

Zooplankton effects on vertical particulate flux: Testable models and experimental results

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Abstract

The effects of herbivorous zooplankton on the sedimentation of particles out of the euphotic zone are examined with mathematical models, a large-scale field experiment, and descriptive data from a eutrophic lake. The theory is rooted in the population dynamics of phytoplankton and zooplankton and so explicitly accounts for the potential effect of zooplankton grazing on primary production and the connection between the rate at which phytoplankton cells sink and sustainable zooplankton biomass. The models predict positive, negative, or unimodal zooplankton effects, depending on the values of four parameters: rate of direct phytoplankton sinking, fraction of zooplankton fecal material exiting the euphotic zone, zooplankton assimilation efficiency, and system productivity. Models were parameterized with data from a eutrophic lake to make a priori predictions about the shape and direction of zooplankton effects. Predictions were tested against the results of an independent experiment in which a gradient of *Daphnia* biomass was established in large enclosures. *Daphnia* negatively affected sedimentation rates of carbon, nitrogen, and phosphorus in the enclosure experiment, which confirmed model predictions. *Daphnia* had a strong negative effect on phytoplankton biomass, and phytoplankton biomass was positively correlated with sedimentation in the enclosures. Experimental results were congruent with relationships between *Daphnia* biomass and sedimentation rate in the lake. Successful application of the theory suggests that these models may be of utility for assessing the direction of zooplankton effects on vertical flux in other systems. More generally, the models help to identify parameters that should be measured in studies of zooplankton effects on downward particle flux.

The rate at which particles sink out of the euphotic zone is an important process driving the seasonal dynamics of nutrients, as well as benthic–pelagic coupling, in stratified water columns (Hinga et al. 1979; Angel 1984; Guy et al. 1994). In addition, the sinking flux of particulate organic carbon fixed by marine phytoplankton is an important component of global carbon cycles (Michaels et al. 1994; Sarmiento and Bender 1994). Consequently, there is considerable interest in understanding and predicting sedimentation flux in both lakes and oceans (Suess 1980; Pace et al. 1987; Wassmann 1991; Baines and Pace 1994). Of particular interest in recent years is the role that primary consumers (zooplankton) play in sedimentation (Noji 1991). This interest has grown out of recognition that marine flux is generally dominated by large particles with high sinking velocities (Angel 1984; Fowler and Knauer 1986) and that fecal pellets of zooplankton are an important class of rapidly sinking particles (Honjo and Roman 1978; Bathmann et al. 1987; Bodungen et al. 1987; Morris et al. 1988).

Most research to date addressing the role of zooplankton in sedimentation has been directed at determining the potential contribution of zooplankton-derived fecal material to the total downward flux of particles (Pilskaln and Honjo 1987; Dilling and Alldredge 1993; Lane et al. 1994). Such studies, however, do not indicate the overall effect of zooplankton

on flux because they provide no information about the influence of zooplankton grazing on the direct sedimentation of phytoplankton, which may form large, rapidly sinking aggregates if not consumed (Peinert et al. 1989). Consequently, such studies are insufficient for predicting the response of total flux to changes in zooplankton abundance.

A relatively small number of researchers have attempted to assess the effect of a change in zooplankton abundance on total sedimentation, either theoretically or empirically. Of the theoretical studies available, only a very few describe models that are simple enough to be of general applicability (Aksnes and Wassmann 1993; Elser et al. 1995a). Further, the general models currently available are not testable in a strict sense because some of the parameters cannot be (or at least have never been) independently estimated. Experimental studies are potentially the most powerful approach to determining zooplankton effects, but they are limited to lakes and to simple designs (+/– macrozooplankton; Uehlinger and Bloesch 1987; Bloesch and Bürgi 1989; Sarnelle 1992). In several studies, zooplankton have been manipulated indirectly by establishing treatments with and without zooplanktivorous fish (Langeland et al. 1987; Carpenter et al. 1988; Mazumder et al. 1989; Reinertsen et al. 1990; Vanni et al. 1997), an approach that may confound mechanistic interpretation because fish can affect phytoplankton abundance and species composition independently of their effects on zooplankton (Vanni and Layne 1997). Studies that include attempts to correlate sedimentation flux with zooplankton abundance from unmanipulated systems are also rare (Bloesch and Bürgi 1989; Elser et al. 1995a). Each of the above approaches has well-described advantages and weaknesses (Cooper and Barmuta 1993).

In this study, I combined the above approaches to examine the effect of zooplankton on vertical particulate flux. I used

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general mathematical models that make testable predictions about the response of sedimentation to changes in zooplankton biomass. All parameters in the basic model can be estimated independently of experiments used to test model predictions. The theoretical analysis is motivated by the obvious need to be able to predict when the effect of zooplankton on sedimentation will be positive (Bloesch and Bürgi 1989) or negative (Sarnelle 1992). I tested model predictions with the results of a large-scale experimental manipulation of zooplankton biomass in a eutrophic lake. This experiment was unique in that a gradient of zooplankton abundance was maintained via direct manipulation in large enclosures. I then examined whether these experimental results were applicable to natural events with an analysis of the relationship between zooplankton biomass and sedimentation in the lake.

Models

The following models were used to examine the response of sedimentation to changes in zooplankton biomass that are independent of changes in the potential productivity (or enrichment level) of the environment. Some potential sources of variation in zooplankton biomass are variation in (1) the abundance or activity of higher trophic levels (top-down effects), (2) overwinter survival of zooplankton (Peinert et al. 1987), and (3) time lags of response by zooplankton populations to algal blooms (Wassmann 1991). A model that can predict the response of total sedimentation to a change in zooplankton biomass should, at a minimum, incorporate two opposing sets of processes (Noji 1991). First, zooplankton feeding and assimilation will reduce the size of the phytoplankton stock that is available to sink out directly. In opposition to this effect, zooplankton package unassimilated phytoplankton into fecal material that may have high sinking velocities relative to the original cells consumed. There is ample evidence that both direct sedimentation of phytoplankton (in the form of aggregates) and zooplankton fecal material (fecal pellets of copepods) can be major components of total flux at different times and in different locations (Bathmann et al. 1987; Pilskaln and Honjo 1987; Wassmann 1991).

A general expression, based on the seminal work by Aksnes and Wassmann (1993), describing total sedimentation flux as the sum of direct phytoplankton sinking and sedimentation of zooplankton fecal material is

$$S_T = S_p + S_f = BvD + (1 - e)BZgDq \quad (1)$$

where S_T , S_p , and S_f are total, phytoplankton, and fecal sedimentation ($\text{mg m}^{-2} \text{d}^{-1}$), B is phytoplankton biomass (mg m^{-3}), v is the loss rate of phytoplankton due to direct sinking (d^{-1}), D is the depth of the euphotic zone (or other depth stratum of interest) (m), e is the assimilation efficiency of herbivorous zooplankton, g is the filtering rate of zooplankton (m^3 cleared mg^{-1} zooplankton biomass d^{-1}), Z is zooplankton biomass (mg m^{-3}), and q is the fraction of zooplankton fecal material that exits the euphotic zone.

A model that assumes that observations are made over a relatively short time scale (a few days or weeks) can be used so that zooplankton biomass can be thought of as a fixed

parameter (the uncoupled model). This model describes phytoplankton dynamics as

$$\frac{dB}{dt} = rB \left(1 - \frac{B}{K} \right) - gZB - vB \quad (2)$$

where r is the maximum division rate of the phytoplankton (d^{-1}) and K is maximum phytoplankton biomass (mg m^{-3}). This expression is a key point of departure from the model of Aksnes and Wassmann (1993). They assumed that phytoplankton divide at a constant rate, whereas here it is assumed that phytoplankton division rate is density dependent, reflecting the possibility that phytoplankton may grow more slowly at the end of a bloom (when phytoplankton abundance is high) than at its initiation. Over a time interval in which phytoplankton biomass is constant ($dB/dt = 0$), equilibrium phytoplankton biomass is

$$B^* = \frac{K(r - v - gZ)}{r} \quad (3)$$

Equation 3 implies that equilibrium phytoplankton biomass will increase linearly with decreases in zooplankton biomass. This model would not be an appropriate description of a system in which a decrease in zooplankton does not result in an increase in phytoplankton abundance. Equation 3 has another important implication, namely that maximum zooplankton biomass is, in part, determined by v , the loss rate of phytoplankton due to direct sinking, which follows from simply assuming that phytoplankton biomass must be greater than zero:

$$Z < \frac{r - v}{g} \quad (4)$$

Equation 4 expresses the reasonable intuition that as the sinking loss of phytoplankton increases, fewer resources will be available for herbivorous zooplankton and so fewer zooplankton can be supported. The potential codependency of Z and v has important implications for the interpretation of nonexperimental data.

By substituting the expression for equilibrium algal biomass (Eq. 3) into the expression for sedimentation (Eq. 1), total sedimentation can be expressed as a function of zooplankton biomass:

$$S_T^* = S_p^* + S_f^* = \frac{KD}{r} [v(r - v - gZ) + (1 - e)(r - v - gZ)gZq] \quad (5)$$

Equation 5 predicts that direct phytoplankton sedimentation (S_p^*) will be a negative linear function of zooplankton biomass (Z), whereas fecal sedimentation (S_f^*) will be a unimodal function of zooplankton biomass, a consequence of a decline in fecal production rate per zooplankter because of the decrease in phytoplankton biomass (Corner et al. 1972; Paffenhöfer and Knowles 1979; Butler and Dam 1994) as zooplankton biomass increases.

The shape of the response of total sedimentation (S_T^*) to changes in zooplankton biomass will depend on the relative contributions of phytoplankton and fecal material to overall flux. These contributions depend most strongly on the mag-

nitude of ν (in part because ν varies widely in nature; Reynolds 1984) and to a lesser extent on q and e (Fig. 1). When ν is high, as might occur when phytoplankton are large or tend to aggregate independent of zooplankton grazing, or when physical conditions are characterized by low rates of mixing, phytoplankton sedimentation will dominate flux and the effect of zooplankton will be to reduce total flux (Fig. 1). Conversely, when ν is low, fecal material will dominate sedimentation and total flux will tend to be a unimodal function of zooplankton biomass. Similarly, as the fraction of fecal material that exits the euphotic zone (q) increases or the assimilation efficiency of zooplankton (e) decreases, the response of sedimentation to changes in zooplankton biomass will become more hump-shaped (Fig. 1), reflecting the importance of fecal material to total flux.

The prediction that sedimentation may be a unimodal function of zooplankton biomass is crucial for the interpretation of field manipulations because a unimodal response cannot be discovered in an experiment with two treatment levels of zooplankton, the design most commonly employed. Under no biologically reasonable circumstances does the uncoupled model predict that the effect of zooplankton on total sedimentation will be monotonically positive over the entire range of sustainable zooplankton abundance.

An analogous model for observations made over longer time scales, where zooplankton biomass could be expected to equilibrate to a change in the rate of predatory mortality (or removal by the experimenter), requires a pair of predator-prey equations, such as Eq. 2, and the following expression for the dynamics of herbivorous zooplankton (the coupled model):

$$\frac{dZ}{dt} = ecgZB - bZ - dZ, \quad (6)$$

where ec is the efficiency with which zooplankton convert ingested phytoplankton into zooplankton (product of assimilation efficiency, e , and growth efficiency, c), and b and d are loss rates via respiration and mortality, respectively, of the zooplankton (d^{-1}). An experiment designed to establish a gradient of zooplankton biomass via a removal manipulation can be thought of as a direct manipulation of d . Solving at equilibrium gives

$$B^* = \frac{d + b}{ecg} \quad (7)$$

$$Z^* = \frac{r \left(1 - \frac{d + b}{ecgK} \right) - \nu}{g}. \quad (8)$$

Equation 8 clearly shows the interdependency noted earlier between zooplankton biomass and the sinking loss rate of the phytoplankton, ν .

Substituting Eq. 7 into Eq. 1 and replacing d with an expression derived from Eq. 8, Eq. 5 can be rederived so that this model makes predictions somewhat similar to those of the uncoupled model about the response of sedimentation flux to a change in zooplankton biomass. However, in contrast to the uncoupled model, zooplankton biomass (Z^*) is now an explicit function of enrichment level (K), as ex-

pected based on observations in lakes (Hanson and Peters 1984). As a consequence, the predicted effect of zooplankton on sedimentation varies qualitatively depending on the productivity of the environment. Model sensitivity to enrichment can be illustrated by considering the relationship between two parameters, maximum zooplankton biomass (Z_{\max}^* , when $d = 0$) and zooplankton biomass at which sedimentation is maximal (Z_{opt}^*). Z_{\max}^* can be derived directly from Eq. 8 by setting $d = 0$:

$$Z_{\max}^* = \frac{r \left(1 - \frac{b}{ecgK} \right) - \nu}{g}. \quad (9)$$

Z_{opt}^* can be derived by setting the derivative, with respect to Z , of Eq. 5 (dS_T/dZ) to zero and solving for Z :

$$Z_{\text{opt}}^* = \frac{r - \nu - \frac{\nu}{(1-e)q}}{2g}. \quad (10)$$

Z_{\max}^* is positively related to K , but Z_{opt}^* is independent of K .

Under conditions where the relationship between total sedimentation and zooplankton biomass is predicted to be unimodal by the uncoupled model (low ν , high q), the coupled model's prediction depends on $Z_{\max}^* : Z_{\text{opt}}^*$, which changes with K . In eutrophic systems, Z_{\max}^* will typically be much higher than Z_{opt}^* , so sedimentation will be a unimodal function of zooplankton biomass (Fig. 2A). In oligotrophic systems, Z_{\max}^* may be equal to or lower than Z_{opt}^* , so the descending portion of the curve relating sedimentation to zooplankton biomass will not be expressed. In the latter case, the coupled model predicts that sedimentation will be a monotonically positive function of zooplankton biomass (Fig. 2C). Consequently, the coupled model suggests that positive effects of zooplankton on total sedimentation may be more likely in low-productivity systems.

Replacing the constant filtering rate of the zooplankton with a saturating functional response (type II) in the coupled model introduces complex behavior into the relationship between phytoplankton and zooplankton biomass, precluding a general analysis. To get an idea of how the functional response influences zooplankton effects, I examined the behavior of a coupled model with a type II functional response, using the values of ν , q , and K shown in Figs. 1 and 2. The functional response was of the form: $I/(B + B_i)$, where I is maximum ingestion rate (d^{-1}) and B_i is the level of phytoplankton biomass at which ingestion rate equals $I/2$. I used values for I and B_i that are reasonable for the common freshwater herbivore *Daphnia* (Nisbet et al. 1991). These limited analyses do not greatly alter the general conclusions regarding how the direction of the sedimentation response is influenced by ν , q , and K . However, in productive systems showing unimodal responses, the peak in the relationship between sedimentation and zooplankton biomass is shifted toward high zooplankton densities in the more complex model (Fig. 3). This result and the truncation of unimodal responses seen in oligotrophic systems (Figs. 2, 3) may reduce the probability of observing unimodal responses in nature.

The models can be modified to examine the effect of other

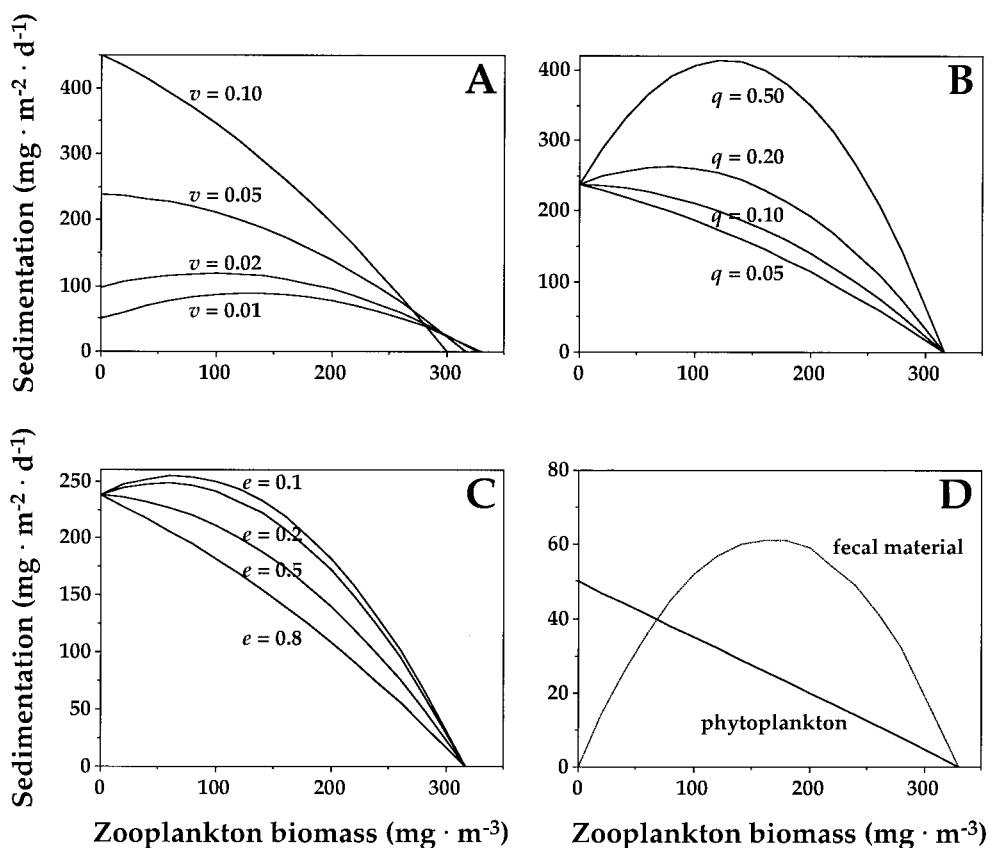


Fig. 1. Predicted effects of zooplankton on sedimentation rate (phytoplankton plus fecal material) for the uncoupled model. Reference parameter values: $r = 1.0 \text{ d}^{-1}$, $K = 1,000 \text{ mg m}^{-3}$, $v = 0.05 \text{ d}^{-1}$, $D = 5 \text{ m}$, $e = 0.5$, $g = 0.003 \text{ m}^3 \text{ mg}^{-1} \text{ d}^{-1}$, $q = 0.1$. (A) Effect of changing v , the sinking loss rate of phytoplankton. (B) Effect of changing q , the fraction of fecal material that exits the euphotic zone. (C) Effect of changing e , the assimilation efficiency of zooplankton. (D) Sedimentation rates of phytoplankton and fecal material for reference parameters and $v = 0.01$.

complicating factors, often without losing analytical tractability. Among these factors are variation among elements, e.g., carbon (C), nitrogen (N), and phosphorus (P), in rates of grazer assimilation (e) and fecal mineralization (q), changes in phytoplankton sinking (v) as a function of zooplankton grazing or phytoplankton biomass, and the contribution of zooplankton-derived material to particle flux. These complications will not be addressed here. The major strength of these models is their testability. Model parameters can be estimated independently of experiments in which the response of sedimentation rate to a manipulation of zooplankton biomass is measured.

Study site

The data for this study were collected from Zaca Lake (7 ha, maximum depth, 13 m) located in the San Rafael Mountains of southern California. Zaca Lake is naturally eutrophic (total phosphorus at overturn averages 10–12 μM), high in dissolved ions, particularly magnesium, sulfate, calcium, and carbonate (Melack and Setaro 1986), and marked by persistent stratification for 6–8 months of the year (see Sarnelle 1993 for detailed lake description). Zaca Lake also under-

goes periodic episodes of massive calcite precipitation (whitings), which typically begin in May (Sarnelle 1992).

Materials and methods

Lake monitoring—Predictions were generated by parameterizing models using previously published values (r , e , c , g , b , and q) and data from Zaca Lake (K , D , and v). Data for parameterization were collected from the lake during 1989–1990. Depth-integrated samples for suspended phytoplankton biomass were collected from the euphotic zone with a tube sampler (27 mm inside diameter). Samples for chlorophyll a were filtered onto Gelman A/E filters and frozen until analysis. Chlorophyll a was measured spectrophotometrically (with acid correction) after extraction in 90% acetone (Parsons et al. 1984).

Estimates of phytoplankton sinking loss were based on sediment-trap studies performed in the lake during 1989–1990 and in enclosures during an experiment in April 1989. Cylindrical sediment traps (5 cm diameter, 25 cm length) were set in the thermocline for 3–4 d throughout March, April, and May (see Sarnelle 1992 for details). Average sinking loss (d^{-1}) for the algal assemblage as a whole was cal-

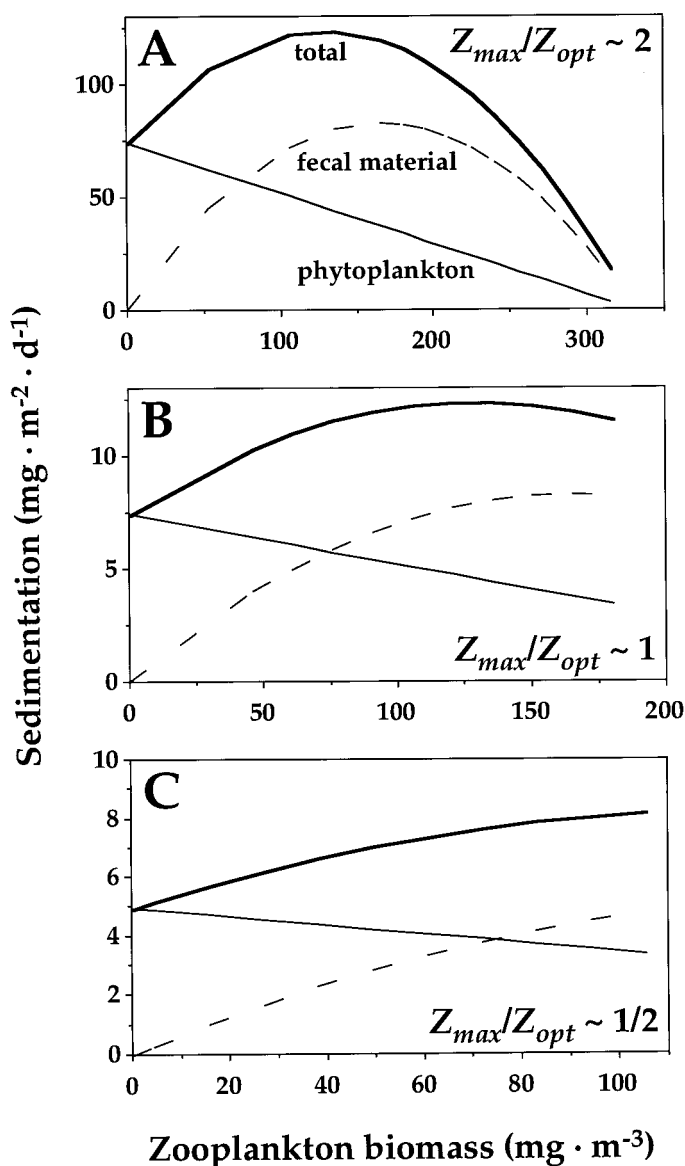


Fig. 2. Predicted effects of zooplankton on sedimentation rate (phytoplankton plus fecal material) for the coupled model, effect of varying system productivity (K). Reference parameter values: $r = 1.0 \text{ d}^{-1}$, $v = 0.01 \text{ d}^{-1}$, $D = 5 \text{ m}$, $ec = 0.5$, $b = 0.10 \text{ d}^{-1}$, $g = 0.003 \text{ m}^3 \text{ mg}^{-1} \text{ d}^{-1}$, $q = 0.1$. (A) $K = 1,500 \text{ mg m}^{-3}$, maximum zooplankton biomass (Z_{max}^*) > zooplankton biomass at which fecal sedimentation is maximal (Z_{opt}^*). (B) $K = 150 \text{ mg m}^{-3}$, $Z_{max}^* \approx Z_{opt}^*$. (C) $K = 100 \text{ mg m}^{-3}$, $Z_{max}^* < Z_{opt}^*$.

culated by dividing chlorophyll *a* sedimentation rate ($\text{mg m}^{-2} \text{ d}^{-1}$) by average suspended chlorophyll *a* concentration (mg m^{-3}) over the trapping interval. Estimates of sinking loss based on chlorophyll sedimentation may underestimate actual loss rates because chlorophyll degrades rapidly after cell death (Leavitt and Carpenter 1990). To examine the magnitude of this bias, sinking loss rates were estimated with microscopic counts of phytoplankton in sediment traps and the euphotic zone during the 1989 enclosure experiment (see Sarnelle 1993 for details on phytoplankton counting meth-

ods). Count-based estimates were made in parallel with chlorophyll-based measurements for four enclosures on one date.

Sedimentation data from the lake were restricted to the time period before the onset of calcite whittings (March–May). Whittings have large effects on sedimentation rates that would obscure patterns resulting from the influence of zooplankton (Koschel et al. 1983; Sarnelle 1992). I also collected samples from sediment traps in 1989–1990 to estimate sedimentation rates of particulate P and N in the lake (see Sarnelle 1992 for analytical details). Zooplankton abundance was monitored in the lake in 1989–1990.

Field experiment—An enclosure experiment designed to quantify the response of sedimentation to a gradient of zooplankton biomass was conducted in Zaca Lake during April–May 1994. Twelve large enclosures made of clear polyethylene sheeting (2.3 m diameter, 8 m deep) were deployed in the middle of the lake on 17 April. Each enclosure was fitted with coarse netting on the bottom, to exclude fish as the enclosure bottom was lowered. Otherwise, enclosure bottoms were open to the anoxic hypolimnion. Enclosures were open to the atmosphere at the top, suspended from rafts, and held open by attaching a weight to a PVC hoop attached to the bottom edge of the polyethylene sheeting.

Enclosures were manipulated by slowly pulling a large, coarse-mesh zooplankton net (1 m diameter, 250- μm mesh) through enclosures 2 days of each week. The objective of this manipulation was to create a gradient of *Daphnia* biomass rather than to manipulate all crustaceans. The same number of net hauls was made in every enclosure to control for mixing effects, and the gradient of *Daphnia* removal was established by varying the number of times the contents of net hauls were either emptied into the lake or emptied back into the enclosure (sham hauls, no zooplankton removed). Zooplankton collected in sham hauls were released back into the enclosure without removing the net from the water.

Enclosures were sampled weekly for suspended phytoplankton biomass (as chlorophyll *a*), particulate elements (C, N, P), and dissolved P. Depth-integrated samples were taken from the euphotic zone with a tube sampler (51 mm inside diameter). Chlorophyll and elemental samples were collected on A/E filters. Samples for chlorophyll *a* and dissolved P were kept frozen until analysis. Samples for particulate elements were screened through 149- μm mesh to remove crustacean zooplankton, air dried in the field, further dried at 35°C in an oven, and stored in a desiccator. Chlorophyll *a* was measured spectrophotometrically (with acid correction) after extraction in 90% ethanol (Sartory and Grobbelaar 1984). P was determined by persulfate oxidation (Valderrama 1981) followed by ascorbic-molybdate colorimetry (Murphy and Riley 1962). Particulate organic C and N were measured with a CHN analyzer (Control Equipment Corp. Model 240XA), after inorganic C was driven off by acid-fuming filters.

Cylindrical sediment traps (7.5 cm diameter, 37.5 cm length) were deployed four times during the experiment, on days 5–7, 13–15, 20–22, and 27–29. Paired traps were filled with enclosure water and suspended at the bottom of the euphotic zone in 9 or 10 of the enclosures on each date. After 2 d of exposure, the contents of paired traps were

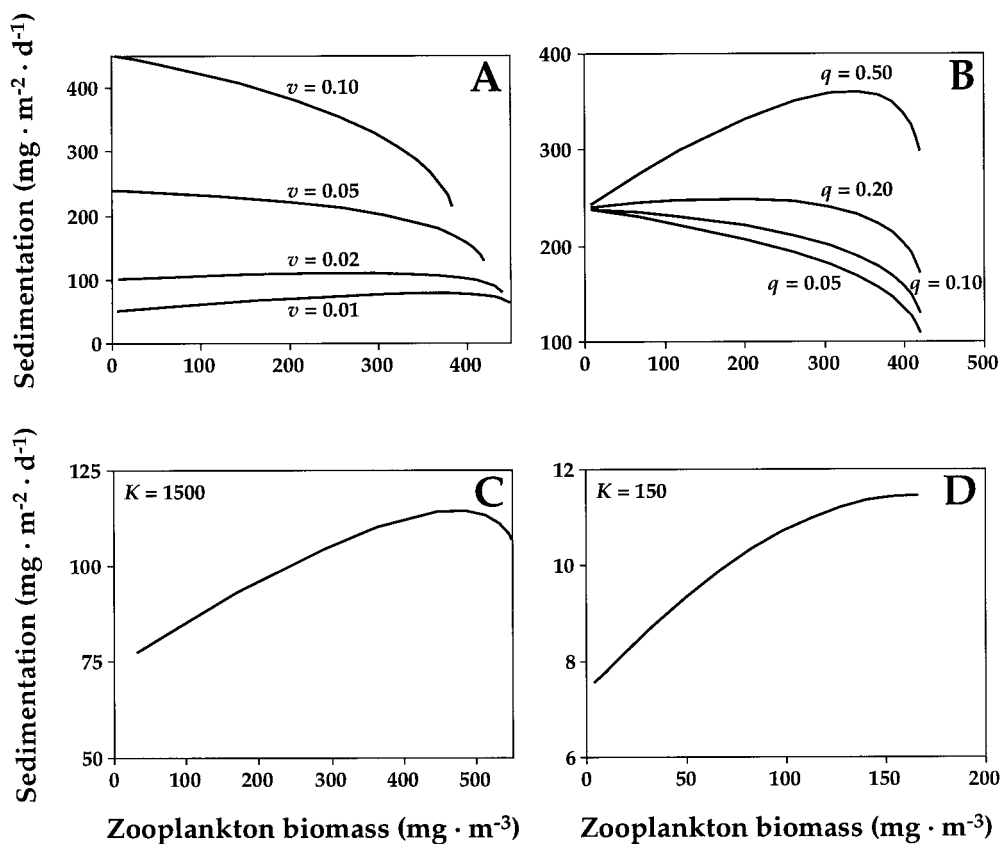


Fig. 3. Predicted effects of zooplankton on sedimentation rate (phytoplankton plus fecal material) for the coupled model with a type II functional response. Reference parameter values: $r = 1.0 \text{ d}^{-1}$, $K = 1,000 \text{ mg m}^{-3}$, $v = 0.05 \text{ d}^{-1}$, $D = 5 \text{ m}$, $ec = 0.5$, $b = 0.10 \text{ d}^{-1}$, $I = 1.0 \text{ d}^{-1}$, $B_i = 350 \text{ mg m}^{-3}$, $q = 0.1$. (A) Effect of changing v , the sinking loss rate of phytoplankton. (B) Effect of changing q , the fraction of fecal material that exits the euphotic zone. (C, D) Effect of varying system productivity (K), when $v = 0.01 \text{ d}^{-1}$.

pooled, screened through 149- μm mesh to remove crustacean zooplankton, and subsampled for particulate elements. Samples for particulate C, N, and P were collected on A/E filters and stored and analyzed as for seston. Suspended particle concentrations in each enclosure at the start of each trap deployment were subtracted from trap concentrations before calculating sedimentation rates. Sedimentation was measured at least once in every enclosure during the experiment, so regression analyses of zooplankton effects that were based on data averaged over all dates of the experiment consisted of 12 independent observations (=enclosures).

Zooplankton were sampled every 3–4 days with vertical hauls of a 13-cm diameter 102- μm -mesh net, which was assumed to have an efficiency of 60% based on previous empirical experience (Sarnelle 1992). Samples were preserved in sucrose–formalin (Haney and Hall 1973). Zooplankton were counted and measured at 40 \times in a Sedgwick-Rafter cell. Measurements of body length were made with a digitizer and drawing tube and were used to calculate dry biomass using equations developed for dried Zaca Lake specimens. Zooplankton carbon was assumed to be 45% of dry biomass (Peters 1987).

Results

Model predictions for Zaca Lake—For both the uncoupled and coupled models (Eqs. 1–8), only the parameters e , c , q , K , and v affect predictions about the direction and shape of the effect of zooplankton biomass on sedimentation rate. The removal manipulation was successful in creating a gradient in *Daphnia* abundance without significantly affecting other crustaceans (Fig. 4), so I parameterized the models using published values for e , c , g , and b for *Daphnia*. Carbon-based units were used. Values for e (0.6), c (0.8), and b (0.10 d^{-1}) were taken from Nisbet et al. (1991). A value for carbon-specific grazing rate of *Daphnia* ($g = 0.003 \text{ mg Daphnia C}^{-1} \text{ d}^{-1}$) was calculated by considering that a 2-mm *Daphnia* (body mass $\sim 30 \mu\text{gC}$, based on *Daphnia* from Zaca Lake) has a filtering rate of $\sim 85 \text{ ml d}^{-1}$ (Knoechel and Holtby 1986). The parameters K and v were based on data from Zaca Lake from 1989–1990. Maximum phytoplankton biomass (K) was estimated from maximum chlorophyll a concentrations during March–May. In both 1989 and 1990, maximum chlorophyll a concentration during this time period was $82 \mu\text{g liter}^{-1}$, which translates to $K \sim 2.5 \text{ mgC}$

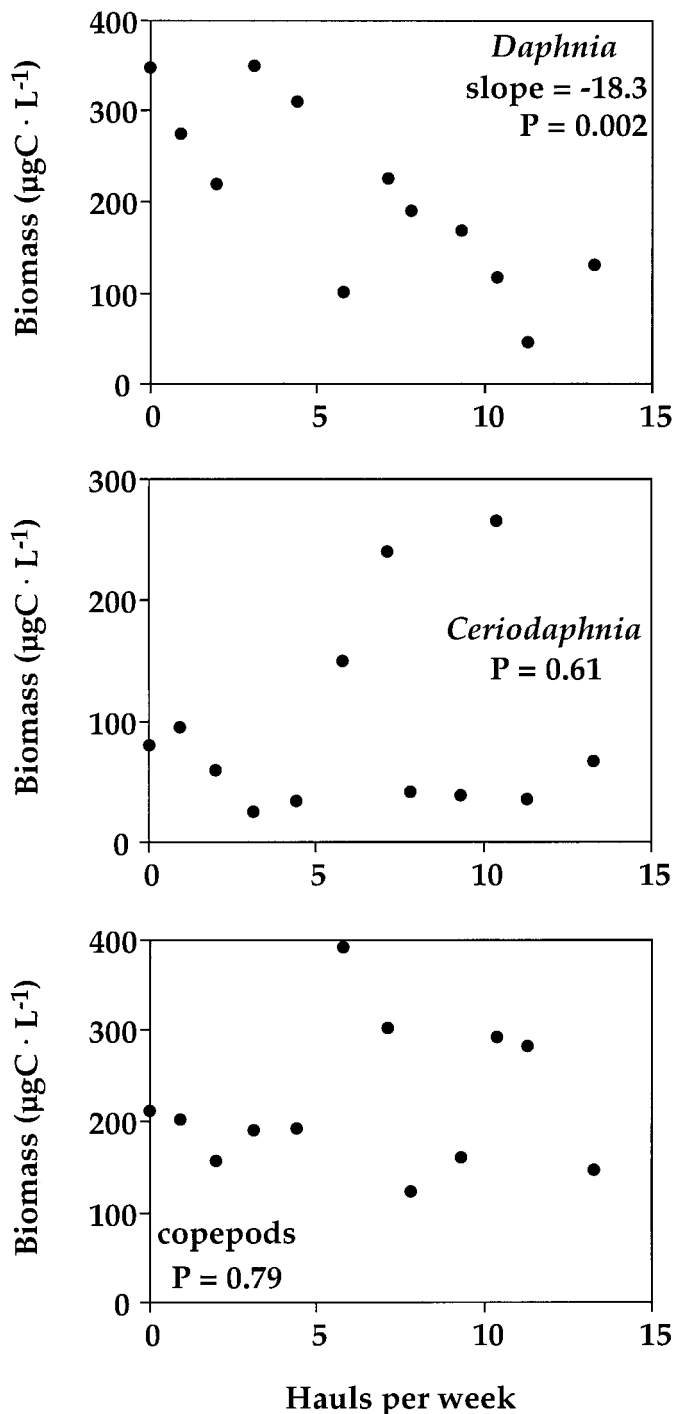


Fig. 4. Effects of the removal manipulation (net hauls per week) on the biomass of crustacean zooplankton in the 1994 enclosure experiment.

liter⁻¹, assuming a chlorophyll:C ratio of 0.033 (Reinertsen et al. 1990). This value for K is similar to the maximum particulate organic C concentration of 2.8 mgC liter⁻¹ found in the lake in 1994.

Sinking loss rates of phytoplankton were estimated based on sedimentation rates of chlorophyll *a* measured in the lake and in enclosures during 1989–1990. These values may be

underestimates because of degradation of chlorophyll in sediment traps, but direct comparisons of chlorophyll-based estimates with estimates derived from cell counts showed good agreement. For the four enclosures analyzed in parallel in 1989, mean sinking loss was similar for the two methods (mean \pm SE for estimates based on chlorophyll and cell counts, respectively: 0.274 ± 0.102 and 0.250 ± 0.121 d⁻¹).

The median sinking loss for 1989–1990 was 0.14 d⁻¹ (range: 0.04 – 1.62 d⁻¹, $n = 34$), and there was congruence between estimates from the lake and estimates from enclosures (lake median: 0.12 d⁻¹, enclosure median: 0.15 d⁻¹). More than 90% of these sinking loss estimates had values ≥ 0.06 d⁻¹. Based on these data, I parameterized the models using values for ν of 0.14 d⁻¹ or 0.06 d⁻¹.

Suitable data with which to estimate the fraction of fecal material exiting the euphotic zone (q) are rare in general and nonexistent for *Daphnia*. Ideally, this fraction could be estimated by comparing the sedimentation rate of fecal material with the rate at which fecal material is produced. Such a comparison was attempted by Ayukai and Hattori (1992) for copepod and euphausiid fecal pellets in an oceanic gyre. They reported a range of 0.001–0.180 for the fraction of fecal material reaching sediment traps set at the base of the euphotic zone (see table 6 of Ayukai and Hattori). These estimates were based on pellet numbers (rather than mass) and so are somewhat crude, but they do agree with data reported by Lane et al. (1994) for a continental shelf system. In the Lane et al. study, fecal pellet production (copepods) was calculated to be 95 mgC m⁻² d⁻¹, whereas pellet flux was estimated as 15 mgC m⁻² d⁻¹, which results in a value of 0.160 for q . *Daphnia* produces amorphous feces rather than compact streamlined pellets, so it is likely that *Daphnia* fecal material sinks more slowly than the fecal pellets of many marine crustaceans. However, the depth of the euphotic zone in Zaca Lake is an order of magnitude smaller than that in the two marine studies cited above, so particles have a shorter distance to travel before being lost from the euphotic zone. Consequently, it is not clear where values of q for *Daphnia* in Zaca Lake fall relative to the range given above. I parameterized the models using $q = 0.001$ and 0.180, a range that is probably wide enough to encompass values likely for *Daphnia* in Zaca Lake.

Predicted relationships between *Daphnia* biomass and sedimentation were identical for the uncoupled and coupled models because of the high productivity of Zaca Lake (Fig. 2, $Z_{\text{max}}^* \gg Z_{\text{opt}}^*$). In general, the models predicted that sedimentation rate should be a negative function of *Daphnia* biomass in Zaca Lake (Fig. 5). Even using $\nu = 0.06$, which is low relative to values typical of Zaca Lake, and $q = 0.180$, which is among the highest estimates currently available and based on large fecal pellets, the models predict that the effect of *Daphnia* should be largely negative. This prediction was tested with the results of the 1994 enclosure experiment.

Experimental results—When the data were averaged over all sampling dates of the 30-d experiment, relationships between *Daphnia* biomass (as set by the removal gradient) and sedimentation rate were suggestive of a negative effect, but regressions were not significant ($P > 0.05$) (Fig. 6). When the data were analyzed separately for each trapping interval,

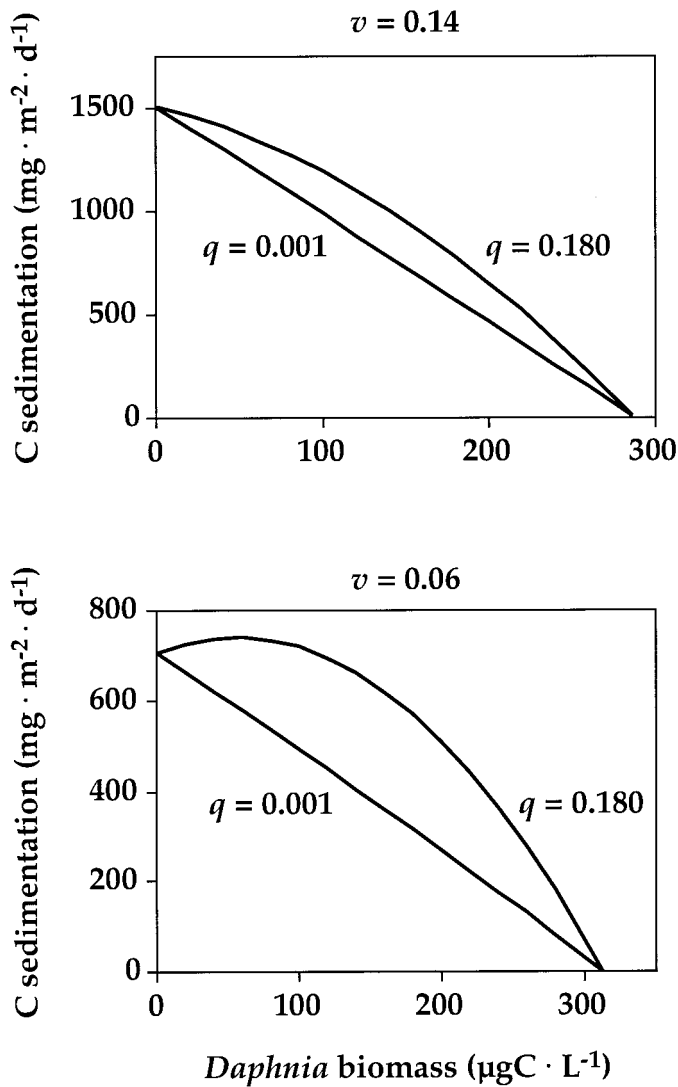


Fig. 5. Predicted effects of *Daphnia* on sedimentation rate (phytoplankton plus fecal material) in Zaca Lake. Parameter values: $r = 1.0 \text{ d}^{-1}$, $K = 2,500 \text{ mgC m}^{-3}$, $D = 5 \text{ m}$, $ec = 0.5$, $g = 0.003 \text{ m}^3 \text{ mgDaphniaC}^{-1} \text{ d}^{-1}$, $b = 0.12 \text{ d}^{-1}$.

slopes of the *Daphnia* effect were always negative (four of four cases), and significant regressions were obtained on the first trapping date ($P = 0.035$, 0.013 , and 0.001 for C, N, and P, respectively) and the last trapping date ($P = 0.046$ for P). In contrast, there were no consistent relationships between sedimentation rates and total zooplankton biomass ($P > 0.59$ in all cases). Total P (dissolved plus particulate) averaged $318 \mu\text{g liter}^{-1}$ across the enclosures and was not affected by the manipulation ($P > 0.20$).

Lake patterns—The relationship between *Daphnia* biomass and sedimentation rate in the lake during 1989–1990 was congruent with the results of the 1994 enclosure experiment. Sedimentation rates at the same level of *Daphnia* biomass tended to be higher in 1989 than in 1990, so I performed an analysis of covariance for the effect of year and *Daphnia* biomass on sedimentation rates of particulate N and

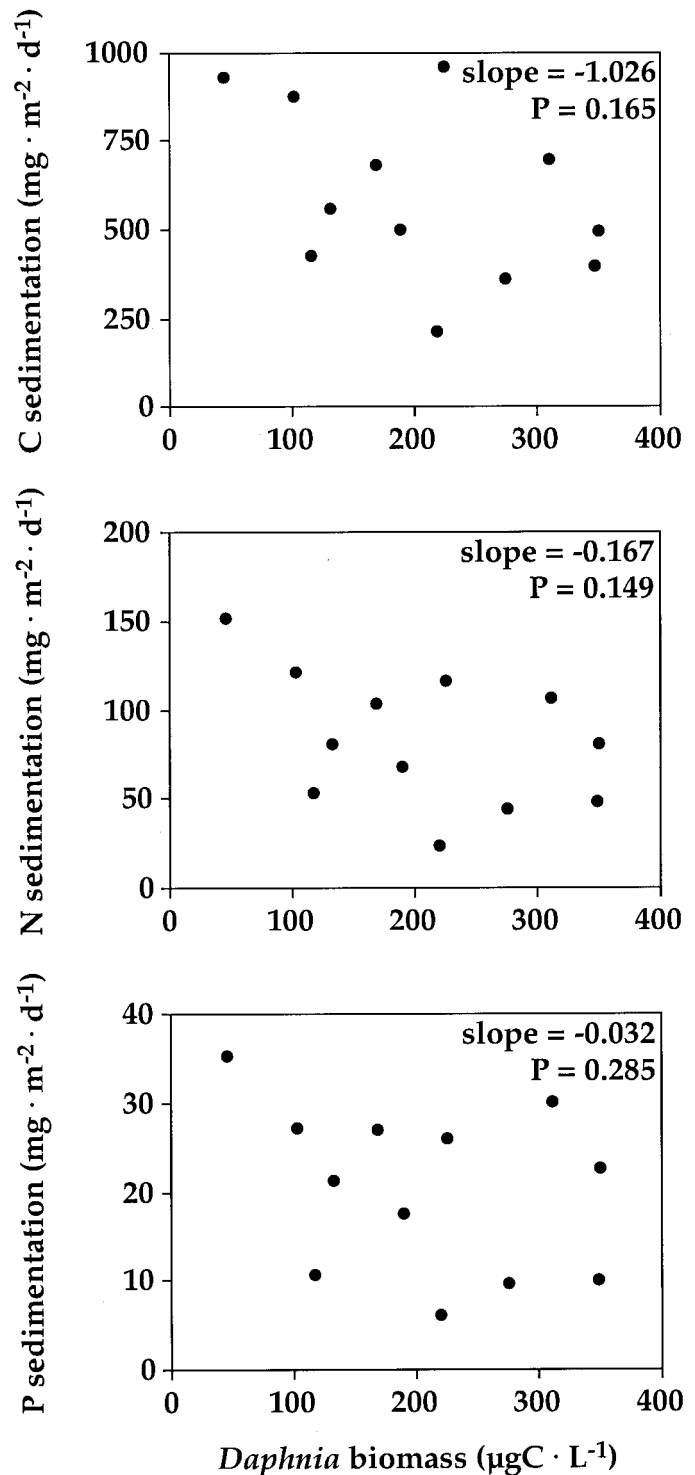


Fig. 6. Effects of *Daphnia* on the sedimentation of carbon, nitrogen, and phosphorus in the 1994 enclosure experiment. Data averaged over all sampling dates.

P. These analyses indicated a significant negative relationship between *Daphnia* biomass and sedimentation for the lake (Fig. 7). The slopes of these relationships were fairly similar to those found for time-averaged data from the en-

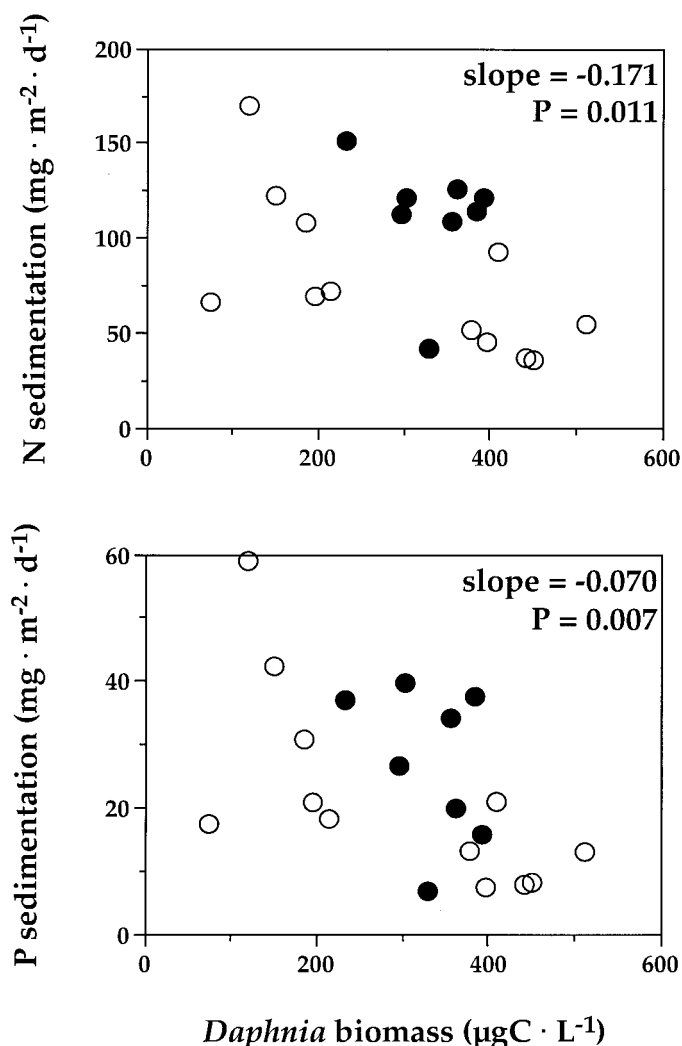


Fig. 7. Relationships between *Daphnia* biomass and the sedimentation of nitrogen and phosphorus in Zaca Lake during 1989 (closed symbols) and 1990 (open symbols). Data are from Sarnelle (1992, 1997). P values are for the effect of *Daphnia* in an analysis of covariance.

closure experiment (Fig. 6), despite differences in methods between 1989–1990 and 1994.

The lake data also showed that *Daphnia* densities in the enclosures were within the range found naturally in the lake (Figs. 6, 7). Zaca Lake is highly eutrophic and had very low densities of zooplanktivorous fish in 1990 (Sarnelle 1993), so high *Daphnia* densities are to be expected. Total biomass of crustacean zooplankton averaged $523 \mu\text{gC liter}^{-1}$ across the enclosures, which is comparable to the predicted value of $477 \mu\text{gC liter}^{-1}$ calculated using Hanson and Peters' (1984) regression of zooplankton biomass versus total P for lakes and average total P in the enclosures.

Discussion

Theory—The models here described were built upon the simple foundation provided by Aksnes and Wassmann

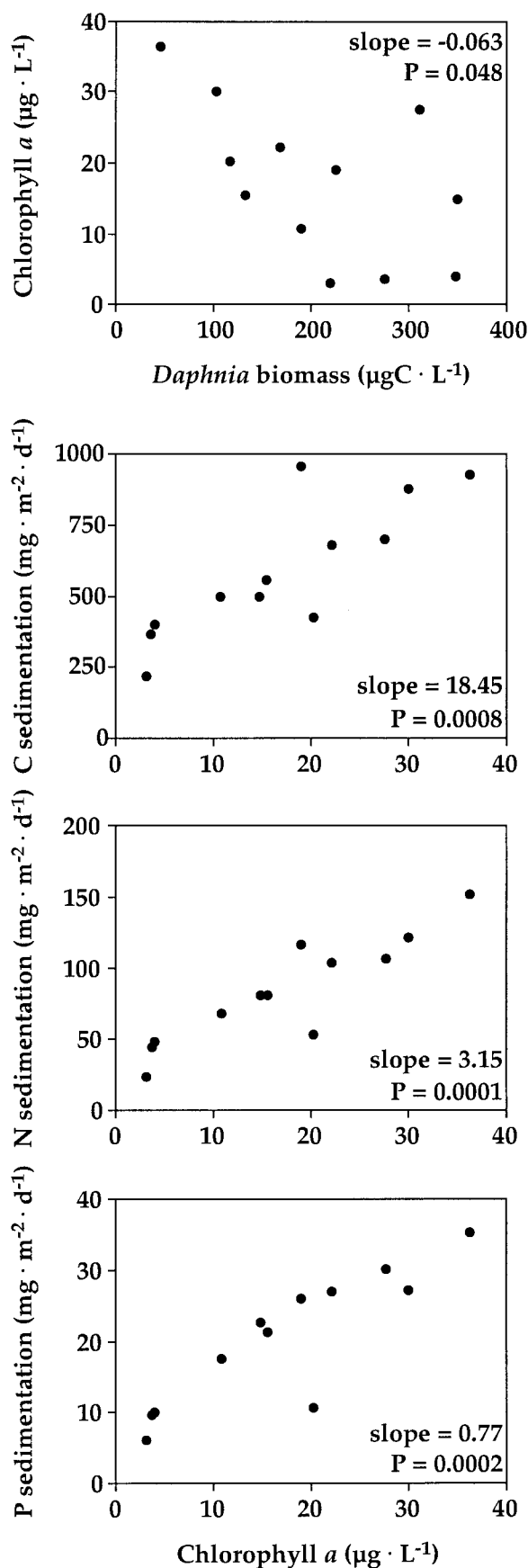
(1993). In their model, only one type of relationship is possible: sedimentation declines to an asymptote with increasing zooplankton biomass. (However, this relationship is not readily apparent because of errors in eqs. 2 and 5 of Aksnes and Wassmann. The correct equations are, respectively, $dB/dt = B[\mu - (w_s/D) - gH]$ and $P_e = \{[w_s + (1 - \alpha)G]/(w_s + G)\}P_e$.) Given that the role of zooplankton is viewed as positive or negative in different studies, there is a clear need for more versatile models, such as the ones described here and by Elser et al. (1995a). The model described by Elser et al. (1995a) incorporates a similar conceptualization about the role of fecal versus direct phytoplankton sinking and can predict positive and negative but not unimodal responses of sedimentation to changes in zooplankton abundance.

In the models of Aksnes and Wassmann (1993) and Elser et al. (1995a), the dynamics of phytoplankton and zooplankton were uncoupled. Neither study included an explicit accounting of the possibility that zooplankton biomass might be influenced by the growth and loss rates of the phytoplankton, in particular sinking loss, v . This point is critical because such coupling may confound attempts to relate sedimentation rates to zooplankton biomass using nonexperimental data. If v influences both sedimentation rate and zooplankton biomass, cause and effect inferences based on relationships between these two variables may be misleading.

Further, the mass-balance modeling approach employed by Elser et al. (1995a) was based on the implicit assumption that primary production is not influenced by zooplankton biomass, an assumption that may be violated in many cases (Brett et al. 1994; Elser et al. 1995b). This assumption is especially problematic if relationships between zooplankton biomass and export ratio (sedimentation rate divided by total primary production), rather than between zooplankton biomass and sedimentation rate, are examined for patterns. Given that a critical element of the zooplankton effect on sedimentation is the reduction of phytoplankton biomass by grazing and that zooplankton populations might be expected to respond dynamically to changes in algal growth and loss, an approach based on population dynamics, as followed here, may provide unique insights.

Experimental results—Despite considerable unexplained variation, the results of the enclosure experiment suggested that increases in *Daphnia* biomass negatively affect sedimentation rates in Zaca Lake (Fig. 6). This conclusion agrees with the results of a previous enclosure experiment performed in the lake using different methods (Sarnelle 1992) and, more importantly, confirms model predictions. Reasonably good quantitative agreement was obtained between model output and experimental data for C (Figs. 5, 6), even though the model was parameterized with data from 1989–1990 and tested with data from 1994.

Negative effects of zooplankton on sedimentation are indicative of a system where direct sinking of phytoplankton dominates flux and zooplankton act to reduce overall flux by reducing suspended phytoplankton concentrations and thus direct phytoplankton sedimentation. In such systems, there should be a negative effect of zooplankton on phytoplankton biomass and a positive relationship between sedimentation rate and phytoplankton biomass. Both of these



expectations were confirmed by experimental results (Fig. 8). These results should not be interpreted to mean that *Daphnia* does not enhance the sinking velocities of particles in this lake. The effect of *Daphnia* on average sinking velocities of C, N, and P (m d^{-1} , sedimentation rate divided by suspended concentration) was significantly positive in the enclosures (C, N, P: $P < 0.06, 0.03, 0.001$). This effect could be the result of packaging of phytoplankton into fecal material (Bloesch and Bürgi 1989) or of grazing-induced changes in phytoplankton sinking velocities. These changes in sinking velocities could be effected, for example, via shifts toward larger, nonmotile algae (Larocque et al. 1996) or changes in phytoplankton vertical distribution. Regardless of the underlying mechanism, the positive effect of *Daphnia* grazing on particle sinking velocities was overridden by the negative effects of *Daphnia* on phytoplankton biomass and direct phytoplankton sedimentation in Zaca Lake.

Few researchers have attempted to experimentally isolate the effect of zooplankton on sedimentation rates, making it difficult to generalize from previously published reports. However, the available experimental data do not contradict model predictions. Negative effects of zooplankton have been reported in eutrophic Zaca Lake (Sarnelle 1992; present study) and Greifensee (Bürgi et al. 1979), whereas positive effects of zooplankton have been found in a series of enclosure experiments conducted in oligomesotrophic Lake Lucerne (Bloesch and Bürgi 1989). Thus, there is very preliminary evidence supporting model predictions that positive effects should be more likely in low-productivity systems (Fig. 2).

All previous manipulations of zooplankton biomass have utilized only two treatment levels. Given the theoretical potential for unimodal responses of sedimentation (Fig. 1), there is a need for experiments that establish gradients of zooplankton biomass. In practice, however, it may be difficult to detect unimodal responses because they may only appear at high grazer densities (as per models with a saturating functional response) in some systems and because high error variance is typical of large-scale field experiments. Error variance associated with the effect of *Daphnia* on sedimentation rates was particularly high in the 1994 experiment (Fig. 6) and was related to high variability in the effect of *Daphnia* on phytoplankton biomass (Fig. 8). The highly variable effect of *Daphnia* on phytoplankton biomass was surprising, given that a previous manipulation of *Daphnia* in this lake showed highly significant effects on phytoplankton biomass (Sarnelle 1993). In contrast, relationships between phytoplankton biomass and sedimentation rates showed relatively little error (Fig. 8).

It is tempting to consider results from studies in which the abundance of zooplanktivorous fish was manipulated (Langeland et al. 1987; Carpenter et al. 1988; Mazumder et

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Fig. 8. Top: Effect of *Daphnia* on phytoplankton biomass (as chlorophyll *a*) in the 1994 enclosure experiment. Bottom: Relationships between phytoplankton biomass and sedimentation rates in the 1994 enclosure experiment. Data were averaged over all sampling dates.

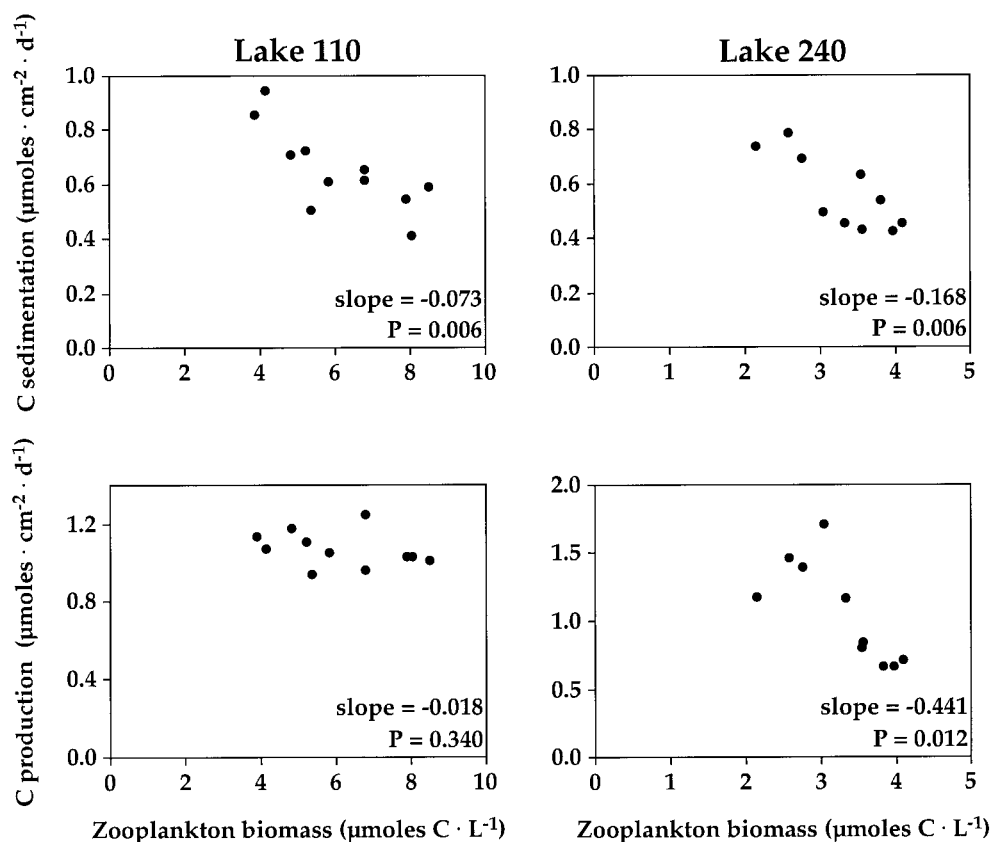


Fig. 9. Reanalysis of data from Lakes 110 and 240 reported by Elser et al. (1995a). Top: Relationships between zooplankton biomass and the sedimentation rate of carbon. Bottom: Relationships between zooplankton biomass and primary production. Data were extracted from figs. 3–6 of Elser et al. (1995a) with a digitizer.

al. 1989; Reinertsen et al. 1990; Larocque et al. 1996) in a synthesis of the effects of zooplankton on vertical particulate flux. These experiments, however, are difficult to interpret in the present context because fish can have direct effects on the nutrient environment and phytoplankton species composition (Vanni and Layne 1997), in addition to effects mediated via changes in zooplankton grazing. In model terms, fish addition may increase K and alter v (in addition to affecting Z), two parameters that strongly influence the shape and direction of zooplankton effects on sedimentation. In addition, fish may favor copepods over cladocerans (Christoffersen et al. 1993), which could affect q , the fraction of fecal material that exits the euphotic zone, because copepod fecal pellets are highly packaged relative to cladoceran feces. Consequently, fish manipulations may involve a host of pathways that can qualitatively modify the functional relationship between zooplankton biomass and sedimentation.

Lake patterns—The negative relationships between *Daphnia* biomass and sedimentation rate in the lake (Fig. 7) are reassuring because they help to validate the enclosure results and rule out experimental artifacts. However, problems may arise when attempting to interpret patterns in nonexperimental data in the absence of contemporaneous experiments. For example, Elser et al. (1995a) contrasted the relationship between zooplankton biomass and export ratio (sedimentation

rate divided by total primary production) in two low-productivity lakes that differed in food-web structure and physical mixing. Although export ratio is a useful concept for understanding the fate of primary production (Berger et al. 1989), interpretational problems may occur when relating this ratio to other variables, because variation in the export ratio can be driven by variation in sedimentation rate or by variation in total production. Elser et al. (1995a) found opposite relationships between zooplankton biomass and export ratio for the two lakes they studied. Although it would be reasonable to conclude from their data that the zooplankton in these two lakes might have different effects on the fraction of total production that is exported, it is not reasonable to conclude that “zooplankton have qualitatively different effects on sedimentation processes” in these two lakes (Elser et al. 1995a, p. 166). Reanalysis of their data shows that the relationship between zooplankton biomass and sedimentation rate was negative in both lakes, despite differences in food-web structure and mixing (Fig. 9). Thus, the influence of zooplankton on particle flux in these lakes was qualitatively similar to that found in Zaca Lake. The contrasting patterns in export ratios reported by Elser et al. (1995a) were driven by contrasting relationships between zooplankton biomass and total production in these two lakes (Fig. 9), not by qualitative differences in sedimentation response. Consequently, it seems advisable to avoid basing

conclusions on correlations of zooplankton biomass with export ratio without also separating the influences of zooplankton on sedimentation rate and primary production.

Negative relationships between primary production and zooplankton biomass are not surprising (Brett et al. 1994; Elser et al. 1995b) and suggest that it is important to explicitly consider the coupling between phytoplankton and zooplankton dynamics when trying to understand zooplankton effects on sedimentation rates and the fraction of primary production that is exported. Use of models that are based on population dynamics thus may be of value in the study of patterns in ecosystem function. Likewise, it is important to be mindful of the potential for zooplankton biomass to be dynamically responsive to changes in phytoplankton sinking velocities (Eqs. 4, 8) when attempting to interpret cause and effect from descriptive data.

Conclusions—The theory provided a reasonably accurate prediction despite its simplicity and equilibrium assumptions. Notably absent from the models were explicit functions describing mineralization of sinking particles, feeding on and disaggregation of fecal material, vertical migration, aggregation of phytoplankton, etc. These processes cannot all be included in a tractable general model, but their effects can be examined in a simple way by varying two model parameters, q and v . For example, mineralization by particle-bound bacteria, and fecal consumption and vertical migration by metazoans will affect q , the fraction of fecal material that becomes sediment. Likewise, processes that lead to phytoplankton aggregation will affect v , the sinking loss rate of the phytoplankton (e.g., v could be made a function of phytoplankton or zooplankton biomass). It seems reasonable initially to quantify the net effects of these complications using simple parameters as a guide (i.e., measure the fraction of fecal material that becomes sediment and the net sinking loss of phytoplankton) before attempting a detailed analysis of all the intervening mechanisms. It is debatable whether exhaustive measurements of all the processes subsumed within the basic parameters will lead to more accurate predictions of the effect of zooplankton.

Both the theoretical and experimental analyses reported here do not account for the contribution of zooplankton-derived material (carcasses, exuviae, etc.) to overall vertical flux. This simplification was made because of a lack of information with which to parameterize models and the difficulty of separating live animals from dead zooplankton tissue in sediment trap samples. Sedimentation rates for C, N, and P were based on particles $<149 \mu\text{m}$ to correspond to particle concentrations in the water column. This size fraction should adequately represent sinking phytoplankton and fecal material but may exclude zooplankton-derived material. The implications of assuming that zooplankton-derived material is negligible can only be adequately assessed with further research.

Peinert et al. (1989, p. 43, emphasis added) stated that “very little is known about the effects of changes in the physical environment, alterations of food supply and life cycles on sedimentation patterns, and the respective impacts are not easily separated.” Mathematical models provide a transparent logic for integrating these multiple influences.

For example, effects of the physical environment may be expressed in v , the rate of direct phytoplankton sinking. Changes in the food supply impact zooplankton assimilation (e) and perhaps also fecal sinking rate (which affects q). Life cycle influences can be examined in a simple way via how they ultimately affect zooplankton biomass. At present, the greatest limitation to application of the theory may be the lack of information about the fraction of fecal material that exits the euphotic zone (q). I used values based on two studies of marine zooplankton because data for *Daphnia* feces are nonexistent and difficult to obtain. Given that high values of q are needed for the models to predict nonnegative (unimodal or positive) effects of zooplankton on sedimentation, the upper value of q that I used needs to be verified by measurements of q for *Daphnia* fecal material.

The models described here are intended as a simple, testable theory to guide examinations of the effect of zooplankton on sedimentation in both freshwater and marine systems. Further testing with field experiments and descriptive data would increase confidence in the theory's applicability, but such tests should ideally be based on parameter estimates that are independent of the data used for testing. When independent tests are impractical, simply measuring critical parameters identified by the theory should improve our ability to interpret relationships between zooplankton biomass and sedimentation in descriptive data. If the theory is a useful guide to these parameters, it could be applied to predict where and when zooplankton are likely to have positive, negative, or unimodal effects on vertical particulate flux. This application may be valuable in systems where it is impossible to manipulate zooplankton at scales large enough to measure the response of sedimentation.

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