Modeling the significance of zooplankton grazing for export production

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$$P_e = [(w_s+(1-a)G)/(w_s+G)] P_t$$

Abstract

We present a theoretical model and different scenarios for the impact of herbivorous zooplankton grazing on planktonic production and vertical flux of particulate organic matter. Sedimentation of phytoplankton and fecal matter from the mixed layer (i.e. export production P_e) is given by $P_e = [(1 - \alpha) G/(w_s + G)]P_t$, where α is a "pelagic assimilation efficiency" of the mixed layer, w_s is phytoplankton sinking rate, G is grazing pressure of the herbivore stock, and P_t is the integrated phytoplankton production in the mixed zone. The parameter α is influenced by herbivorous assimilation and decomposition of fecal matter in the upper water column. In the above expression the influence of grazing acts like a Michaelis-Menten limitation term $[G/(w_s + G)]$, where sinking rate is the half-saturation parameter and pelagic assimilation efficiency represents the maximal influence from grazing. The model seems predictive as it gives reasonable explanations to $P_e : P_t$ relationships for both freshwater and marine systems, and therefore improves our understanding of several empirical models presented in the literature linking export production to primary production.

During the last decade a variety of approaches measuring and predicting the magnitude and dynamics of primary production and export of carbon from the surface layers (e.g. time series of sedimentation measurements, satellite imaging, interpretation of undisturbed sediment cores, mathematical modeling) have been used. Discussions of the "biological pump," i.e. the biologically mediated export of carbon from the surface layer and storage in the oceans's interior, frequently apply the concept of new production (P_{new}), i.e. primary production based on allochthonous, inorganic N (Dugdale and Goering 1967). This concept is of utmost importance for understanding pelagic ecosystems because the fraction $f = P_{new} : P_t$, where P_t is total primary production, represents the upper limit of organic matter and energy that can be removed or extracted from the surface waters of the ocean without destroying the long-term integrity of pelagic systems (Vézina and Platt 1987; Legendre 1990). Unfortunately, the biological pump is not well understood even on a quite elementary level and topics like nutrient limitation of primary production, the relationship between new and regenerated production, and the conditions for export of carbon from the euphotic layer are debated. The relationships are particularly important for understanding the dynamics of ocean productivity and its role in the global carbon cycle.

Models from the literature

While these discussions are going on, biological oceanographers and geochemists use sediment traps to measure seasonal and annual variability of vertical carbon flux despite the present controversy on trap-collecting efficiency. Empirical models of P_{new} and export production (P_e) have been suggested (*see* Berger et al. 1989). Most of these models are based on sedimentation and primary production measurements that rarely consider the temporal and spatial scales to which the data may apply. In order to overcome these problems of interpretation, Wassmann (1990) presented literature data on long-term, simultaneous measurements of P_t and P_e. Sufficient data were available only from the coastal zone of the boreal North Atlantic. Comparison with published models predicting the vertical flux of

particulate organic carbon from the upper water column by Eppley and Peterson (1979), Suess (1980), Betzer et al. (1984), and Pace et al. (1987) revealed that they do not adequately predict P_e from P_t in these coastal environments. It was suggested that P_e in the boreal coastal zone of the North Atlantic should be calculated with

$$P_e = 0.049 \ P_t^{1.41} \qquad (r_2 = 0.94; \ n = 14). \qquad (1)$$

Because $f = P_{new} : P_t$ and P_e estimates as measured by sediment traps come close to P_{new}, but must be smaller (organic matter sedimentation rates derived from traps refer usually to particulate matter since dissolved organic matter in the overlying water inside the sediment traps is infrequently analyzed), calculating f with P_e gives rise to underestimates (Wassmann and Slagstad 1991). Therefore the term $e = P_e : P_t$ should be applied to approximate f. In boreal, coastal areas where steady state can be assumed only for intervals of months (e.g. the time of the productive period), e is meaningful as a base for estimating f for lengthy periods only, expressed by the term $\langle e \rangle$. $\langle e \rangle$ is positively, nonlinearly correlated with P_t, and the upper limit for $\langle e \rangle$ is ~0.6 in boreal coastal environments of the North Atlantic (Wassmann 1990).

The empirical models predicting P_e and $\langle e \rangle$ as reviewed by Berger et al. (1989) and Wassmann (1990), however, pay little attention to the biological processes determining P_{new} and P_e. To understand some of the basic biological processes giving rise to the empirical relationships presented by Wassmann (1990) and additional data from subalpine lakes (Weilenmann 1986; Bloesch and Uehlinger 1990), a theoretical model is presented to explore the effect of zooplankton grazing on vertical carbon flux. Different scenarios of grazing pressure and assimilation efficiency are shown to evaluate the biological conditions required to make the theoretical models fit empirical observations of P_e and $\langle e \rangle$.

Our model for export production

The vertical flux of particulate organic matter is a dynamic variable reflecting temporal variability in water movement, phytoplankton production and sinking, animal grazing, assimilation, and vertical migration. Such dynamics can be represented by a set of partial differential equations including the relevant processes (Wassmann and Slagstad 1991). By integrating these equations, vertical flux of particulate organic matter can be derived (for any depth) as a "true" result of the mechanisms represented in the equations. In the following, we will not deal with the instantaneous dynamic situation, but will relate vertical flux to biological mechanisms on a longer time scale. Specifically, we want to analyze theoretically how export production, as measured by sediment traps, is related to primary production, sinking, grazing, and assimilation. First, we derive a simple expression for the steady state phytoplankton biomass. This expression is inserted into a definition of export production and then we arrive at an equation relating export production to plankton parameters.

Phytoplankton has two nutrient sources: new nutrients and regenerated nutrients. Both, however, give rise to growth resulting in new biomass. This biomass may sink, degrade in the upper layer, or be grazed by herbivores. Depending on assimilation efficiency and decomposition in the mixed layer, some mass must leave the herbivores as fecal matter (Fig. 1). The temporal change in phytoplankton biomass in the surface layer can be expressed as (an explanation of symbols is given in the notation)

$$dB/dt = B[\mu - (w_s/D_m) - gH] \qquad (2)$$

where B is the local phytoplankton concentration averaged over the depth of D_m, w_s/D_m the instantaneous loss rate from the water column above the mixing depth (D_m), and gHB the grazing term depending on the densities of both phytoplankton and herbivores (H) (Fig. 1). For simplicity we assume a linear functional response. The term gHB in Eq. 2, however, can be replaced by a more realistic feeding representation, including satiation at high food availability.

We consider here the export production from the mixed layer $z = D_m$. For other applications it may be convenient to deal with other depth layers, such as the euphotic zone given by the compensation depth (D_c). Considering phytoplankton biomass constant $(dB/dt = 0)$ over the time period Δt, Eq. 2 gives the (equilibrium) biomass:
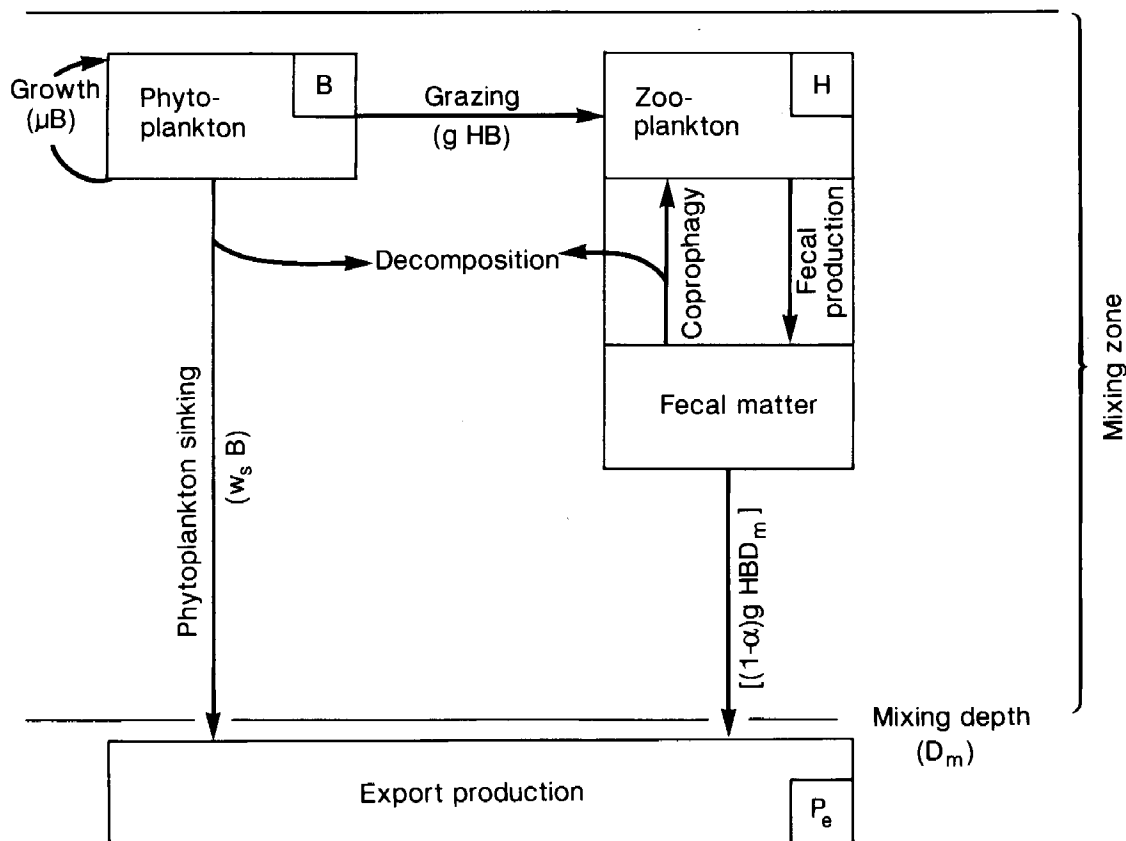
Fig. 1. Schematic representation of the theoretical model indicating how phytoplankton (B) and grazing of the herbivores (H) give rise to export production (P_e) at the bottom of the mixing depth (D_m).

$$B = P_t/[\Delta t(w_s + gHD_m)] \qquad (3)$$

where $P_t = \mu BD_m\Delta t$ equals the depth-integrated production (above D_m) over the time period Δt (g C m^{-2}). We define export production (P_e; *see Fig. 1*) during period Δt as the sum of phytoplankton sinking out of the mixed layer and sinking of fecal matter out of that layer:

$$P_e = [w_sB + (1 - \alpha)gHBD_m]\Delta t \qquad (4)$$

where $(1 - \alpha)$ represents the unassimilated fraction of the grazed phytoplankton. In the present model α is the pelagic assimilation efficiency of the water column above D_m. Therefore, α cannot be readily interpreted as the herbivorous assimilation efficiency, but rather as a composite parameter reflecting both herbivorous assimilation and degradation of fecal matter (e.g. bacterial decomposition and coprophagy) above D_m. It is likely that α will be dominated by herbivorous assimilation when

phytoplankton and grazers are relatively large and fecal pellets sink rapidly. With small phytoplankton and grazers, however, degradation may dominate and increase α above the level expected from herbivorous assimilation alone (i.e. the material is assimilated several times). Nevertheless, α is reflecting the impact of zooplankton on export of particulate matter from the euphotic zone.

Inserting Eq. 3 into 4 gives

$$P_e = [(w_s+(1-a)G)/(w_s+G)] \, P_t \qquad (5)$$

where $G = gHD_m$ (m s^{-1}) is the grazing pressure inside the mixed layer represented as a clearance rate along the vertical axis. Generally, the influence of grazing on export production is assessed by scaling grazing pressure against sinking rate of phytoplankton [the term $G/(w_s + G)$ in Eq. 5]. It should be noted that the influence of grazing acts like a Michaelis-

Notation

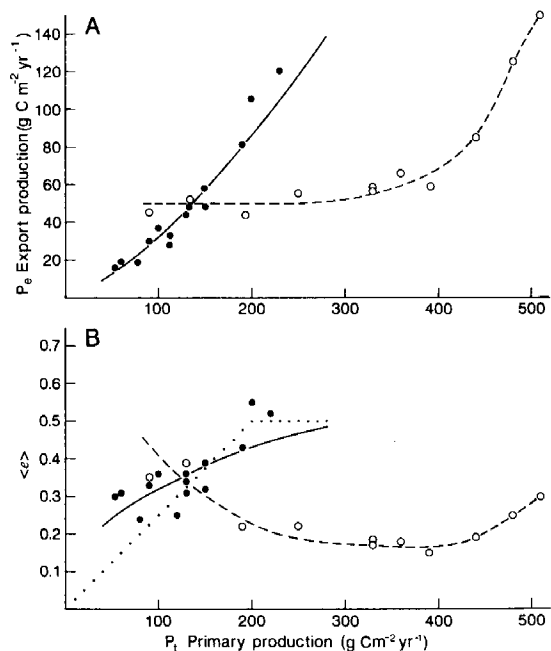|	
α	Pelagic assimilation efficiency of the water column above D_m (*see text*), dimensionless
B	Mean phytoplankton concentration above D_m, g C m^{-3}
D_c	Phytoplankton compensation depth, m
D_m	Mixing depth, m
e	Ratio between export production (P_e) and total production (P_t), dimensionless
$\langle e \rangle$	e for lengthy periods of time, dimensionless
f	Ratio between new and total production, dimensionless
g	Grazing rate of herbivores, m^3 (g C)$^{-1}$ s^{-1}
$G = gHD_m$	Herbivorous clearance of the water column above D_m, m s^{-1}
H	Mean herbivore concentration above D_m, g C m^{-3}
P_e	Export production (at D_m) during time period Δt, g C m^{-2}
P_t	Total phytoplankton production above D_m during time period Δt, g C m^{-2}
w_s	Phytoplankton sinking rate, m s^{-1}
μ	Instantaneous phytoplankton growth rate, s^{-1}

Fig. 2. A. Sedimentation of particulate organic C close to the bottom of the photic zone (i.e. P_e) as a function of P_t from simultaneous long-term measurements from coastal, marine environments of the boreal North Atlantic (g C m^{-2} yr^{-1}) (●—redrawn from Wassmann 1990). The regression line (solid line) is given by Eq. 1. Also shown is P_e as a function of P_t from simultaneous long-term measurements (g C m^{-2} yr^{-1}) in subalpine lakes (O—data presented by Weilenmann 1986; Bloesch and Uehlinger 1990). Broken line is visually fitted. B. $\langle e \rangle = P_e/P_t$ from coastal, marine environments (●) and subalpine lakes (O) (data: *see above*). The solid line represents $\langle e \rangle = 0.049P_t^{1.41}/P_t$ and the broken line is fitted by inspection. Dotted line is the f-ratio according to Eppley and Peterson (1979).

Menten limitation term, where sinking rate is the half-saturation parameter and the pelagic assimilation efficiency represents the maximal influence from grazing.

When phytoplankton sinking is low ($w_s \approx 0$), Eq. 5 reduces to the trivial result $P_e = (1 - \alpha)P_t$. Hence, export production is a function of total phytoplankton production and pelagic assimilation efficiency. However, if grazing pressure (G) becomes insignificant (i.e. $G \ll w_s$), Eq. 5 reduces to $P_e = P_t$.

Model test

Several marine studies have revealed non-linearity between export production and total production (*see* Wassmann 1990). Specifically, there is a tendency for export production to increase more rapidly with increasing total production than total production itself (Fig. 2A). This means that the increase of $\langle e \rangle$ slows with increasing total production (Fig. 2B). The opposite pattern, however, has been described for subalpine lakes (Fig. 2). Here, there is no increase in export production with increased total primary production up to ~400 g C m^{-2} yr^{-1} (Fig. 2A), and consequently $\langle e \rangle$ decreases with increasing total production in this inter-

val (Fig. 2B). Decreasing $\langle e \rangle$ values with increasing P_t have also been found in other northern, temperate lakes (Baines and Pace 1993).

The emphasis given to the representation of $\langle e \rangle$ as a function of P_t is based on the importance of this relationship in calculations of global new production. The variability of $\langle e \rangle$ vs. P_t relationships which can be expected in different aquatic ecosystems might be crucial for the precision of new production estimates. However, the substantial scatter in results derived from coastal, marine environments in Fig. 2B makes the interpretation of the relationship between $\langle e \rangle$ and P_t difficult. Also, when replacing P_e vs. P_t by P_e/P_t vs. P_t, a substantial negative, nonlinear correlation is automatically installed even when P_e and P_t are

uncorrelated, random variables. However, for the marine data the line in Fig. 2B is derived from Eq. 1. Despite the scatter in the data, $\langle e \rangle$ seems to increase nonlinearly up to a maximum of ~0.6.

The data presented here are from ecosystems characterized by blooms dominated by large phytoplankton species, large herbivores, and pronounced seasonality in abiotic factors. Such scenarios support the assumption that α in the present data sets is dominated by herbivore assimilation rather than fecal decomposition and coprophagy above D_m (Fig. 1). Such situations are found in boreal coastal zones, North Atlantic shelf ecosystems (e.g. the Barents Sea), and lakes of the temperate zone. However, in ecosystems characterized by small phytoplankton and zooplankton species, the grazing impact of larger herbivores on phytoplankton is low (e.g. Longhurst 1991). Protozooplankton, copepod nauplii, etc., producing small fecal material (slowly settling), coprophagy (Lampitt et al. 1990), and "floating" of fecal pellets (Alldredge et al. 1987) give rise to ecological situations where α is dominated by fecal decomposition rather than herbivorous assimilation. Before applying Eq. 5 to data sets one should consider the composite processes represented by α.

Discussion

In the following discussion we apply our theoretical model to ecosystems and situations where large phytoplankton and herbivore species play a dominating role. Both patterns shown in Fig. 2 can be explained in terms of Eq. 5 by assuming a dependency between assimilation efficiency and grazing pressure on the one hand and total production on the other. We first investigate the effect of decreased assimilation efficiency with increased total production and then the effect of increased grazing pressure with increased total production.

Accelerated increase in export production is to be expected if herbivorous assimilation efficiency (now assumed to be the major contributor to α) decreases with increasing total production (Eq. 5). It has been documented that individual zooplankton assimilation efficiency decreases significantly with food ingestion (Gaudy 1974). Valiela (1984) concluded that assimilation efficiency depends on the abundance of food particles up to the point

where the maximum ingestion rate is reached. At higher densities of food, assimilation rate is likely to be independent of food density as occurs in copepods (Conover 1978) and bivalves (Navarro and Winter 1982). It is likely that food density increases with total primary production in some situations. The influence of food density-dependent assimilation efficiency on export production is demonstrated in Fig. 3A. Here, we assume that food density increases with total primary production. We obtain two slopes: the first with accelerating P_e as a consequence of decreased α; the second with linear increase in P_e as the minimal (constant) α is reached. Similarly, the ratio between export production and total production, $\langle e \rangle$ (termed the $\langle f \rangle$ ratio by Wassmann 1990), reaches a constant value when the minimal assimilation efficiency is reached (Fig. 3B). Such satiation of $\langle e \rangle$ is supported by Eppley and Peterson (1979) (Fig. 2B).

Increased primary production may lead to increased herbivore stock and thereby to increased grazing pressure (G in Eq. 5). This mechanism will rely heavily on the time scale for possible herbivore response to altered primary production. The response time (i.e. the numerical response) is sensitive to aggregation behavior, generation time, and fecundity, but also to predation on the herbivores themselves. High fecundity, short generation time, and low predation will all lead to a short response time allowing the herbivore stock to increase. A larger herbivore stock will have a higher potential clearance rate (G), which the phytoplankton cannot escape as they must concentrate in the narrow euphotic zone. Thus, grazing pressure is likely to increase with primary production (top-down control). This mechanism reduces the increase in export production with increasing primary production (Fig. 3C).

Consequently, $\langle e \rangle$ may decrease as long as G increases with primary production (Fig. 3D).

The data obtained from subalpine lakes deviate significantly from the marine data (Fig. 2). Higher herbivore control on phytoplankton (i.e. shorter response time) in freshwater may explain the discrepancy between freshwater and marine systems. Higher herbivore control on phytoplankton is partly supported by the fact that several freshwater herbivores (e.g. Cladocera) have a high reproductive potential due
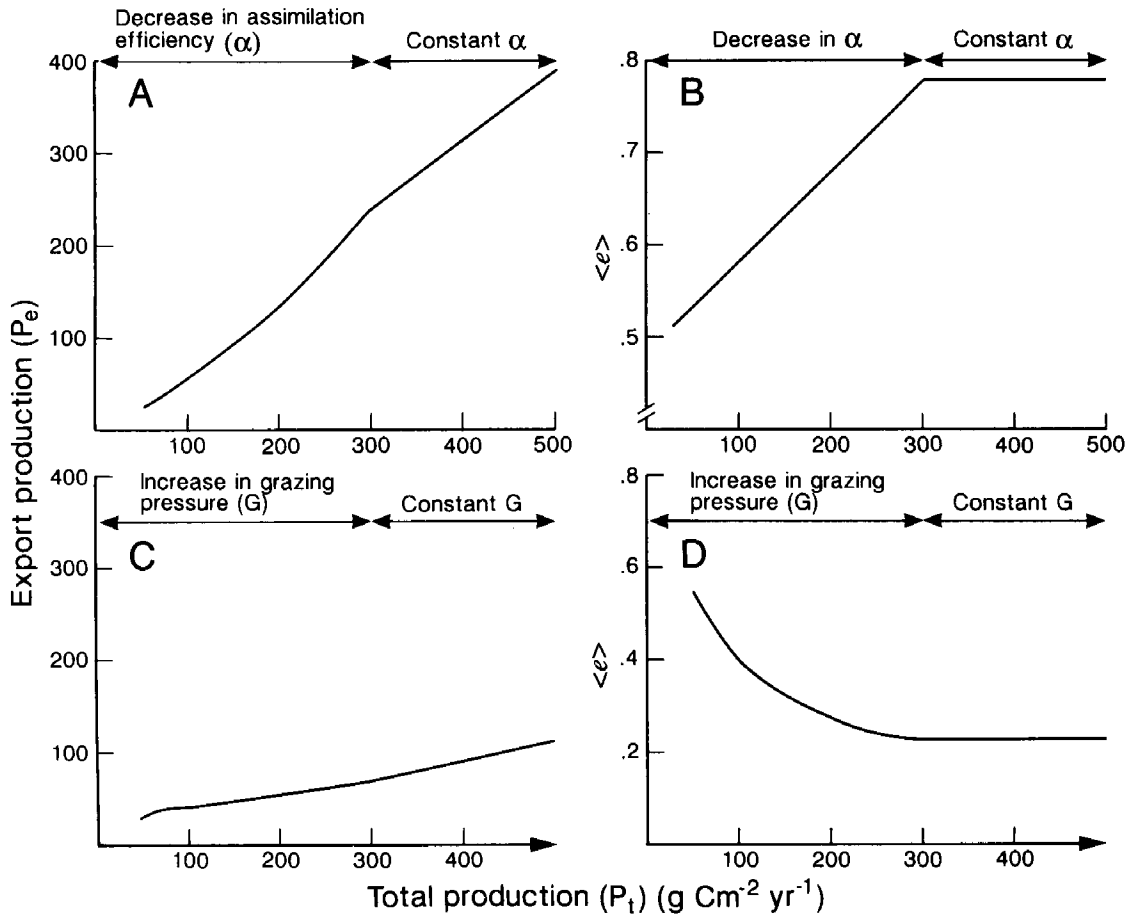
Fig. 3. Hypothetical influence of alterations in assimilation efficiency and grazing pressure on export production (P_e) (A, C) and ratio between export and total production ($\langle e \rangle$) (B, D). The relationships are computed according to Eq. 5. In panels A and B, α decreases (0.95–0.45) with increasing P_t for the interval 50–300 g C m^{-2} yr^{-1}, while G is constant (1 m d^{-1}). In panels C and D, G increases (1–6 m d^{-1}) with increasing P_t for the interval 50–300 g C m^{-2} yr^{-2}, while α is constant (0.9). Sinking rate (w_s) is constant (1 m d^{-1}).

to short generation times and parthenogenetic reproduction. Given the strong reproductive potential, coupling between phytoplankton and zooplankton is supposed to be different in lakes dominated by cladocerans (e.g. subalpine lakes) and those where copepods dominate (e.g. large, African lakes). Lakes dominated by copepods may show P_e vs. P_t relationships comparable to coastal, marine environments.

The data obtained from freshwater systems show a peculiar trend in that $\langle e \rangle$ decreases up to a primary production of ~300–400 g C m^{-2} yr^{-1}, and then increases with higher production (Fig. 2B). According to our model (Eq. 5) this trend can be interpreted as grazing pressure increases (which may be due to an increase

in herbivore stock) with increased primary production up to a maximum in the region 300–400 g C m^{-2} yr^{-1}. At this production level the increase in grazing pressure has ceased (or diminished) and $\langle e \rangle$ approaches a constant value. For higher production rates, grazing becomes less effective and assimilation efficiency decreases, which finally results in increased $\langle e \rangle$ values. Such a scenario is demonstrated in Fig. 4 where G is assumed to double for each doubling in P_t for the interval 50–300 g C m^{-2} yr^{-1}, while α is assumed to decrease by 0.1 for each 100 g C m^{-2} yr^{-1} increase in P_t for the interval 300–500 g C m^{-2} yr^{-1}. A decrease in α at $P_t > 400$ g C m^{-2} yr^{-1} might be caused by phytoplankton size because the limit for
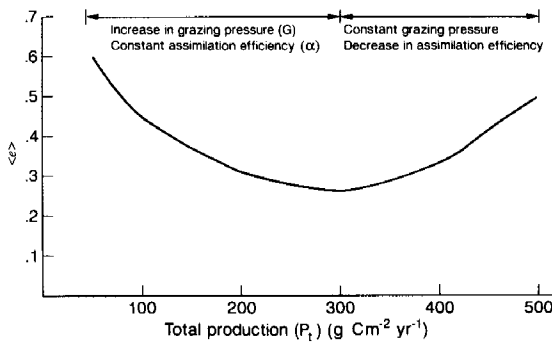
Fig. 4. Hypothetical influence of alterations in grazing pressure and assimilation efficiency on the ratio between export and total production ($\langle e \rangle$). The relationship is computed according to Eq. 5. G increases (0.8–4.8 m d^{-1}) with total production for the interval 50–300 g C m^{-2} yr^{-1}, while α is constant (0.9). α decreases (0.9–0.6) with increased P_t for the interval 300–500 g C m^{-2} yr^{-1}, while G is constant (4.8 m d^{-1}). Sinking rate (w_s) is constant (1 m d^{-1}).

cladoceran grazing is ~30 μm (M. Simon pers. comm.).

Current understanding of planktonic ecosystems implies that communities become less efficient at retaining nutrients in the water column as they become more productive (e.g. Harris 1986). While such a decrease in efficiency with increasing productivity seems to be true for boreal coastal ecosystems of the North Atlantic, the opposite is found in northern temperate lakes (Fig. 2; Baines and Pace 1993), revealing that sinking biomass is more important for carbon cycling in oligotrophic than in eutrophic lakes. Negative P_e vs. P_t relationships have also been reported from oligotrophic oceans (e.g. Lohrenz et al. 1992). $\langle e \rangle$ values of 0.24, i.e. 2.5 times lower than predicted by Eq. 1, are reported at average P_t rates of 345 g C m^{-2} yr^{-1} from Dabob Bay, a fjord in the boreal coastal zone of the North Pacific (Hedges et al. 1988). The low $\langle e \rangle$ value indicates that Dabob Bay, where fecal pellet sedimentation (high grazing rate) comprises a dominating part of the vertical carbon flux (Downs and Lorenzen 1985), might experience a less steep increase in the $\langle e \rangle$ vs. P_t relationship. Relationships of $\langle e \rangle$ vs. P_t are, therefore, far more variable than our current understanding of planktonic C cycling suggests.

With a simple, theoretical model, variable grazing pressure and assimilation efficiency alone were sufficient to explain the empirical

P_e/P_t relationships presented in the literature. Obviously, the impact of zooplankton grazing has a dominating influence on the export of particulate organic matter from the euphotic zone in limnetic as well as in marine environments (Bloesch and Bürger 1989; Peinert et al. 1989). This conclusion has crucial consequences for investigations of the mechanisms of the biological pump that are currently a priority in biological oceanography. The transport of particulate organic matter to depth, as a fraction of a given rate of phytoplankton production, depends on the formation of settling particles as well as on their subsequent consumption and modification (e.g. Banse 1990; Noji 1991). The structure and function of the particular food webs obviously play an important role for P_e/P_t relationships, supporting the view that taxonomically oriented zooplankton programs will be a necessary component of future particle flux projects in aquatic environments.

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