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Big Soda Lake (Nevada). 4. Vertical fluxes of particulate matter: Seasonality and variations across the chemocline

James E. Cloern, Brian E. Cole, and Sally M. Wienke
U.S. Geological Survey, 345 Middlefield Road, Menlo Park, California 94025

Abstract

Vertical fluxes of particulate organic matter were measured with sediment traps above and below the chemocline of Big Soda Lake to define the seasonality of sinking losses from the mixolimnion and determine the effectiveness of the chemocline (pycnocline) as a barrier to the sinking of biogenic particles. Seasonality of sedimentation rates reflected seasonal changes in the community of autotrophs. During summer–autumn, when production is dominated by autotrophic bacteria, vertical fluxes were small: ≅100 mg C m^{-2} d^{-1} and ≅0.5 mg Chl *a* m^{-2} d^{-1}. Following the winter diatom bloom, vertical fluxes increased markedly: ≅570 mg C m^{-2} d^{-1} and 23 mg Chl *a* m^{-2} d^{-1}. The bulk of the seston (>80%) and particulate carbon (≅65%) sinking to the chemocline passed through it, showing that this very sharp density discontinuity does not effectively retard the sinking of particulate matter. However sinking losses of particulate carbon were generally small (≅10%) relative to previous measures of primary productivity, indicating that the mixolimnion is a zone of efficient carbon cycling. Exceptions occurred following the winter bloom when sinking losses were a larger fraction (≅40%) of productivity.

Because density discontinuities inhibit vertical mixing, a potential function of the chemocline (pycnocline) in meromictic lakes is to cause the vertical flux of particulate organic matter (POM) to be unidirectional and downward. Particles sinking to the lower layer (monimolimnion) will be trapped and either buried in the sediments or decomposed. The only mechanisms for re-entry into the upper layer (mixolimnion) are through bubble ebullition of gaseous decomposition products (e.g. methane) or very slow diffusion across the chemocline. Under this circumstance, a significant fraction of primary production in the trophogenic mixolimnion may be lost to the monimolimnion, and an important mechanism of nutrient regeneration is absent from the surface layer.

The chemocline may also be the site of localized accumulations of seston (Culver and Brunskill 1969; Hamner et al. 1982; Cloern et al. 1983*a*), suggesting that it retards the sinking of biogenic particles. If the chemocline is a perfectly efficient "filter" for sinking POM, then it may be an active site of nutrient regeneration and decomposition for POM produced in the trophogenic zone (Culver and Brunskill 1969). Hence, the efficiency of the chemocline as a filter for sinking seston influences the fate of organic matter produced autotrophically in meromictic lakes. If the chemocline is an inefficient filter, then the monimolimnion can be a sink for nutrients and organic matter; if the chemocline is an efficient filter, then nutrient cycling in the mixolimnion is similar to that in holomictic lakes.

The first objective of this study was to estimate the filtering efficiency of the chemocline in Big Soda Lake. It was done by measuring sinking fluxes of POM just above and below the chemocline, which is an extreme density discontinuity (42 kg m^{-3}: Kimmel et al. 1978) that allows a robust test of the hypothesis that density differences retard the sinking of biogenic particles. A second objective was to determine the seasonality of vertical fluxes to the chemocline and relate them to seasonal changes in the pelagic autotrophs. During summer–autumn when the mixolimnion is thermally stratified, phytoplankton biomass is low and autotrophic production is dominated by photosynthetic and chemosynthetic bacteria localized in a layer near the oxycline (*see* figure 2: Zehr et al. 1987). During winter mixing the bacterial layer is disrupted but ammonia is brought to the surface and stimulates a phytoplankton bloom dominated by the pennate diatom *Nitzschia palea*. Our study was designed around this annual cycle and included measurements during the anticipated period of the winter diatom bloom,

the spring transition period, and the summer–autumn period of low phytoplankton biomass.

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Methods

Sampling was done over the deepest part of the lake in July and October 1984 and in February and May 1985. Vertical profiles (to 30 m) of temperature and dissolved oxygen (DO) were obtained with an Orbisphere Laboratories thermistor and DO sensor. Water samples were collected at 10–15 depths with a 2.2-liter PVC Kemmerer bottle; sample depths were chosen on the basis of temperature and DO profiles to ensure sampling around the thermocline and oxycline. Samples were always taken at the depths of sediment trap deployment (30 m, 40 m) and at the chemocline (34.5 m). Water samples were placed in opaque containers, chilled on ice, and processed within 12 h of collection.

After sampling, replicate sediment traps were placed above (30 m) and below (40 m) the chemocline. The traps were PVC tubes (65 cm long, 7.5-cm diam) suspended from a buoyed and anchored line. Rates of POM decomposition were measured with replicate 150-ml BOD bottles that were filled with 30- or 40-m water and attached to the line at the depth of collection. After 6–10 d, sediment traps and BOD bottles were recovered, and their contents were drained into containers and processed immediately.

Concentrations of particulate carbon (PC) and particulate nitrogen (PN) were measured in water samples collected with the Kemmerer bottle as well as those from the sediment traps and BOD incubations. Aliquots were filtered on precombusted 13-mm GF/AE filters that were loaded into nickel capsules and dried in a desiccator. They were later analyzed for PC and PN with an elemental analyzer (Perkin-Elmer model 240B) with acetanilide as a standard. Replicate aliquots were analyzed from the sediment traps and BOD bottles. Particulate carbon collected in the sediment traps was size-fractionated by analyzing aliquots of unscreened sample and aliquots after screening with a 60-μm Nitex mesh.

The contents of the BOD bottles, water samples, and material from sediment traps were also analyzed for photosynthetic pigments (Chl *a* and Bchl *a*). Replicate aliquots were collected on 47-mm GF/AE filters and frozen. In the laboratory they were ground with 90% acetone and extracted overnight in a refrigerator. Concentrations were determined spectrophotometrically with the pheopigment correction of Lorenzen (1967) for Chl *a* and the equation of Takahashi and Ichimura (1970) for Bchl *a*. Figure 1 compares absorption spectra of pigment extracts taken in the aerobic epilimnion (phytoplankton) and in the photosynthetic bacterial (PSB) layer. Since Bchl *a* is calculated only from the absorbance peak at 772 nm and algal pigments do not absorb at this wavelength (*see Fig. 1A*), calculation of Bchl *a* was straightforward even for water samples containing both phytoplankton and these photosynthetic bacteria.

However, Bchl *a* interferes with the determination of algal Chl *a*. Calculation of Chl *a* includes subtraction of a turbidity blank at 750 nm, typically with very small values (Strickland and Parsons 1972). Acetone extracts of PSB from Big Soda Lake absorb strongly at 750 nm (Fig. 1B), and the Lorenzen (1967) equation could not be applied directly to samples containing PSB. To calculate Chl *a* in anoxic waters, we subtracted the value $0.69 \times A_{772}$ from the measured absorbance at 750 nm, where A_{772} is the absorbance at 772 nm. The constant 0.69 defines the PSB contribution to absorbance at 750 nm and was determined from the mean value of the ratio $A_{750}:A_{772}$ for all samples collected in anoxic waters.

Aliquots of each sediment trap were preserved in Lugol's solution for microscopic examination. The remaining contents of each trap were used to measure the total mass of seston collected during the deployment period. We did this gravimetrically by collecting sediment on Nuclepore filters (0.2 μm) and then reweighing them after air-drying.

PC, PN, and pigment profiles of the water column were used to calculate total standing

stocks by depth integration (0–30 m) with trapezoidal quadrature. Vertical fluxes of PC, seston, and pigments were calculated from measured concentration changes in the sediment traps and BOD bottles. We assumed that two processes determine the accumulation rate of biogenic seston in sediment traps: decomposition (or production) of POM during the deployment period, and sedimentation. These processes are defined by

$$dC/dt = rC + G, \quad (1)$$

where C is the concentration of a seston constituent (PC, Bchl *a*, Chl *a*), t is time, r is the specific rate constant of decomposition for constituent C, and G is the accumulation rate from sinking of constituent C. The solution to Eq. 1 yields a measure of the sedimentation rate (mg m^{-3} d^{-1}) corrected for decomposition (*see* Ducklow et al. 1982):

$$G = r[C_T - C_0\exp(rT)]/[\exp(rT) - 1], \quad (2)$$

where r is the specific rate of decomposition (d^{-1}), C_T is the mean final concentration in sediment traps (mg m^{-3}), C_0 is the mean initial concentration (mg m^{-3}), and T is deployment time (d). Vertical fluxes were then calculated as

$$F \text{ (mg m}^{-2} \text{ d}^{-1}) = VG/A, \quad (3)$$

where V is the volume of the sediment traps and A is the surface area of the sediment trap opening.

We determined values of the coefficient r from in situ incubations using the relationship:

$$r = \ln(C_T/C_0)/T,$$

where C_T is the final concentration in the BOD bottles following recovery of the sediment traps. Mean values of r were 0.006 d^{-1} for PC (i.e. there was a small net production of particulate carbon in the BOD bottles) and -0.007 d^{-1} for Bchl *a*. We assumed that the anaerobic decomposition rate for Chl *a* was equal to that for Bchl *a*. This correction for in situ decomposition/production was small; vertical fluxes calculated with and without the correction agreed within 10–20%.

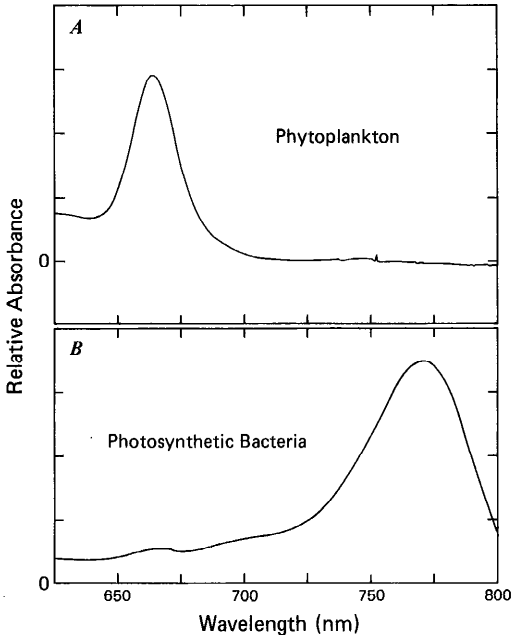

Fig. 1. Typical absorption spectra of acetone extracts taken from samples collected (A) in the epilimnion of Big Soda Lake (showing the algal Chl *a* peak at 665 nm), and (B) in the PSB layer (showing the Bchl *a* peak at 772 nm).

Results

Seston composition and standing stocks—Vertical distributions of oxygen, temperature, and photosynthetic pigments were similar in July and October 1984 (Fig. 2) to those observed in July and November 1981 (Cloern et al. 1983*a*). These sampling dates were representative of the summer–autumn period of thermal stratification. Oxygen disappeared at a depth of 18–20 m, phytoplankton biomass was low (<1.5 mg Chl *a* m^{-3}), and there was a layer of purple photosynthetic bacteria just below the depth of oxygen disappearance (max Bchl *a* = 130 mg m^{-3}). Depth distributions of PC and PN paralleled those of pigments: concentrations were low in the epilimnion and peaked at the depth of the Bchl *a* maximum. A second peak in PC and PN, at the chemocline (*see October*), was not associated with Bchl *a*. During the period of thermal stratification, there were variations in the ratio of particulate carbon to nitrogen across the oxycline. For example during July, PC : PN ratios were

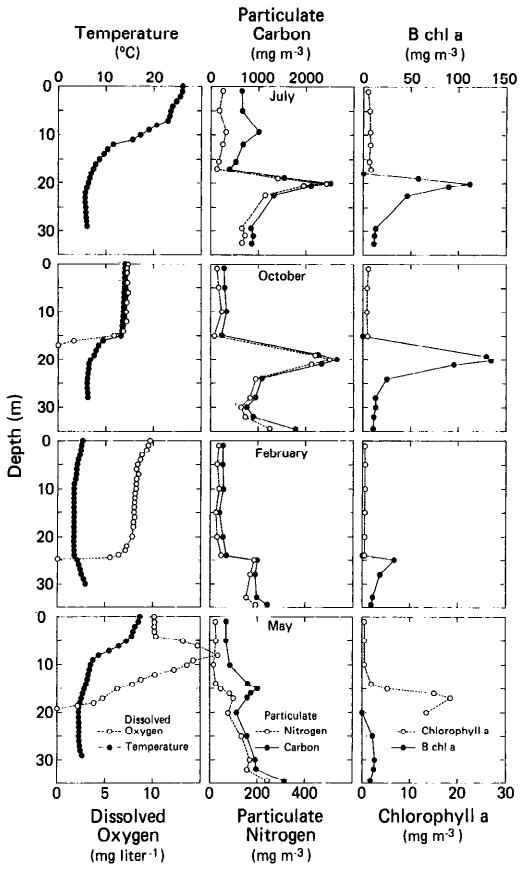

Fig. 2. Vertical profiles of the Big Soda Lake mixolimnion. Left—depth distributions of temperature and dissolved oxygen; center—distributions of particulate carbon and particulate nitrogen; right—distributions of photosynthetic pigments: Chl *a* in the aerobic zone and Bchl *a* in the anaerobic zone.

high (13) in the epilimnion but low (5) in the PSB layer. These differences presumably reflect nitrogen limitation in the epilimnion, consistent with DIN profiles obtained in previous studies (Cloern et al. 1983*a*).

The February sampling occurred during the period of surface cooling and enhanced vertical mixing, shown by the nearly isothermal conditions extending to 24 m (Fig. 2). Dissolved oxygen was present down to 24 m and the PSB populations were reduced. Similar conditions were observed in February 1982. However in February 1985 thermocline depth was 4–5 m higher and phytoplankton biomass remained lower than in February 1982. It appears that the deeper mixing into DIN-rich anoxic waters is required to initiate the winter bloom. Subsequent sampling in May (Fig. 2) showed that deeper mixing and a winter bloom did occur after February 1985. Low winter biomass of the phototrophs was reflected in low PC and PN concentrations during February.

Vertical distributions of temperature and Chl *a* showed that the May sampling occurred at the end of the winter bloom. Thermal stratification was re-established with a thermocline at 6–7 m, and phytoplankton biomass was again low in the surface layer but it was high (20 mg Chl *a* m^{-3}) below the thermocline (Fig. 2). We speculate that this distribution resulted from the decline of the winter phytoplankton bloom in the surface layer after the onset of thermal stratification in spring. The subsurface Chl *a* peak indicates that residual DIN was still sufficient to sustain high phytoplankton biomass there, but that DIN was depleted in the epilimnion. PC : PN ratios support this interpretation (PC : PN was 9–13 in the epilimnion, but 5–7 below 18 m).

Although we did not sample during the peak of the winter bloom, there was considerable variation in the standing stock and nature of seston among the four sampling periods. Standing stock of PC varied almost threefold (Table 1) and the relative contributions of phytoplankton and PSB varied even more: standing stock of Chl *a* varied by an order of magnitude (maximum in May of 145 mg m^{-2}) and PSB biomass varied fivefold (maximum in July–October of about 500 mg Bchl *a* m^{-2}).

Vertical fluxes—Vertical fluxes of seston, PC, and Chl *a* were low and stable from July to February (Fig. 3). During this period fluxes to the chemocline ranged from 336 to 442 mg dry wt m^{-2} d^{-1}, 63 to 113 mg C m^{-2} d^{-1}, and 0.14 to 0.52 mg Chl *a* m^{-2} d^{-1}. However during May, fluxes of all three constituents were substantially higher—about fivefold for seston and PC, and almost 50-fold for Chl *a* (Fig. 3). Agreement among replicate sediment traps gives an indication of the precision of these values: the mean deviation among all paired measurements averaged 20% for PC and 15% for Chl *a* fluxes. This "variance" is similar in mag-

Table 1. Standing stocks of three seston constituents in Big Soda Lake during 1984–1985; values are depth integrals from 0 to 30 m. Shown in parentheses are specific sinking rates (percent lost per day = 100% × vertical flux ÷ standing stock).

	Jul	Oct	Feb	May
Particulate C (g m^{-2})	28.7 (0.4)	25.1 (0.3)	10.7 (0.9)	18.2 (3.1)
Phytoplankton (mg Chl *a* m^{-2})	42.7 (1.2)	33.7 (1.2)	10.5 (1.4)	145 (15.4)
Photosynthetic bacteria (mg Bchl *a* m^{-2})	500 (0.1)	530 (0.1)	130 (1.0)	90 (0.1)

nitude to that of replicate measures of PC concentration within individual sediment traps, so most of the measurement error is associated with sampling and analytical error rather than poor agreement among replicate traps. Given this level of precision, we conclude that measured vertical fluxes of seston, PC, and Chl *a* did not change significantly between July 1984 and February 1985, but that the fluxes in May were larger. Unlike the other constituents, vertical flux of Bchl *a* was highest in February, following the onset of winter mixing (Fig. 3).

From ratios of vertical flux to standing stock, we calculated specific sinking rates (i.e. turnover rates due to sedimentation) for PC and photosynthetic pigments (Table 1). During July and October these turnover rates were 0.3–0.4% d^{-1} for PC, 1.2% d^{-1} for Chl *a*, and 0.1% d^{-1} for Bchl *a* (=residence times in the mixolimnion of 83 d for phytoplankton and 1,000 d for PSB). The specific sinking rate of PSB increased 10-fold in February, following winter mixing and disruption of the bacterial layer. Similarly, the turnover rate of phytoplankton increased 10-fold (residence time = 6 d) in May, after decline of the winter bloom.

Measured rates of sedimentation are summarized in Fig. 3 (the deep sediment traps were lost in July). For all constituents, seasonal changes in vertical fluxes below the chemocline (at 40 m) paralleled those above it (30 m). The ratio of these fluxes (F_{40} : F_{30}) is an index of the efficiency of the chemocline in trapping sinking particulates. For total seston this ratio was high (>86%), showing that the chemocline retained only a small fraction of sinking particulate matter (this ratio was >100% in October, but the difference between F_{40} and F_{30} was less than the precision of the measurement). This ratio was similar for Chl *a* (>80%), but was smaller for PC (mean among three sampling dates of 67%) and Bchl *a* (mean of 54%).

Composition of sinking particles—Several different approaches were used to characterize the particulate matter collected in sediment traps (Table 2). Microscopic examination revealed no obvious differences in seston collected above or below the chemocline. However there were seasonal differences. For example, *Oocystis* colonies and cladoceran molts were present in July, fecal pellets were prominant in October and February, and *N. palea* dominated in May. These seasonal changes mirrored those in the water column: *Oocystis* is the dominant phytoplankton taxon in summer, and the cladoceran *Moina hutchinsoni* is most abundant in summer–autumn (Cloern et al. 1983*a*); the copepod *Diaptomus sicilis* is abundant in spring and maintains a small winter population; and the winter phytoplankton bloom is composed almost entirely of the diatom *N. palea.* Most (>65%) of the PC passed a 60-μm mesh (both above and below the chemocline), showing that large particles (e.g. fecal pellets, crustacean carcasses) composed a small fraction of the sinking POM (Table 2). In May virtually all PC passed the 60-μm mesh, consistent with the observation that seston then was dominated by *N. palea.* A third characteristic of the seston, the organic carbon fraction (PC flux/seston flux), was consistently about 20% above the chemocline. There was always a reduction in this fraction below the chemocline (Table 2), and this depletion of organic carbon was the only apparent difference in seston composition across the chemocline.

Photosynthetic bacteria or phytoplankton (depending on season) composed a large fraction of POM in the mixolimnion. To estimate PSB and algal contributions to the

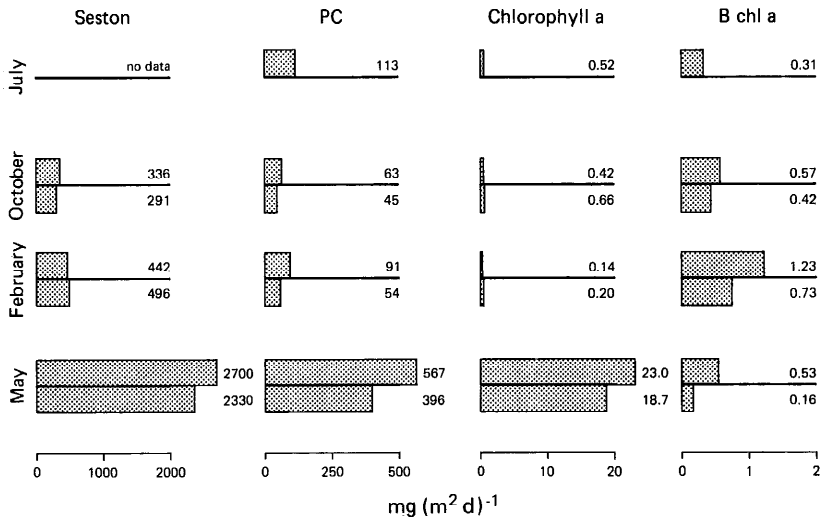

Fig. 3. Vertical fluxes of seston, PC, Chl *a*, and Bchl *a* in Big Soda Lake during 1984–1985. Values over the horizontal lines represent measured fluxes above the chemocline (at 30 m) and values under the horizontal lines are fluxes below the chemocline (at 40 m).

PC flux at the chemocline, we multiplied measured vertical fluxes of pigments (Fig. 3) by a carbon : pigment conversion factor. For PSB, the conversion factor was obtained from linear regression (model 2: Laws and Archie 1981) of PC against Bchl *a* for all data collected around the PSB layers (=19–22 m; Fig. 2). The regression was highly significant (Fig. 4), and the slope yielded a C : Bchl *a* ratio of 15.2. Calculated vertical fluxes of PSB, in carbon units, were a small component (4%) of the total PC flux in July when the bacterial layer was well defined and maintained by thermal stratification. In February, however, when the bacterial layer had dissipated due to winter mixing, the PSB component of PC flux increased to 21% (Table 2). Except during winter mixing, then, the vertical flux of photosynthetic bacteria was small even though this community comprised a large fraction (25% in summer–autumn) of the total standing stock of PC.

Analogous calculation of the phytoplankton component of PC flux was not possible, because there was no correlation between

Table 2. Characteristics of seston in Big Soda Lake during 1984–1985.

	Jul	Oct	Feb	May
Microscopic examination:				
Predominant components	*Oocystis*	Organic aggregates	Fecal pellets	*Nitzschia palea*
	Crustacean molts	Crustacean molts Fecal pellets Pennate diatoms	Organic aggregates Pennate diatoms	
Size fractionation:				
Percentage of PC passing a 60-μm mesh	65	78	77	99
Organic content (%C) at 30 m/40 m	—	19/15	21/11	21/17
Phytoplankton (PP) or photosynthetic bacterial (PSB) component (%) of vertical PC flux at 30 m:				
PP	12	17	4	Most
PSB	4	14	21	1

PC and Chl *a* concentration. In May, the ratio of the PC flux to the Chl *a* flux at 30 m was 24.7 mg C (mg Chl *a*)$^{-1}$—near the lower limit of expected C : Chl *a* ratios for phytoplankton (e.g. Cullen 1982). It implies that most of the PC in May was composed of phytoplankton cells, consistent with microscopic examination of the sediment trap contents (Table 2). Assuming a constant phytoplankton C : Chl *a* ratio of 25, we estimate that during other times of the year the phytoplankton component was a smaller fraction (4–17%) of PC flux (Table 2).

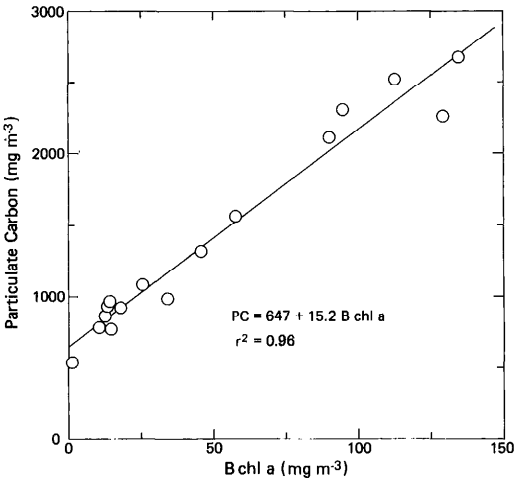

Fig. 4. Model 2 (geometric mean) regression of PC against Bchl *a* for all samples collected at or near the bacterial layer of Big Soda Lake.

Discussion

Seasonality of vertical fluxes—The mixolimnion of Big Soda Lake shows large seasonal variations in the vertical flux of seston, characterized by a relatively constant and low sedimentation rate from summer to winter, followed by a large increase during spring (Fig. 3). This seasonality does not result from temporal variations in the standing stock of seston, because PC standing stock was highest in summer (Table 1). Rather, it results from temporal changes in the specific sinking rate of the seston. During summer and autumn only about 0.4% of the PC standing stock is lost to sedimentation per day, but this fraction increases almost 10-fold in spring (Table 1). This change results from differential sinking rates of the predominant autotrophs. During summer and autumn most (≅85%: Cloern et al. 1983*b*) production is by chemosynthetic and photosynthetic bacteria. These organisms sink very slowly. Note, for example, that the specific sinking rate of Bchl *a* was only 0.1% d^{-1} during summer–autumn (Table 1). On the other hand, phytoplankton are the dominant producers after winter mixing and their sinking rates are much higher, particularly following thermal stratification and subsequent nutrient depletion in the epilimnion during spring (16% daily loss in May). Smetacek et al. (1978) observed similar rapid sinking losses of phytoplankton following blooms in the Baltic, and in his review Smetacek (1985) showed that rapid mass sedimentation of diatoms is common in lakes and the ocean after nutrients are depleted. An analogous event with the PSB layer followed enhanced mixing in winter; PSB standing stock decreased from 530 to 130 mg Bchl *a* m^{-2} between October and February, and the specific sinking rate of PSB increased 10-fold in February (Table 1). This accelerated sinking of PSB could be a consequence of physiological stress (exposure to oxygen or depletion of reduced sulfur compounds) resulting from vertical mixing in winter.

Our results suggest an annual cycle of sedimentation. After thermal stratification is established in early summer (and for most of the year), autotrophic production is dominated by bacteria localized in a layer at or below the oxycline; maintenance of this layer is facilitated by slow turbulent mixing below the thermocline. Phytoplankton biomass is low because of nutrient limitation in the epilimnion, and vertical fluxes (seston, PC, pigments) are also low (July, October—Fig. 3). During the initial stage of winter mixing the bacterial layer is disrupted by turbulent mixing, and there is an increased flux rate of PSB to the chemocline (February—Fig. 3). After the near-complete circulation of the mixolimnion in winter, DIN from the hypolimnion is brought to the surface, phytoplankton biomass increases, and primary productivity is dominated by planktonic diatoms. Vertical fluxes were not measured during this stage, but it is likely that fluxes of PC and Chl *a* are

higher than measured in our study. During the winter bloom of 1982, we measured phytoplankton biomass as high as 945 mg Chl *a* m^{-2}, over six times higher than during our flux measurements in May 1985. During the re-establishment of thermal stratification in spring, the phytoplankton bloom collapses, and the vertical flux of senescent diatoms is large (May—Fig. 3). The vertical flux of POM is therefore controlled by qualitative changes in seston that, in turn, are driven by seasonal changes in the physical structure of the water column, as in other pelagic systems (Hargrave and Taguchi 1978).

The chemocline as a localized site of mineralization—Both seston and bacteria accumulate at the chemocline of Big Soda Lake (Zehr et al. 1987), suggesting that this density discontinuity may be an important site of POM mineralization. However, sinking losses of PC are small relative to productivity. For example, autotrophic productivity is about 700 mg C m^{-2} d^{-1} during summer–autumn (Cloern et al. 1983*b*) when vertical fluxes ranged from 63 to 113 mg C m^{-2} d^{-1}. Hence only about 9–16% of daily productivity sinks to the chemocline during summer–autumn. In addition, most particulate carbon (≅70%) reaching the chemocline passes through it, so only about 3–5% of daily productivity accumulates there. Recent measurements show that ATP and protein concentrations are not elevated at the chemocline (Oremland et al. 1987), and assimilation rates of thymidine are low there (Zehr et al. 1987). Hence the large localized population of bacteria observed at the chemocline must play a minor role in lake metabolism and nutrient regeneration.

Because vertical fluxes of seston below the chemocline were about 90% of those measured above it (Fig. 3), we conclude further that the chemocline of the lake is an inefficient filter for sinking particulate matter. In addition, microscopic examination showed similar compositions of seston collected at 30 and 40 m. These observations demonstrate that an extreme density discontinuity (42 kg m^{-3} over <1 m) does not greatly inhibit the sinking of bulk POM or pelagic diatoms. Consequently the much smaller density gradients characteristic of the open ocean and freshwater lakes should not greatly influence the vertical flux of suspended particles. Our observations support other mechanisms for the formation of chlorophyll peaks in the deep ocean (e.g. Cullen 1982). On the other hand, the chemocline of Big Soda Lake does inhibit more strongly the sinking of bacteria, as evidenced by the accumulation of bacterial cells there and the reduced vertical fluxes of Bchl *a* across the chemocline (Fig. 3).

Implications for the lake carbon budget—Comparison of vertical PC fluxes with our previous measures of productivity indicates that sinking losses are a minor component of the carbon budget in Big Soda Lake, at least during summer–autumn, as is illustrated by a simple population model of PSB biomass:

$$\Delta B/\Delta t = P - S - H. \quad (4)$$

Here $\Delta B/\Delta t$ represents the rate of biomass increase (mg C m^{-2} d^{-1}), P is the productivity, S is the sinking loss rate from the mixolimnion, and H is the rate of all in situ processes that consume PSB (including grazing, lysis, and decomposition of senescent cells). From July to October 1984, PSB biomass increased from 500 to 530 mg Bchl *a* m^{-2}—equal to a daily population growth rate of 4.9 mg C m^{-2} d^{-1}. PSB productivity ranged from 180 to 210 mg C m^{-2} d^{-1} in summer–autumn 1981 (Cloern et al. 1983b), and measured sinking losses ranged from 0.31 to 0.57 mg Bchl *a* m^{-2} d^{-1} (=4.7–8.7 mg C m^{-2} d^{-1}). Using mean values for P and S, we calculate that heterotrophic processes in the water column (H) are the dominant sink for PSB production:

$$4.9 = 195 - 6.7 - H,$$

or

$$H = 183 \text{ mg C } m^{-2} d^{-1}.$$

For this community, the estimated consumption rate is 97% of daily productivity. Similar calculations for phytoplankton indicate that $H/P = 89\%$ during summer and autumn. This consumption must take place in the mixolimnion.

Mechanisms responsible for this high re-

cycling efficiency (≅90%) are not known. Among microbial processes, rates of methane production are negligible (Iversen et al. 1987), denitrification has not been detected (Oremland et al. 1987), and sulfate reduction in the mixolimnion can account for a maximum mineralization rate of only 100 mg C m^{-2} d^{-1} (Smith and Oremland 1987), which is <20% of the difference between productivity and PC sedimentation rate. Zehr et al. (1987) speculate that fermentation processes are the predominant mechanism of decomposition of the anaerobic mixolimnion. Zooplankton may also be important in recycling PC. Sorokin (1965) demonstrated that crustaceans can feed from bacterial layers associated with an oxycline. Sorokin and Donato (1975) observed ciliates active in the anoxic zone of meromictic Lake Faro. And there is growing evidence that microzooplankton grazing can be a large sink for production by small autotrophs and bacteria; for example, Sherr et al. (1984) showed that heterotrophic nanoplankton (microflagellates) graze up to half the daily bacterioplankton production in Georgia coastal waters. Unfortunately, the zooplankton community has been largely ignored in Big Soda Lake.

The fate of POM produced during the winter bloom remains an open question because vertical PC fluxes were not measured during the winter peak in phytoplankton biomass and productivity. The high specific sinking rate in May (0.16 d^{-1} for Chl *a*) is about 40% of our upper estimate of phytoplankton growth rate (Cloern et al. 1983*b*). Sinking losses of this magnitude (≅30–40% of daily productivity) are common during winter–spring diatom blooms (Ducklow et al. 1982; Forsskåhl et al. 1982) when recycling is slowed by cold temperatures and low zooplankton biomass (Smetacek 1980).

Although Big Soda Lake is unusual in its extreme vertical zonation (distinct chemocline, thermocline, and oxycline) and its community of autotrophs (seasonal alternation of bacteria and algae), the patterns of carbon cycling described here are similar to those observed in holomictic lakes and the ocean. As a general rule, most production (≅90%) is mineralized before sinking from the trophogenic zone (e.g. Bloesch et al. 1977; Eppley and Peterson 1979; Karl and Knauer 1984). Exceptions to this rule occur only after the winter diatom bloom, when sedimentation losses become a large component of the carbon budget.

References

BLOESCH, J., P. STADELMAN, AND H. BUHRER. 1977. Primary production, mineralization, and sedimentation in the euphotic zone of two Swiss lakes. Limnol. Oceanogr. **22:** 511–526.

CLOERN, J. E., B. E. COLE, AND R. S. OREMLAND. 1983*a*. Seasonal changes in the chemistry and biology of a meromictic lake (Big Soda Lake, Nevada, U.S.A.). Hydrobiologia **105:** 195–206.

———, ———, AND ———. 1983*b*. Autotrophic processes in meromictic Big Soda Lake, Nevada. Limnol. Oceanogr. **28:** 1049–1061.

CULLEN, J. J. 1982. The deep chlorophyll maximum: Comparing vertical profiles of chlorophyll *a*. Can. J. Fish. Aquat. Sci. **39:** 791–803.

CULVER, D. A., AND G. J. BRUNSKILL. 1969. Fayetteville Green Lake, New York. 5. Studies of primary production and zooplankton in a meromictic marl lake. Limnol. Oceanogr. **14:** 862–873.

DUCKLOW, H. W., D. L. KIRCHMAN, AND G. T. ROWE. 1982. Production and vertical flux of attached bacteria in the Hudson River plume of the New York Bight as studied with floating sediment traps. Appl. Environ. Microbiol. **43:** 769–776.

EPPLEY, R. W., AND B. J. PETERSON. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. Nature **282:** 677–680.

FORSSKÅHL, M., AND OTHERS. 1982. Seasonal cycle of production and sedimentation of organic matter at the entrance to the Gulf of Finland. Neth. J. Sea Res. **16:** 290–299.

HAMNER, W. M., R. W. GILMER, AND P. P. HAMNER. 1982. The physical, chemical, and biological characteristics of a stratified, saline, sulfide lake in Palau. Limnol. Oceanogr. **27:** 896–909.

HARGRAVE, B. T., AND S. TAGUCHI. 1978. Origin of deposited material sedimented in a marine bay. J. Fish. Res. Bd. Can. **35:** 1604–1613.

IVERSEN, N., R. S. OREMLAND, AND M. J. KLUG. 1987. Big Soda Lake (Nevada). 3. Pelagic methanogenesis and anaerobic methane oxidation. Limnol. Oceanogr. **32:** 804–814.

KARL, D. M., AND G. A. KNAUER. 1984. Detritus-microbe interactions in the marine pelagic environment: Selected results from the Vertex experiment. Bull. Mar. Sci. **35:** 550–565.

KIMMEL, B. L., R. M. GERSBERG, L. J. PAULSON, R. P. AXLER, AND C. R. GOLDMAN. 1978. Recent changes in the meromictic status of Big Soda Lake, Nevada. Limnol. Oceanogr. **23:** 1021–1025.

LAWS, E. A., AND J. W. ARCHIE. 1981. Appropriate use of regression analysis in marine biology. Mar. Biol. **65:** 13–16.

LORENZEN, C. J. 1967. Determination of chlorophyll

and pheopigments: Spectrophotometric equations. Limnol. Oceanogr. **12:** 343–346.

OREMLAND, R. S., AND OTHERS. 1987. Microbial and biogeochemical processes in Big Soda Lake, Nevada, in press. *In* K. Kelts et al. [ed.], Lacustrine petroleum source rocks. Geol. Soc. Lond.

SHERR, B. F., E. B. SHERR, AND S. Y. NEWELL. 1984. Abundance and productivity of heterotrophic nanoplankton in Georgia coastal waters. J. Plankton Res. **6:** 195–202.

SMETACEK, V. S. 1980. Annual cycles of sedimentation in relation to the plankton ecology in western Kiel Bight. Ophelia Suppl. 1, p. 65–76.

———. 1985. Role of sinking in diatom life-history cycles: Ecological, evolutionary and geological significance. Mar. Biol. **84:** 239–251.

———, K. VON BRÖCKEL, B. ZEITZSCHEL, AND W. ZENK. 1978. Sedimentation of particulate matter during a phytoplankton spring bloom in relationship to the hydrological regime. Mar. Biol. **47:** 211–226.

SMITH, R. L., AND R. S. OREMLAND. 1987. Big Soda Lake (Nevada). 2. Pelagic sulfate reduction. Limnol. Oceanogr. **32:** 749–803.

SOROKIN, J. I. 1965. On the trophic role of chemosynthesis and bacterial biosynthesis in water bodies. Mem. Ist. Ital. Idrobiol. **18(suppl.):** 187–208.

———, AND N. DONATO. 1975. On the carbon and sulphur metabolism in the meromictic Lake Faro (Sicily). Hydrobiologia **47:** 241–252.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis, 2nd ed. Bull. Fish. Res. Bd. Can. 167.

TAKAHASHI, M., AND S. ICHIMURA. 1970. Photosynthetic properties and growth of photosynthetic sulfur bacteria in lakes. Limnol. Oceanogr. **15:** 929–944.

ZEHR, J. P., AND OTHERS. 1987. Big Soda Lake (Nevada) 1. Pelagic bacterial heterotrophy and biomass. Limnol. Oceanogr. **32:** 781–793.

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