

Effects of zooplankton on sedimentation in pelagic ecosystems: Theory and test in two lakes of the Canadian shield

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Abstract. A simple heuristic theory based on conservation of matter and describing the fate of autotrophic production in pelagic ecosystems was developed to assist in conceptualizing how zooplankton affect sedimentation processes in lakes and oceans. The theory predicted that effects of zooplankton on the fraction of autotrophic incorporation that sediments (the “export ratio”) will be a function of factors related both to zooplankton digestion and egestion and to tendencies of particulate matter to sediment directly prior to mineralization. As a result, effects of zooplankton grazing on the export ratio were predicted to be site-dependent, a function of physical conditions and zooplankton communities characterizing an ecosystem. The theory was tested by monitoring autotrophic production of C, N, and P, sedimentation of C, N, and P, and zooplankton biomass in two lakes of the Canadian shield characterized by contrasting morphometry and food-web structure. In Lake 110, a small elongate lake protected from wind exposure, export ratios of C, N, and P declined strongly with zooplankton biomass. In contrast, in L240, a larger lake with considerably greater wind exposure, export ratios increased with zooplankton biomass. These results were consistent with predictions of our theory that effects of zooplankton on sedimentation processes will depend on the tendency of particulate matter to directly sediment relative to the tendency of egested materials to sediment. However, no significant differences in relationships between export ratios for C, N, and P and zooplankton biomass were found.

Key words: export ratio, grazing, nutrients, sedimentation, zooplankton

Introduction

In contrast to pronounced horizontal variability of aquatic benthic and most terrestrial ecosystems, the primary axis of spatial heterogeneity in pelagic ecosystems is vertical (Harris 1986). This vertical heterogeneity is created by density layering due to differences in temperature and/or salinity. Thus, processes that affect vertical movement of water, organisms, and materials are a central focus of biogeochemical studies of pelagic ecosystems. One process that leads to substantial downward fluxes of materials in pelagic ecosystems is sedimentation of suspended particulate matter. Sedimentation of particulate matter is critically important in pelagic ecosystems for several reasons. First, sedimentation is a potentially significant loss of key limiting nutrients that

support phytoplankton production in lighted surface layers (Capblancq 1990). Second, sedimentation can be a major flux of material to deep waters where materials may be stored for considerable periods (e.g., in the deep ocean, Walsh et al. 1981; Pace et al. 1987) or further metabolized, altering chemical properties of deep water layers. For example, high rates of organic matter sedimentation and subsequent bacterial decomposition can lead to deep-water oxygen depletion and shifts in oxygen- and redox-sensitive processes (Suess 1980; Bishop 1989). Third, sedimenting material contributes the bulk of potential food for profundal benthos (Parsons et al. 1977; Smetacek 1984). Processes that affect rates of sedimentation, and biochemical and elemental composition of sedimenting material, are therefore critical in supporting profundal benthos production.

While many studies have evaluated the roles of physical properties of the water column and characteristics of suspended particles in influencing sedimentation rates in marine and freshwater ecosystems (Smayda 1970; Reynolds 1984), our understanding of the role of trophic interactions such as zooplankton grazing in influencing sedimentation is incomplete. This topic has received particular attention in marine ecosystems, where rapidly-sinking zooplankton fecal pellets are considered to be a primary means by which sinking particulate material reaches the deep ocean prior to being mineralized (Knauer et al. 1979; Angel 1984; Valiela 1991; but see Silver & Gowing 1991). Such zooplankton-mediated fluxes have been shown to have pronounced biogeochemical effects even in relatively shallow marine environments (Parsons et al. 1977). Recent studies in lakes have also evaluated the role of zooplankton in influencing sedimentation of particulate elements. In particular, several studies have shown that changes in zooplankton community structure resulting from alterations in intensity of fish predation can produce substantial changes in sedimentation processes (Uehlinger & Bloesch 1987a,b; Bloesch & Burgi 1989; Mazumder et al. 1989; Samelle 1992). Various mechanisms may determine effects of zooplankton on sedimentation. For example, copepod zooplankton encapsulate their fecal pellets in a distinct peritrophic membrane; this enhances pellet integrity and potentially increases the likelihood that pellets will sink out of the water column prior to microbial degradation (Ferrante & Parker 1977; Honjo & Roman 1978). In contrast, other zooplankton, such as cladocerans (e.g. *Daphnia*), egest a loose aggregate that is subject to breakage and rapid bacterial colonization. Nevertheless, even loose fecal production by cladocerans may enhance sedimentation rates by transforming small, slow-sinking food particles into larger, more rapidly sinking particles (Uehlinger & Bloesch 1987b). An additional mechanism of zooplankton effects on sedimentation may involve differential elemental requirements of zooplankton taxa. It is now known that many

copepods have characteristically high body N:P ratios while cladoceran taxa, especially *Daphnia*, have low body N:P ratios (Andersen & Hessen 1991; Sterner et al. 1992). If elementally-contrasting zooplankton species differentially assimilate N and P during digestion then contrasting zooplankton species might produce fecal matter with a differing elemental constitution, thus disproportionately affecting the sedimentation of N and P via their fecal production.

Despite the work just described, our view of the role of zooplankton in influencing sedimentation processes is still somewhat unclear (Angel 1989; Peinert et al. 1989; Silver & Gowing 1991). Zooplankton grazing is alternately seen as enhancing or retarding transport of particulate matter out of surface water layers under various conditions (Paffenhöfer & Knowles 1979; Suess 1980; Williams & von Bodungen 1989). Conditions under which these qualitatively different effects occur are not clearly defined and remain a research priority (Williams & von Bodungen 1989). The purpose of the work reported here was two-fold. First, we wished to develop a heuristic theory of sedimentation and grazing as a formal framework for understanding how zooplankton might affect sedimentation of particulate matter produced by phytoplankton in surface layers. Second, we attempted to test general predictions of this theory by monitoring dynamics of phytoplankton production, sedimentation, and zooplankton in two lakes of contrasting morphometry, food web structure, and zooplankton community composition.

Theory development and predictions

Suspended particulate matter will sink out of the water column unless kept in suspension by turbulent water motion. These direct losses of particle-bound elements are potentially diminished if elements comprising sinking particulate matter are returned to solution before loss from the water column. Losses of particulate production may also occur via indirect means, when phytoplankton are grazed by zooplankton and non-assimilated matter is egested and sinks, subject to potential mineralization prior to loss from the surface waters. This simple description of processes contributing to particulate sedimentation underlies our theoretical consideration of effects of zooplankton on sedimentation in pelagic ecosystems. We develop this theory primarily as a heuristic device to organize formally a strategy of thinking about these processes and the theory is likely incomplete and overly simplistic. We specifically focus on sedimentation processes affecting C, N, and P in a stratified water column during the growing season and do not attempt to generate predictions regarding the role of sedimentation in whole-ecosystem nutrient budgets over annual or longer time scales or regarding long-term accumulation of sediments. We

also focus only on the fate of pelagic autotrophic production and do not incorporate import of allocthonous materials or transport of littoral zone production in our approach.

The model we describe below is based on dichotomies describing the fate of autotrophic production in the water column. The approach bears a superficial resemblance to the bifurcation model of export production of Legendre & Le Fèvre (1989). However, the resemblance is in many respects a superficial one, as our model is largely based on mass balance of material transfers whereas Legendre and Le Fèvre's approach involves dichotomies of fundamental processes and conditions affecting sedimentation that are not necessarily directly constrained by mass balance (e.g., dominance of small vs. large phytoplankton, grazing by large zooplankton vs. microzooplankton). Our model also resembles in some ways that of Aksnes & Wassman (1993) who presented an analytical model of the effect of zooplankton grazing on export production. The primary goal of this model was to understand variation in export ratio as a function of total production. However, our primary goal was to understand the nature of the effect of zooplankton on sedimentation as a function of water column physical conditions. In addition, our effort is distinct from theirs in that we delineate the fate of grazed production into three components (assimilated by zooplankton, unassimilated by zooplankton and lost as intact fecal pellets, or unassimilated by zooplankton by mineralized during sinking) while they do not distinguish between grazed production that is retained in the water column due to assimilation or due to mineralization by bacteria. Thus our approach may be more suitable for specific consideration of physiologically-based perspectives on the fate of zooplankton grazed production. This distinction is discussed more extensively later in the paper.

Using the principle of mass balance for all autochthonous production, consider the fate of phytoplankton production in the water column of a lake or ocean (Fig. 1). By "production rate" we refer to the rate at which C, N, or P is incorporated into phytoplankton biomass due to autotrophic activity. Let P_x be total net production rate of an element (x) per unit area during an interval. This production can be grazed or not be grazed:

$$P_x = gP_x + (1 - g)P_x, \quad (1)$$

where g is fraction of production grazed. g will be a function of total zooplankton biomass and zooplankton species composition, as well as of phytoplankton biomass (when algal biomass exceeds the incipient limiting concentration (ILC) of the grazers) and susceptibility of phytoplankton to grazing and of environmental factors such as temperature (Sterner 1989).

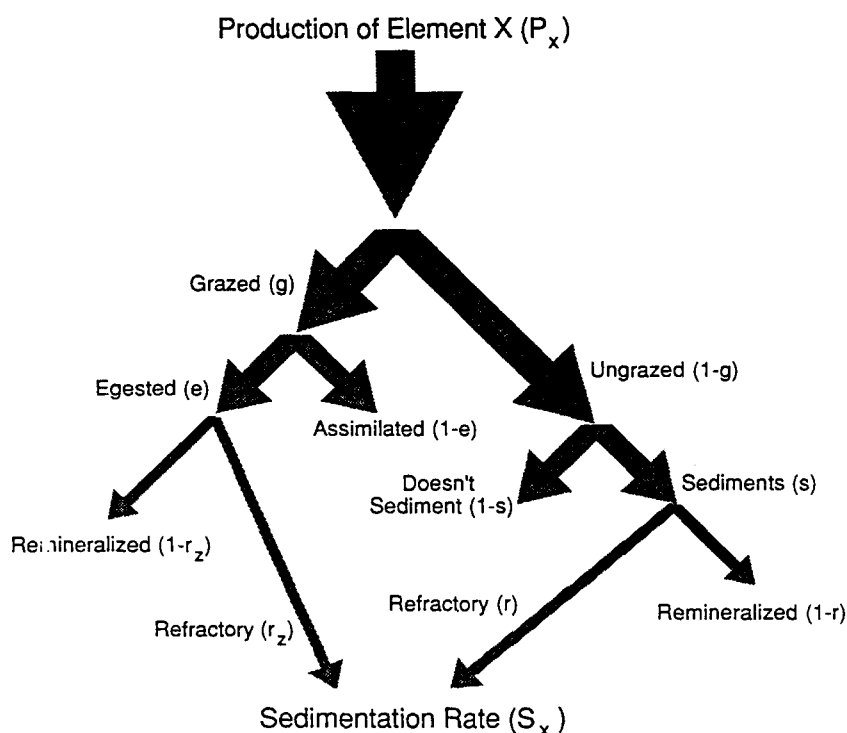


Fig. 1. Illustration of the fate (with associated coefficients) of autotrophic production in a pelagic ecosystem. The bottom arrows represent fluxes contributing to sedimentation and show that one component arises from direct sedimentation of ungrazed production and the other from sedimentation of unassimilated, grazed production.

Of ungrazed production some fraction will sediment (s_x) and some will not ($1 - s_x$):

$$P_{t,x} = gP_x + s_x(1 - g)P_x + (1 - s_x)(1 - g)P_x. \quad (2)$$

Physical factors such as mixed-layer depth, wind intensity, and water column turbulence are likely to affect s_x , as would characteristics of the phytoplankton themselves, such as their size distribution and specific gravity. Aggregation of small algal cells into larger particles (e.g., "marine snow") also affects direct sedimentation (Alldredge & Silver 1988).

Of sedimenting, non-assimilated production a fraction will be refractory and not be mineralized in the water column (r_x) but some will be mineralized ($1 - r_x$):

$$P_{t,x} = gP_x + r_x s_x(1 - g)P_x + (1 - r_x)s_x(1 - g)P_x + (1 - s_x)(1 - g)P_x. \quad (3)$$

The refractory nature of sinking particulate matter will likely depend on its biochemical and elemental composition as well as abundance and activity of bacteria (as modulated by factors such as temperature and other bacterial limiting factors). In our approach the term $(1 - r_x)$ refers to the *net* fraction of sinking particulate matter that is remineralized; this incorporates the possibility that particulate matter will be colonized by bacteria that may extract elements from particulate matter and incorporate them into their own biomass, without releasing them to the environment. A possible complicating factor that should nevertheless be considered is that particle-associated bacteria might extract inorganic nutrients from the water column during sedimentation. This would clearly raise the apparent r_x for element x .

Of ingested production, a fraction will be egested (e_x) and the rest $(1 - e_x)$ will be "assimilated" (taken across the gut wall):

$$P_x = e_x g P_x + (1 - e_x) g P_x + r_x s_x (1 - g) P_x + (1 - r_x) s_x (1 - g) P_x + (1 - s_x) (1 - g) P_x. \quad (4)$$

e_x likely depends on a number of factors, including identity of dominant zooplankton species and their growth efficiency, various aspects of digestive processes (including differential assimilation, discussed below), and overall food concentration (DeMott 1989).

Of egested production, a fraction will be refractory ($r_{z,x}$) and will sediment without mineralization or leaching while the rest $(1 - r_{z,x})$ will be released to inorganic form via bacterial mineralization or leaching:

$$P_x = (1 - e_x) g P_x + r_{z,x} (e_x) g P_x + (1 - r_{z,x}) (e_x) g P_x + r_x s_x (1 - g) P_x + (1 - r_x) s_x (1 - g) P_x + (1 - s_x) (1 - g) P_x. \quad (5)$$

Whether or not egested material is mineralized before sedimenting is likely to be influenced by properties of the egested material itself that influence its sinking velocity (Fowler & Knauer 1986; Alldredge et al. 1987), relative importance of easily leached nutrients, and susceptibility to microbial proliferation (pellets vs. loose feces, discussed above), its biochemical and elemental make-up relative to bacterial requirements, as well as by numerous factors influencing microbial activities (temperature, alternative substrates) (Honjo & Roman 1978). We point out that in the approach developed here "coprophagy" (reingestion of egested fecal material, with potential assimilation of residual nutrients; Paffenhöfer & Strickland 1970) and "coprorhexy" (breakage of fecal pellets by zooplankton, potentially enhancing mineralization; Lampitt et al. 1990) are included within processes parameterized by $r_{z,x}$. Note that, as for r_x , $r_{z,x}$ also should be interpreted in terms of the net outcome of bacterial remineralization and uptake of elements.

In equation (5), the terms in **bold face** potentially contribute to sedimentation. So, sedimentation rate of element x (S_x) per unit area is given by the expression:

$$S_x = r_{z,x}e_xgP_x + (r_x)s_x(1 - g)P_x. \quad (6)$$

As defined, S_x does not include direct sedimentation of bacterial cells not associated with particles or sedimentation of materials produced during secondary production. Note that for any given time interval we can express the sedimentation of element x as a fraction of element incorporated by autotrophic activity during that interval. In prior studies (Eppley & Peterson 1979; Baines & Pace 1994), this metric is referred to as the "export ratio" (ER) and can be defined for any element x (ER_x):

$$ER_x = (S_x/P_x) = r_{z,x}e_xg + (r_x)s_x(1 - g), \quad (7)$$

which simplifies to:

$$ER_x = r_x s_x + g(r_{z,x}e_x - r_x s_x). \quad (8)$$

Note that this expression defines a relationship between export ratio and grazing intensity (g) in which ER_x is a linear function of g with a Y-intercept of $r_x s_x$ and a slope of $(r_{z,x}e_x - r_x s_x)$.

Equation (8) formalizes the expected relationship between sedimentation processes and grazing intensity and makes explicit the implicit joint dependence of sedimentation effects of zooplankton on relative tendencies for grazed and ungrazed production to sediment prior to mineralization. To provide a more tangible interpretation of these relationships, we next develop a set of alternative scenarios describing potential field situations involving zooplankton of different types and activities and evaluate predicted relationships between grazing intensity and ER_x that apply.

Microconsumer scenario

In this situation all grazing is done by microconsumers (ciliates, microflagellates, etc.), which produce small, slowly sinking, rapidly mineralized feces (i.e., $r_{z,x}$ approaches zero). In this situation, equation (8) simplifies to:

$$ER_x = r_x s_x + g(-r_x s_x)$$

or,

$$ER_x = r_x s_x - r_x s_x g. \quad (9)$$

In this situation, the export ratio should be $r_x s_x$ when there is no grazing ($g = 0$) and approach zero for intense grazing (as g approaches 1 and all production

is grazed). Thus, the theory predicts that under heavy microconsumer grazing sedimentation losses are minimal and the water column efficiently retains materials.

Macroconsumer scenarios: Copepods vs. cladocerans

Differences in the nature of egested material between major zooplankton groups (such as copepods and cladocerans) can also be incorporated in our approach. For example, cladocerans like *Daphnia* produce loose fecal aggregates that are subject to breakage, slow sinking, and rapid mineralization. Predicted effects of such consumers on sedimentation may approach those described in the microconsumer scenario. In contrast, encapsulated pellets of copepods have high sinking rates and are more resistant to microbial breakdown; thus, for copepod-dominated zooplankton $r_{z,x}$ may approach 1 and equation (8) simplifies to:

$$ER_x = r_x s_x + g(e_x - r_x s_x). \quad (10)$$

Thus, when there is no grazing ($g = 0$), $ER_x = r_x s_x$ (as above), but when grazing by copepods is intense ($g = 1$), $ER_x = e_x$. Thus, when copepods dominate, export ratio may increase or decrease with g depending upon the relative magnitudes of $r_x s_x$ and e_x :

- if $r_x s_x = e_x$, then there will be no relationship between ER_x and g ;
- if $r_x s_x > e_x$, then ER_x will *decrease* with g ;
- if $r_x s_x < e_x$, then ER_x will *increase* with g .

This result emphasizes the simultaneous dependence of sedimentation effects of zooplankton on digestive physiology (which affects e_x) and the physical environment in which they live (which affects s_x). Zooplankton communities in nature are unlikely to be completely dominated by either cladocerans (or similar) or copepods; in other words, it more likely that $r_{z,x}$ will fall between 0 and 1. In this more general case, the nature of the relationship between ER_x and g is dependent upon the sign of the term $(r_{z,x}e_x - r_x s_x)$.

The predicted joint dependence of export ratio on zooplankton grazing and hydrodynamic conditions is similar to patterns predicted by the bifurcation model of “new vs. recycled” production by Legendre & Le Fèvre (1989). Their conceptual model predicts that the importance of “export production” (i.e., “new production”, which is available to sediment) will be high under conditions that enhance direct sinking of autotrophic production or increase grazing by macrozooplankton. However, our prediction that export ratio may increase or decrease with zooplankton grazing is in contrast to the results of Aksnes & Wassman’s (1993) analysis. Their model predicted that export ratio scales hyperbolically with grazing intensity and thus that there should only be

regions of grazing intensity where ER_x increases or is invariant with increasing grazing intensity. Several considerations are relevant in this regard. First, in the Aksnes and Wassman model, grazing intensity (*their* “G”) is the product of the biomass-specific filtering rate, zooplankton biomass, and mixed-layer depth. Thus, water-column mixing processes that affect mixed layer depth and thus also the probabilities of direct sedimentation and sedimentation of egested materials are somewhat confounded with grazing intensity and complicate interpretation. Second, one of primary predictions of the model of Aksnes and Wassman is of a U-shaped relationship between export ratio and total production, in which the descending portion of the relationship is attributed to increasing grazing pressure with a constant assimilation efficiency and the ascending portion is ascribed to a maximization of grazing pressure accompanied by decreasing assimilation efficiency. Thus, the decline or increase in export ratios with zooplankton biomass observed in our study lakes (see below) might have occurred if zooplankton biomass and total production were significantly correlated in our systems and if productivity variation in L110 and L240 lie in different portions of the predicted U-shaped curve. Both possibilities are unlikely, as total production and zooplankton biomass do not co-vary in either lake (L110: Fig. 3 vs. Fig. 5; L240: Fig. 5 vs. Fig. 6) and levels of production are similar in both systems and do not nearly approach the values driving variations in export ratio delineated by Aksnes and Wassman’s model.

Macroconsumer scenarios: Stoichiometric implications

Species-dependent differences in body N:P ratios have potential implications for sedimentation processes explored here because of the possibility that digestive processes might lead to differential transport of elements (C, N, P) across the gut wall and thus to potential differences in e_x when zooplankton are dominated by elementally-contrasting species. According to equation (8), efficient utilization of food elements (i.e., low values of e_x) will tend to lead to situations in which export ratios decline with increasing zooplankton grazing. Thus, the theoretical framework developed here provides a means for assessing stoichiometric implications of zooplankton grazing on sedimentation of biologically-important elements such as C, N, and P, as well as for assessing whether processes leading to direct sedimentation differ for different elements.

Consider effects of zooplankton on sedimentation of N and P, in which:

$$ER_N = r_{NS}N + g(r_{z,N}e_N - r_{NS}N)$$

and

$$ER_P = r_{PS}P + g(r_{z,P}e_P - r_{PS}P).$$

The relative tendency of N and P to directly sediment is given by the ratio of the intercepts (I_x) estimated from relationships between ER_N and g and ER_P and g :

$$I_N/I_P = r_{NsN}/r_{PsP}. \quad (11)$$

If we make the simplifying assumption that factors affecting s_x are largely physical in nature and thus there is likely no difference in the probability of particle-bound N vs. particle-bound P sedimenting (i.e. $s_N = s_P = s$), then the ratio of intercepts provides a direct measure of the relative refractory nature of particulate N and P undergoing direct sedimentation (r_N / r_P).

Information regarding relative magnitudes of zooplankton effects in enhancing or retarding sedimentation of different elements can be obtained by considering the ratio of the slopes (m_x) of the relationships between ER_x and g for different elements. For N and P, this has the form:

$$m_N/m_P = (r_{z,NeN} - r_{NsN})/(r_{z,PeP} - r_{PsP}).$$

If we make the same simplifying assumption that $s_N = s_P = s$ then the ratio is given as:

$$m_N/m_P = (r_{z,NeN} - r_{Ns})/(r_{z,PeP} - r_{Ps}). \quad (12)$$

This ratio may be viewed as a measure of the relative (i.e., N vs. P) "egestion effect" of zooplankton in altering sedimentation of elements from what sedimentation would be occurring directly without zooplankton grazing. In this example, a high value of m_N / m_P would be indicative of a stronger zooplankton-driven alteration (over direct sinking, i.e. $r_x s$) in the export ratio of N relative to the effect on the P export ratio. It is also conceivable that the slope for one element's relationship might be negative and the other slope positive; such an occurrence would be strong evidence that zooplankton differentially alter sedimentation of elements. However, as equation (12) makes clear, such differences might arise not only from stoichiometrically-based differences in e_x but also from differences between elements in $r_{z,x}$ and r_x . Analyses of slopes and intercepts just described for N and P can also be applied to C and P, C and N, or any pair of elements for which appropriate data are available.

Shortcomings of the theory

Like any simplification of complex natural processes, the theory just developed has a number of potentially important deficiencies. Some of these are inherent in the theoretical development itself, while others are related to difficulties in evaluating predictions of the theory using real data. First,

the theory assumes that parameters (i.e. r_x , $r_{z,x}$, s_x , e_x) do not vary with g . This is certainly an incorrect assumption. For example, as grazing intensity increases, size structure of the phytoplankton assemblage is likely to shift towards larger cells (Schoenberg & Carlson 1984) with higher inherent sinking rates (i.e., s_x might increase). Similarly, increases in grazing intensity that decrease phytoplankton biomass (i.e., food levels) might also lead to changes in zooplankton digestion efficiency (i.e., alterations in e_x). Complex, higher-level interactions between sedimentation processes and zooplankton may also arise from processes like coprophagy and coprorhexy, implying that $r_{z,x}$ may also scale with g . Second, the theory also does not address changes in parameters that are not necessarily associated with changes in g . For example, seasonal changes in water column physical structure will alter s_x . A theory incorporating ecological, physiological, and physical realities such as these would be much more complicated than the one developed here but might also be too complex for interpretation. Nevertheless, the possibility of such changes in sedimentation parameters must be kept in mind when interpreting relationships such as those investigated here.

An additional complication that should be considered involves time scales and may be particularly important in evaluating real data. The theory described above considers fates of produced material during a given interval. Those fates are essentially 4-fold in our approach: production may sediment directly, it may sediment after passing through a zooplankter's gut, it may be incorporated into a zooplankter or excreted by that zooplankter, or it may be mineralized by bacterial activity (either while sedimenting directly or sedimenting as egesta). Our theory makes no assumptions regarding steady-state conditions and thus does not take into account the possibility that production during an interval may accumulate as increased water column biomass and be subject to either direct or zooplankton-mediated sedimentation at a later time. This difficulty is not likely to be important over long time intervals during which cumulative vertical fluxes are large compared to changes in water column standing stock of particulate matter or for data in which production rates and sedimentation rates are integrated over an entire growing season. However, many studies monitor sedimentation at relatively short time intervals, as does ours. In these situations, non-steady state water column biomass might complicate tests of the theory developed here.

Finally, patterns predicted by the theory essentially involve analyses of the relationship between the export ratio of an element (ER_x) and grazing intensity (g , fraction of production grazed by zooplankton). Measurements necessary for assessment of ER_x , while requiring relatively sophisticated techniques, are commonly made in oceanographic and limnological studies. However, measuring g is laborious and such data are difficult to obtain on a

routine basis. This constraint can be overcome by evaluating not relationships between ER_x and g but relationships between ER_x and a more easily measured variable that scales with g . A likely candidate for such a variable is total zooplankton biomass (ZB; units of mass per unit volume), as grazing intensity (fraction grazed per unit time) imposed by zooplankton is given by:

$$g = ZB \cdot F,$$

where F is the biomass-specific clearance rate (units: volume filtered per unit mass per unit time). This approach is valid provided that phytoplankton biomass does not exceed grazer ILC. This assumption is valid for the oligotrophic lakes in our study but will not hold in eutrophic systems. In an analysis of relationships between ER_x and ZB, equation (8) still holds but now slopes of relationships will be $F \cdot (r_{z,x}e_x - r_x s_x)$; intercepts are unchanged. Likewise, the stoichiometric analysis just described remains valid under the assumption that zooplankton grazing is non-selective with respect to elements (i.e., F is the same for all elements and cancels out of the ratio in equation (12)).

Field tests of the theory

Study sites

Study sites were located at the Experimental Lakes Area (ELA) on the Precambrian Shield in southwestern Ontario (93°30'–94°00' W, 49°30'–49°45' N, altitude 360–380 m asl). Morphometric maps and summaries of morphometric and ecological characteristics are provided in Fig. 2. Lake 110 (L110) is a small, relatively deep, elongate lake protected from wind by ridges and cliffs on its northern and southern shorelines. In contrast, Lake 240 (L240) is considerably larger but has a similar maximum depth. The lake is relatively circular, surrounded by low hills, and exposed to wind from all directions. Ecological characteristics of the lakes also differed. L110 lacked piscivorous fish and its fish community was dominated by cyprinids. Metazoan zooplankton were dominated by copepods with small cladocerans and rotifers also present. In L240, piscivorous species (northern pike; *Esox lucius*), as well as a mixed planktivore assemblage that includes lake herring (*Coregonis artedii*), yellow perch (*Perca flavescens*), and some cyprinids comprised the fish assemblage while zooplankton included larger cladocerans (*Holopedium gibberum* and *Daphnia galeata mendotae*) along with various copepods and small cladocerans.

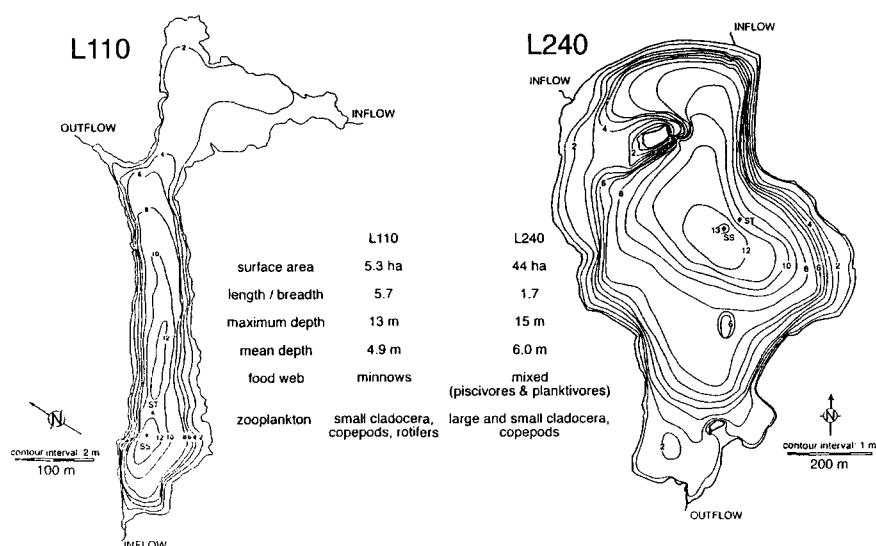


Fig. 2. Morphometric maps, along with morphometric and ecological summary information, for the study sites. Note the difference in scale for the two maps; L240 is considerably larger than L110. Locations of the main sampling station (SS) and sediment trap deployment (ST) are indicated.

Methods

Lakes were monitored at weekly intervals from 15 June (JD 166) to 27 August (JD 239), 1992 during the strongly stratified period to obtain data necessary to estimate sedimentation rates of C, N, and P, areal production rates of C, N, and P, and zooplankton biomass in terms of C, N, and P concentrations.

Sedimentation was monitored using triplicate sediment trap arrays deployed in the upper hypolimnion in each lake (6 m in L110, 8 m in L240). Each replicate array consisted of three PVC cylinders of 5.2-cm diameter and 36-cm height; this diameter:height ratio exceeds the minimum ratio recommended for efficient trapping under low-turbulence conditions of the upper hypolimnion (Bloesch & Burns 1980). Traps were set for 1-week intervals, after which a trap lid was sent down the suspension rope to cover traps during retrieval. Traps were retrieved at night to reduce the possibility that living zooplankton might be included in the trap contents. Immediate inspection of the samples rarely encountered living animals in the trap collections; quantitative microscopic examination of preserved trap samples indicated that zooplankton contributed little directly to trap contents (J.J. Elser, unpublished data). To the extent that zooplankters contributed to trap contents, overestimates of sedimentation would result, artificially raising export ratios. Contents of each

cylinder in an array were combined to produce one replicate. In addition, a water sample from the depth of trap deployment was taken for analysis of particulate concentrations in order to correct trap contents for ambient particulate matter. After being emptied, traps were immediately re-suspended for continued sampling. In the laboratory, material from each replicate (and from the trap depth water sample) was filtered onto two pre-combusted GF/F filters, which were dried and stored in a desiccator until later analysis of particulate P content (by persulfate oxidation followed by colorimetric analysis of phosphate; APHA 1992) or particulate C and N content (using a Perkin-Elmer model 2400 CHN analyzer).

Areal sedimentation rate for each replicate was estimated based on volume of trap material collected, amount of material filtered, amount of C, N, or P on the filter (corrected for ambient quantity of C, N, and P in that volume of lake water at trap depth), and total area of three trap cylinders (63.7 cm^2). Examination of uncorrected sedimentation data indicated export ratios that frequently exceeded 1, suggesting that sediment focussing was occurring (Likens & Davis 1975). We corrected areal sedimentation rates for effects of sediment focussing by multiplying rates by the ratio of lake surface area at thermocline depth to total lake surface area; thermocline depth was 3 m in Lake 110, 5 m in Lake 240 and varied by less than 0.5 m during the monitoring interval. This correction approach was also used by Findlay et al. (1994) who found that sedimentation data corrected in this way are in close agreement with observed sediment burial rates determined from sediment cores and also lead to realistic values of material sedimentation in the context of whole-lake material budgets. However, it should be noted that sediments do accumulate to some degree in shallow epilimnetic regions of these lakes (as in most) and so this correction likely over-compensates to an unknown extent for effects of sediment focussing.

Production rates of C were measured using the ^{14}C method in laboratory incubations (Fee 1990). Surface irradiance was continuously monitored at a central meteorological station at the ELA for later use in estimating daily production based on light extinction and photosynthesis-light parameters. Light extinction was measured in situ at approximately 2-week intervals using surface and in situ quantum cells. Observed light extinction coefficients were used to estimate irradiance flux at a large number of depths (~ 20) for each value of surface irradiance. Lake samples taken at 2-week intervals were incubated in a laboratory light gradient to estimate parameters of the light-photosynthesis relationship so that production at each irradiance level could be estimated. In this manner daily estimates of primary production were made based on the continuous record of surface irradiance by use of the numerical integration methods of Fee (1990). Primary production for L240

was estimated directly in the manner just described. However, L110 was not included in the routine suite of ELA lakes monitored for primary production in 1992 and so we estimated primary production in L110 using data from nearby L109 (which was monitored in 1992). In 1993 simultaneous rates of primary production in L109 and L110 were strongly correlated ($p < 0.001$; $r^2 = 0.60$); other years in which L109 and L110 were simultaneously monitored for PPr indicate a similarly strong correlation (R.E. Hecky, unpublished data). In addition, more in-depth analysis of PPr data at the ELA has also indicated a very high degree of inter-lake similarity in photosynthetic performance such that estimates of PPr using photosynthetic parameters estimated from one lake are remarkably accurate in predicting PPr in other ELA lakes (E.J. Fee, unpublished data). So we estimated L110 primary production on sampling dates in 1992 using 1992 L109 production data for each date and the relationship between L110 and L109 production determined in 1993 (L110 production = $54.7 + 0.62(\text{L109 production})$; units: $\text{mg C m}^{-2} \text{ d}^{-1}$). Any uncertainty in this estimation is likely to detract from our ability to find interpretable relationships between production and sedimentation in L110. Thus, the reasonably strong relationships between export ratio and zooplankton in L110 that we found (see below) indicate that discrepancies in PPr between L110 and L109 were probably minor.

Once areal production rates of C were estimated for both lakes, production rates of N and P were estimated by multiplying C production by N:C and P:C ratios of phytoplankton-sized particles obtained during weekly monitoring of the two lakes. N:C and P:C ratios were estimated by passing epilimnetic water samples through a $1.0\text{-}\mu\text{m}$ polycarbonate filter and then filtering whole lakewater and $<1.0\text{-}\mu\text{m}$ water onto pre-combusted GF/F filters for later analysis of C, N, and P content as described above. Elemental ratios (N:C and P:C) used to estimate autotrophic N and P production were calculated after correcting estimates of whole-water C, N, and P concentrations for contribution of bacterial-sized particles ($<1.0\text{ }\mu\text{m}$). Values of particulate N:C and P:C for estimating weekly N and P production were calculated as geometric mean values of triplicate observations at the beginning and end of each weekly sedimentation interval.

Zooplankton biomass, as an index of grazing intensity, was monitored at weekly intervals in conjunction with sampling of suspended particulate matter and sedimentation rates. As zooplankton undergo pronounced diurnal vertical migration, zooplankton were sampled during both day and night. Zooplankton samples were produced by combining collections from three depths in the epilimnion (generally 0.5 m, 1.5 or 2 m, and 3 or 4 m) taken with a 15-L clear Schindler trap sampler fitted with an $85\text{-}\mu\text{m}$ Nitex mesh collector. Thus, our sampling procedure likely did not include microconsumer biomass. Three

epilimnetic composite samples were taken in this manner and returned for laboratory processing. Each sample was split into three equal portions, with one portion preserved for later identification and enumeration of animals (data not presented), one portion filtered onto a pre-combusted, pre-weighed filter for analysis of C and N content (as above, after drying and re-weighing), and one portion filtered onto a pre-combusted, pre-weighed filter for analysis of P content (as above, after drying and re-weighing). Zooplankton biomass in terms of C, N, and P concentration was then calculated by accounting for total volume of the water sampled using the Schindler trap, splitting of the sample, and C, N, or P content measured.

Data necessary for evaluating relationships between ER_x and grazing intensity was obtained by estimating ER_x for each element by dividing areal sedimentation rate of that element ($\mu\text{moles cm}^{-2} \text{ d}^{-1}$) for a given weekly interval by average areal production rate of that element (same units) during that week. Average areal production rates of N and P were calculated by multiplying average areal C production rate during a week by mean N:C and P:C ratios of epilimnetic phytoplankton measured on the first and last day of the sampling interval. Indices of grazing intensity calculated for regression with estimates of ER_x were calculated as follows. First, we calculated day-night averages of triplicate determinations of zooplankton biomass (in terms of C, N, and P) for sampling dates at the beginning and end of each weekly sampling interval; day-night averages were not weighted to correct for differences in daylength as daylength changed by only ~ 2 h during our relatively short study interval. Then we determined the mean value of these averages for sampling days preceding and succeeding each weekly interval. When these data were available for each interval, regressions between ER_x (for C, N, and P) and ZB_x (in terms of C, N, and P) were performed for each lake. We also tested for potential effects of time lags between water column processes and sedimentation by regressing ER_x and ZB_x at various time lags. No qualitative changes in relationships were observed for short time lags (1 to 2 weeks) although relationships were generally weaker. For longer time lags relationships between ER_x and ZB_x generally disappeared.

Results and discussion

Areal production rates of C, N and P generally exceeded sedimentation rates in L110 (Fig. 3). Production rates for C were relatively constant but autotrophic production in terms of N and P was more dynamic (Fig. 3a) due to variation in N:C and P:C ratios. Sedimentation rates began the season at low values for all elements and peaked around JD 208 (Fig. 3b). In L240, rates of production also generally exceeded sedimentation rates, especially early in

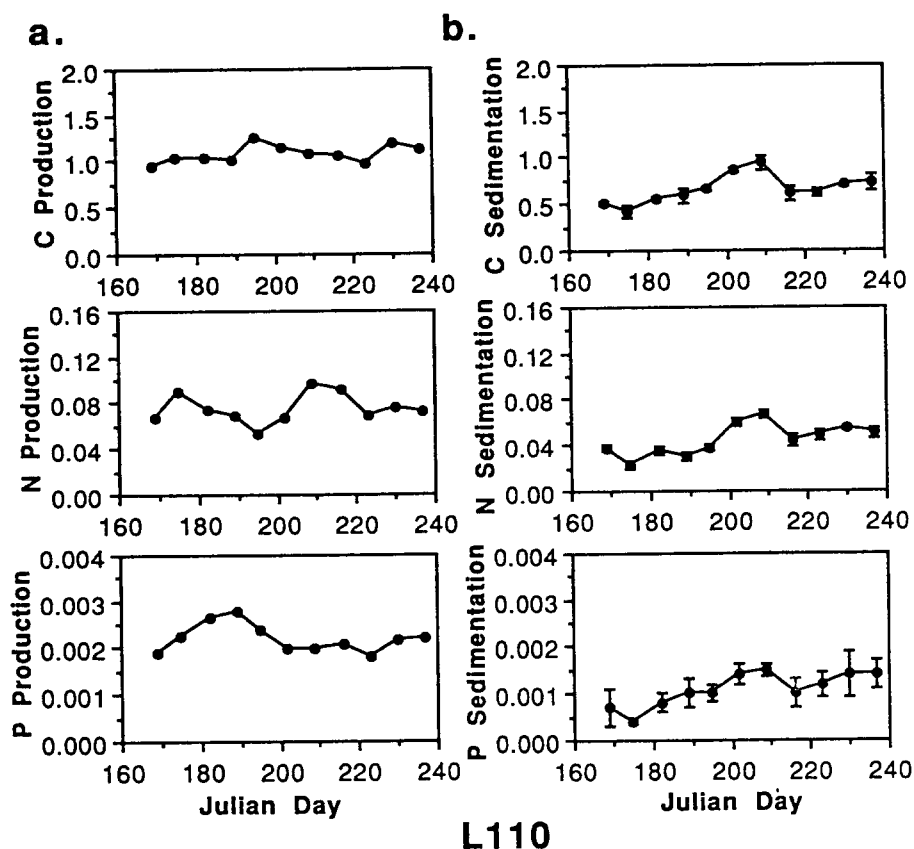


Fig. 3. Dynamics of production and sedimentation rates for C, N, and P in L110. (a) production rates (units: $\mu\text{moles cm}^{-2} \text{d}^{-1}$). (b) Sedimentation rates (units: $\mu\text{moles cm}^{-2} \text{d}^{-1}$). Confidence intervals for sedimentation rates indicate ± 1 s.e. for triplicate sedimentation determinations (on most dates). No confidence intervals for production rates are presented as water column production was estimated based on PPr determinations of a single euphotic zone profile for each date. Julian Day 160 = 9 June 1992.

the observation period (Fig. 4). Production rates showed a maximum centered around JD 190 (Fig. 4a) but sedimentation rates were much less dynamic, declining slowly during most of the study period (Fig. 4b).

ER_x varied from a minimum of 0.2 in L110 on JD 174 to a maximum of 1.3 (for ER_P) in L240 on JD 165 (Figs. 5a and 6a). In L110, export ratios were variable (Fig. 5a), with ER_x being low during the early season prior to two late-season peaks. In L240, export ratios were less dynamic (Fig. 6a) and, following a high value during the first week of monitoring, increased steadily during the sampling season, although changes were more abrupt for ER_P . In L110, zooplankton biomass (in terms of C, N, and P)

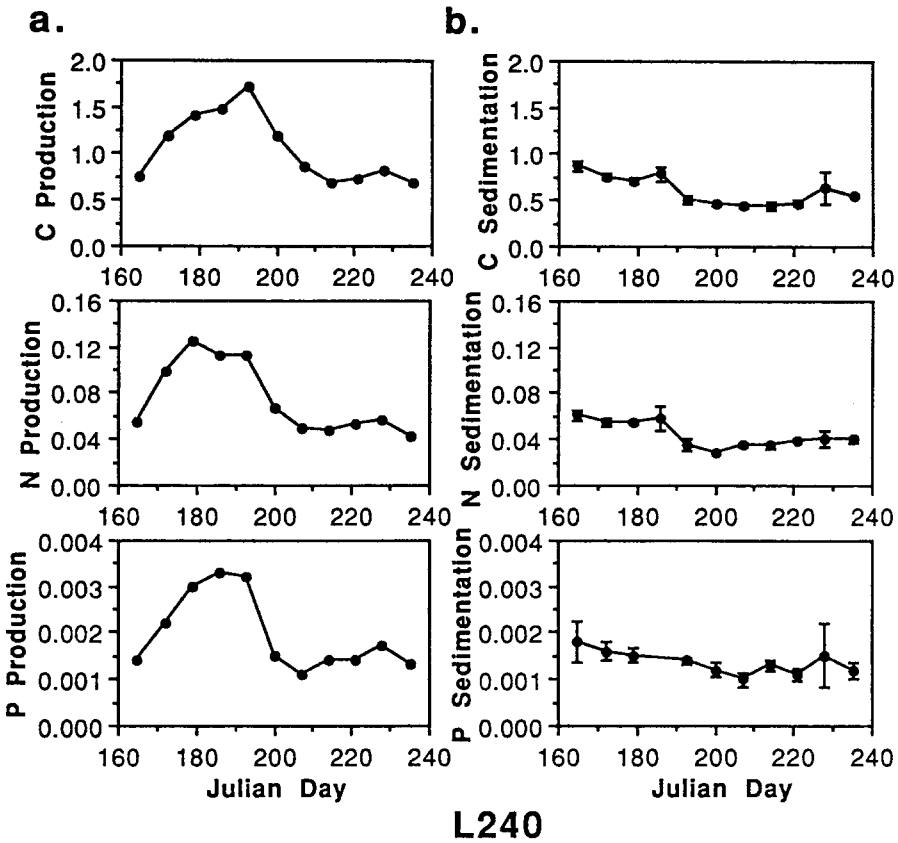


Fig. 4. As for Fig. 3 but for L240.

was highest early in the sampling period with a late-season peak around JD 220 (Fig. 5b). The late-season peak in zooplankton biomass was not reflected in zooplankton P concentration, indicating that zooplankton community N:P increased on those dates. In L240, zooplankton biomass increased steadily during the study period (Fig. 6b). Increases were similar for all elements, indicating that zooplankton community C:N:P was relatively constant.

The effects of zooplankton on sedimentation rates described in the theoretical development outlined above will likely only be functionally important under conditions in which zooplankton grazing contributes significantly to fluxes of materials in the system. Levels of zooplankton biomass observed in these systems (Figs 5b, 6b) are somewhat low but we have no direct measures of grazing intensity. A rough estimate of range of values for fraction of production consumed by zooplankton and egested (and thus contributing directly to sedimentation fluxes) can be made by assuming that zooplank-

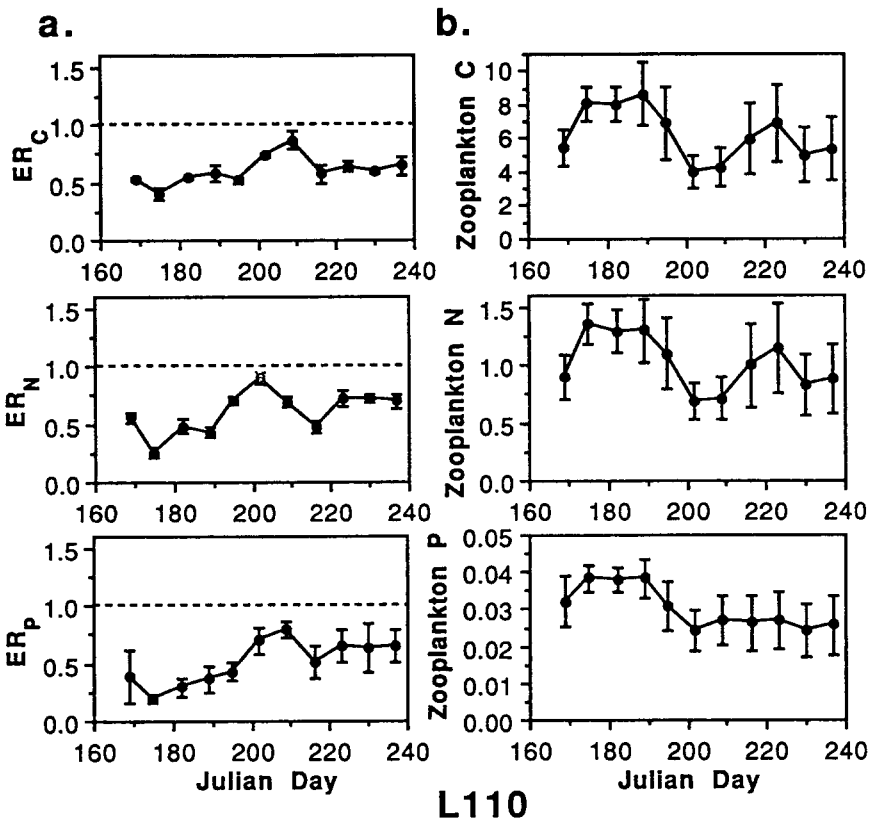


Fig. 5. Dynamics of export ratios (ER_x) of C, N, and P and zooplankton biomass in terms of C, N, and P in L110. (a) export ratios (units: dimensionless). The dotted line indicates $ER_x = 1.0$; subject to appropriate time-scale considerations, mass balance constrains ER_x to be less than 1. (b) Zooplankton biomass (units: μM). Confidence intervals for ± 1 s.e. For ER_x these confidence intervals entirely reflect variability arising from sedimentation determinations. The relative large confidence intervals for ZB_x result primarily from day-night differences as a result of diurnal vertical migration by zooplankton. Julian Day 160 = 9 June 1992.

ton graze $\sim 10\%$ of their biomass per d (low estimate of grazing intensity) or that zooplankton graze 100% of the daily production (high estimate of grazing intensity) and that zooplankton egest $\sim 30\%$ of what they ingest. When this range is compared to observed sedimentation fluxes it appears that zooplankton in these lakes may directly contribute 10–60% of observed sedimentation fluxes. If the actual situation in these lakes was close to the low end of the range then direct zooplankton effects were likely unimportant. However, values close to the high end of this range would indicate that direct egestion effects of zooplankton on sedimentation were important in these sys-

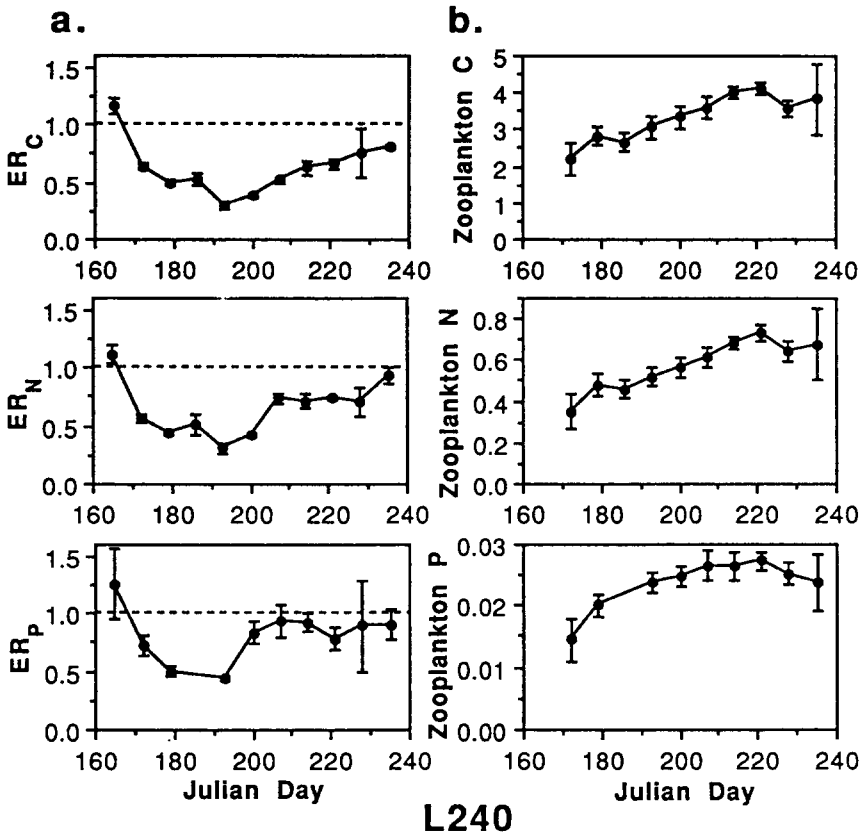


Fig. 6. As for Fig. 5 but for L240.

tems. Given the relatively strong correlations between zooplankton biomass and export ratios that we observed (Fig. 7), it is more likely that the latter was the case. However, uncertainty surrounding direct contributions of zooplankton egestion to sedimentation fluxes suggests that it will be important in the future to better assess the magnitude of, and constraints on, zooplankton contributions to sedimentation in natural systems, facilitating tests of existing hypotheses about effects of grazers on material fluxes.

Values of ER_x exceeded 1.0 only once, in L240 on JD 165, the first observation in the sampling season. This value may reflect contributions of allochthonous materials associated with spring run-off and mixing or a pulse of production missed by the first sampling date. Zooplankton data for this date were not available and so this high observation did not influence the associations between export ratio and zooplankton biomass (below). While the lack of ER_x values exceeding 1.0 indicates that methodological or other artifacts

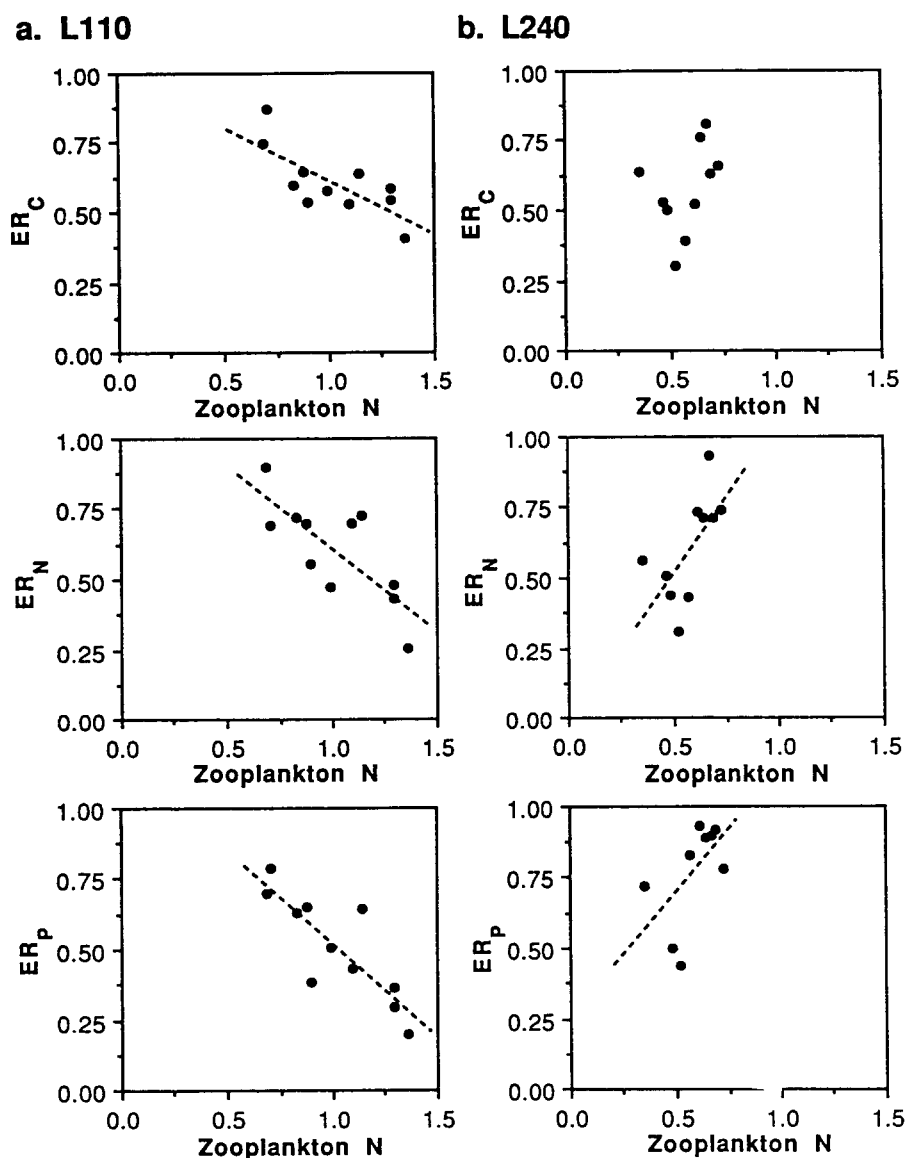


Fig. 7. Relationships between export ratios of C, N, and P and zooplankton biomass in the study lakes: (a) ER_x vs. zooplankton N (units: μM) in L110. (b) ER_x vs. zooplankton N (units: μM) in L240. A dashed line indicates the line of best fit (when $p < 0.10$). Statistical summaries along with estimated slope and intercept for each relationship (with confidence limits) are provided in Table 1.

have not strongly influenced our data, several factors that may contribute to inaccurate assessments of export ratios should be considered before proceeding. First, as discussed above ("Shortcomings of the theory"), we assume that material sedimenting during a given interval was produced during that interval. However, accumulation of phytoplankton biomass that sediments at a later date may lead to situations in which materials sedimenting during an interval were produced during previous intervals. Second, as mentioned above, allochthonous materials or organic matter produced by sources other than pelagic autotrophs (e.g., bacterial production, littoral zone production transported to the pelagic zone) might contribute to sedimentation but are not included in our measure of production, artificially elevating export ratio estimates. Finally, difficulties in assessing pelagic production might also lead to inaccuracies in measures of ER_x . For example, the ^{14}C method for estimating C production is generally considered to overestimate net production of particulate matter (Peterson 1978); this would tend to produce artificially low estimates of ER_x . However, if detritus (low in N and P relative to C) contributed to the seston measured to determine autotrophic N:C and P:C ratios then estimates of N production and P production rates might be too low. However, detailed examinations of elemental ratios of particulate matter in ELA lakes indicated that detrital contributions do not strongly influence seston ratios (Hecky et al. 1993; Elser et al., 1995). In any case, the complicating factors discussed here would need to co-vary with zooplankton biomass, and do so in qualitatively different ways in the two lakes, in order to compromise our main finding that zooplankton had qualitatively different impacts on export ratio in these two lakes (below).

All possible combinations regressions between ER_x for each element (ER_C , ER_N , ER_P) and ZB_x (ZB_C , ZB_N , ZB_P) were performed. Relationships between ER_x and the three ZB_x parameters were qualitatively similar (Table 1) but regressions using ZB_N generally produced highest R^2 and so we focus on regressions using ZB_N here to facilitate comparison between lakes. In L110, export ratios of C, N, and P decreased with increasing ZB_N (Fig. 7a; $p < 0.01$, $R^2 = 0.55 - 0.69$). In contrast to L110, in L240 export ratios for N and P increased with increasing ZB_N although the relationship for ER_P was only marginally significant (Fig. 7b; $p < 0.10$, $R^2 = 0.34 - 0.44$). The relationship between ER_C and ZB_N was positive but non-significant ($p = 0.23$). Comparison of confidence limits on slope estimates for ER_x and ZB_x for the two lakes (Table 1) indicated that slopes for ER_N vs. ZB_N relationships were significantly different for the two lakes ($p < 0.05$) while differences in slopes for ER_P vs. ZB_N and ER_P vs. ZB_P were marginally significant ($p < 0.10$). The finding that export ratios increased or decreased with zooplankton biomass in

Table 1. Results of all possible regressions between export ratios for C, N, and P and zooplankton biomass estimators (ZB_C, ZB_N, and ZB_P). Estimates of intercept and slope for each regression are presented along with their 95% confidence limits.

Zooplankton estimator	Statistics	L110			L240		
		ER _C	ER _N	ER _P	ER _C	ER _N	ER _P
ZB _C	P, R^2	0.015, 0.49	0.009, 0.54	0.002, 0.66	0.31, 0.13	0.04, 0.42	0.09, 0.35
	Intercept \pm c.i.	0.94 \pm 0.27	1.13 \pm 0.35	1.11 \pm 0.32	0.27 \pm 0.65	-0.25 \pm 0.63	0.18 \pm 0.71
	Slope \pm c.i.	-0.054 \pm 0.04	-0.08 \pm 0.05	-0.096 \pm 0.05	0.09 \pm 0.19	0.19 \pm 0.18	0.17 \pm 0.21
ZB _N	P, R^2	0.009, 0.55	0.006, 0.59	0.002, 0.69	0.23, 0.17	0.04, 0.44	0.10, 0.34
	Intercept \pm c.i.	0.99 \pm 0.27	1.20 \pm 0.36	1.17 \pm 0.33	0.26 \pm 0.58	0.015 \pm 0.56	0.25 \pm 0.64
	Slope \pm c.i.	-0.38 \pm 0.26	-0.58 \pm 0.35	-0.66 \pm 0.32	0.54 \pm 1.0	1.0 \pm 0.96	0.88 \pm 1.1
ZB _P	P, R^2	0.04, 0.39	0.003, 0.64	0.001, 0.79	0.97, 0.00	0.40, 0.10	0.25, 0.18
	Intercept \pm c.i.	1.0 \pm 0.39	1.36 \pm 0.41	1.38 \pm 0.32	0.56 \pm 0.89	0.22 \pm 1.0	0.28 \pm 0.93
	Slope \pm c.i.	-13.3 \pm 12.5	-25.2 \pm 13.4	-29.1 \pm 10.5	0.67 \pm 37	16.7 \pm 42.6	20.6 \pm 39.1

the two lakes indicates that zooplankton have qualitatively different effects on sedimentation processes in these systems.

The contrasts in sedimentation processes for different elements and for the two lakes can be more explicitly evaluated by specifically comparing regression results (Table 1). In L110, intercept values for ER_C seemed consistently lower than those for ER_N and ER_P (Table 1). However, these differences were not statistically significant ($p \gg 0.05$) and thus these data provide no evidence for differences among elements in the importance of direct sedimentation processes. However, differences between lakes in direct sedimentation processes were considerably stronger. In L240, intercepts were small (< 0.27) while in L110 intercepts were substantial ($0.99 - 1.20$). Comparison of confidence limits on intercept estimates (Table 1) indicates that these between-lake differences were statistically significant ($p < 0.05$) for the ER_N vs. ZB_N relationship and marginally significant ($p < 0.10$) for the ER_P vs. ZB_N relationship. According to equation (8), the intercept of the relationship between ER_x and ZB_x is an estimate of $r_x s_x$. Thus, estimates for L110 are somewhat problematic, as r_x and s_x are constrained to be between 0 and 1 and therefore $r_x s_x$ should also lie between 0 and 1. However, 95% confidence limits on intercept estimates generally encompassed 1 (Table 1) and we can only conclude that direct sedimentation processes were apparently quite efficient in this system. In any case, the sizable difference in intercepts for L110 and L240 relationships suggests that direct sedimentation processes were considerably stronger in L110 than in L240.

The observed difference between lakes in the contribution of direct sedimentation processes is consistent with differences in lake morphometry and in likely influences of wind-induced turbulent mixing between the two systems. L240 has a deeper mixed-layer (4–6 m during summer) than does L110 (2.5–4 m) and a less pronounced thermocline. The argument that the difference in importance of direct sedimentation in these two lakes is related to morphometric differences is supported by recent observations from the Northwest Ontario Lake Size Series (NOLSS) study which examined ecological characteristics of a series of lakes of increasing size (Fee & Hecky 1992). In this lake size series, apparent rates of mineralization of suspended particulate matter increased, and degree of water column thermal stratification decreased, with increasing lake size, indicating that as lake size increases particulate matter is more efficiently retained in the water column due to enhanced water column turbulence (Fee et al. 1994). Although the NOLSS lakes do not include lakes as small as L110 and L240 (the smallest lake included in NOLSS is 89 ha in area), the association of water column physical structure and particle dynamics with lake size in their study showed little tendency to diminish at small lake size. Thus, it is reasonable to expect that these size-associated

effects likely also hold for differently sized lakes encompassed by the increase in size from L110 to L240.

Above we described how the theory we have developed permits an assessment of the interaction of stoichiometric aspects of zooplankton digestive processes with direct sedimentation processes in potentially differentially affecting export ratios for C, N, and P. This assessment proceeds via a comparison of the slopes of ER_x and ZB_x relationships (i.e., estimates of $r_{z,x}e_x - r_x s_x$). In our data, slopes for ER_C relationships were generally shallower than those for ER_N and ER_P relationships (Table 1), suggesting a stronger impact of zooplankton in modulating sedimentation fluxes of N and P relative to C. However, confidence limits on these slopes were generally large (Table 1) and thus no significant differences in slopes for different elements were observed within individual lakes. More effective tests for stoichiometric impacts of zooplankton on multiple element sedimentation will require more extensive data sets where slope estimates are more precisely determined.

The most striking difference between lakes in the slope of ER_x vs. ZB_N relationships is that slopes are negative for L110 and positive for L240 (Fig. 7). This observation has important implications for understanding how ecological interactions affect biogeochemical cycles in pelagic ecosystems. It indicates that changes in zooplankton biomass, such as might be induced by changes in food web structure (Carpenter et al. 1985), will have qualitatively different effects on the fate of autotrophic production in different ecosystems. In situations such as L110 (small, low turbulence lakes or embayments), increases in zooplankton biomass will decrease the proportion of epilimnetic production that reaches lower waters via sedimentation. The opposite will be true in situations like L240 (larger lakes and open oceans): increases in zooplankton grazing will decrease the efficiency with which materials are retained in the water column. This site-dependence of the effects of zooplankton on sedimentation processes may have contributed to current uncertainty about the impacts of grazing on sedimentation in pelagic ecosystems.

Summary and conclusions

In this paper we have presented a simple, heuristic theory based on conservation of mass that formalizes the expected relationship between the fate of autotrophic production via sedimentation (the export ratio) and zooplankton grazing. The theory explicitly predicts that effects of zooplankton grazing on the export ratio will depend on relative tendencies of suspended particulate matter and zooplankton egested material to sediment. This prediction directly implies that effects of zooplankton grazing on the export ratio will be site dependent. The bifurcation model of Legendre & Le Fèvre (1989) makes a

similar prediction. The predicted site-dependence of the zooplankton-export ratio relationship was supported by our field observations, which revealed qualitatively different relationships between zooplankton grazing and the export ratio in two lakes of contrasting morphometry. Strong relationships between export ratios and zooplankton biomass reported here lead us to suggest that more extensive studies of ecological determinants (zooplankton dynamics, community composition, food web structure) of sinking fluxes are warranted for both freshwater and marine pelagic ecosystems.

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