. Likewise the relationship between $\delta^{15}N$ values and marker of allochthonous material, e.g. chlorite, C:N ratio and Chl a concentration in sedimenting material was less tight than those relationship observed for $\delta^{13}C$ values. This is mainly due to the broad distribution of $\delta^{15}N$-values observed for terrestrial and aquatic organic matter (Fry, 2006), which above all results from the strong discrimination effects occurring during metabolic processing of nitrogen compounds (Saino and Hattori, 1987). For this reason $\delta^{15}N$ values are generally less suitable for indication of the origin of the organic matter but they rather indicate the state of biotic processing of it. This was exemplified for phytoplankton as well as for terrestrial fresh plant material which tend to have lighter values than biotically processed matter as soil organic matter (Adams and Sterner, 2000; Bernasconi et al., 1997; Fuentes, 2010; Owens and Law, 1989) or "aged" phytoplankton detritus (Bernasconi et al., 1997; Van der Nat et al., 2003) which previously had undergone passages through food chains and/or was metabolised by microbial communities (Hodell and Schelske, 1998; Teranes and Bernasconi, 2000). In this context, lighter $\delta^{15}N$ values would indicate a higher portion of "young" algae in the sedimenting material, whereas heavier values would indicate a higher portion of aged or biotically processed material.

Seasonal dynamics of sedimentation

The seasonal dynamics of overall sedimentation fluxes was strongly influenced by the discharge of the river Rhine, which increased sedimentation rates, especially at site AL, during May/June, when the melting of snow and glaciers in the Alpes results into increased inflow and rising water levels in the lake (Jöhnk et al., 2004), and in late August, when an extreme flood event caused a rapid rise of water levels within a few days. This flood increased sedimentation fluxes strongly at site AU, but resulted also in the annual maximum of TPM, total and organic carbon sedimentation at site AL (see above). The seasonal dynamics of $\delta^{13}C$ values seem to be also strongly influenced by seasonal variability in inflow. The comparatively heavy values observed during winter became lighter after the onset of phytoplankton growth in April, but become heavier again after alpine snow melting. Remarkably, this trend is visible at both sites, but was again delayed and less pronounced at site AU. This observation is also a major argument against the alternative explanation of the observed seasonal changes of $\delta^{13}C$ values, i.e., to result from succession of phytoplankton communities with changing isotope signatures (Lehmann et al., 2004a; Vuorio et al., 2006; Wu et al., 1999). Because autochthonous sedimentation was shown to be rather similar at both sites (Fig. 3f), no delay would be expected if the changes were mainly due to phytoplankton succession.

In contrast, seasonal variability of $\delta^{15}N$ values seemed to be less influenced by the riverine inflow. $\delta^{15}N$ values at both sites declined at both sites from winter towards spring and summer approaching values similar to those observed for the seston of the lake (Table 2; Fuentes, 2010). This seasonal pattern is consistent with observations in various other lakes and in marine seston (Bernasconi et al., 1997; Hodell and Schelske, 1998; Teranes and Bernasconi, 2000; Wu et al., 1999). As the degree of biotic processing seems to increase $\delta^{15}N$ values (see above) the seasonal decline of $\delta^{15}N$ indicates that the contribution of "young" phytoplankton to the sedimenting organic matter had increased from winter towards summer at both sites.

A comparison of the seasonal course of epilimnetic concentrations of chlorophyll a (Fig. 2b) with the seasonal development of chlorophyll a sedimentation rates (Fig. 3f) makes apparent that the latter is not necessarily a complete reflection of the simultaneous algal development in the euphotic layer. The reason is on the one hand a delay due to different residence times of phytoplankton in the euphotic layers, secondly it is due to the different sinking properties of the respective algal taxa and thirdly the amount of sinking losses of phytoplankton depends strongly on its susceptibility for use as food source and/or for microbial degradation before sinking down to the bottom. All three effects seem to be relevant in this case study: the summer peak of Chl a in the water column resulted in a maximum of chlorophyll a sedimentation after a delay of roughly two weeks. The general dominance of large diatoms observed in the sediment traps shows also that these algae contribute overproportionally to the autochthonous supply of organic sedimentation. Finally, the fact that a much lower percentage of the phytoplankton spring bloom reached the sediments compared to the summer bloom can presumably be explained by a much higher percentage of "edible" algae and hence higher grazing losses during spring bloom compared to the summer bloom (Kümmerlin, 1998).

Conclusions and outlook

In summary, the study has demonstrated that in a large nonhumic oligotrophic lake at least locally the sedimentary flux of organic matter may be dominated by allochthonous matter. The occurrence of a major flood in our study year could have principally baised our estimates of the importance of "normal" allochthonous sedimentation in oligotrophic Lake Constance. However, water levels throughout most of the year remained below its long-term average suggesting an overall reduced hydraulic load. This is confirmed by measurements of POC loads in the upper river Rhine prior to its entrance into Lake Constance: The average POC load in 2005 (0.42 kg/s) was despite the flooding event lower than the long-term average from 1984 to 1998 (0.54 kg/s) suggesting that our conclusions with respect to the relative importance of allochthonous POM_{sed} are rather conservative.

The allochthonous contribution to sedimentary fluxes varies strongly between aquatic systems and ranges from <5 to 90% based on estimates from stable isotope signatures (Bernasconi et al., 1997; Eddins, 2000; Hodell and Schelske, 1998; Leventhal, 2004; Lehmann et al., 2004a,b). High percentages are observed in systems having large river inflows, whereas they are small in lakes with low river inflows such as Lake Lugano (Bernasconi et al., 1997). Our results show that within one lake large spatial variability in the relative importance of allochthonous to autochthonous sedimentation exists, which makes it difficult to quantitatively upscale the results from two sediment traps to the overall lake. However, our results support calculations relating primary productivity to allochthonous carbon input (see Table 1) and lake wide surveys of sediment characteristics (IGKB, 2009) suggesting that also in deep oligotrophic lakes allochthonous material can make an important contribution not only locally but to overall sedimentary flux. This suggests that allochthonous material is an important source for energy and growth of profundal benthic communities in Lake Constance. This assumption is supported by the observed horizontal distribution of macrobenthic communities which was characterised by strongly increased abundances in the allochthonously dominated northeastern areas of the lake (IGKB, 2009). Because a major part of the allochthonous POM sedimentation appears to be recalcitrant and becomes therefore permanently buried in sediments (Sobek et al., 2009), certainly only a minor part of the allochthonous material is really available for nutrition of benthic communities. Nevertheless, related to available autochthonous carbon supply this part seems to be sufficiently high to provide an important additional source of nutrition for the benthic community (Fuentes, 2010).

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