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Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator–prey weight ratio, and taxonomic group

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Abstract

A comprehensive dataset on the gross growth efficiency (GGE) of planktonic protozoans and metazoans was gathered from the literature in order to (1) identify typical ranges of values, (2) to reexamine the taxon specificity of GGE, and (3) to evaluate the impact of food concentration, predator–prey weight ratio, and temperature on GGE. All taxa (i.e. nano/microflagellates, dinoflagellates, ciliates, rotifers, cladocerans, and copepods) were found to have mean and median GGE of ~20–30%. Contrary to the common practice of using different values of GGE for ciliates and crustaceans, I found that the GGE hardly differed between taxa. Variability within all taxa was high and could only partially be attributed to the independent variables mentioned above. The dependency of GGE on food concentrations was the most reliable relationship identified by multiple regression. Establishing further generalizations regarding the dependency of GGE on other factors was hampered by methodological differences among studies and taxa and the lack of information on other potentially important factors such as the elemental composition of prey items. Future studies of GGE should recognize the importance of these factors.

Knowledge of fluxes of matter and energy within ecosystems is a prerequisite for the understanding of food web regulation and of the role that oceans and lakes play in the global carbon cycle (Longhurst 1991). However, quantifying carbon fluxes reliably in particular ecosystems is hampered by many difficulties. The complexity of aquatic food webs outpaces our capacity to make all the necessary measurements at any one site (Vézina and Platt 1988). This fact forces ecologists to infer unknown fluxes from those that have been measured. A relative straightforward and therefore common approach is to estimate ingestion rates, I, of a group of organisms (of a guild) from measured growth rates, G, and a fixed gross growth efficiency, GGE: $I = G/\mathrm{GGE}$. The crucial ratio GGE (G/I) is the fraction of prey carbon consumed converted to predator carbon. Despite its importance and abundant use in numerous models and applied studies, e.g. on the estimation of fish yield, the literature on GGE is not well developed and provides no or only a few weak generalizations.

Searching the literature of carbon flux modeling, one finds that one generalization in particular has reached modelers' ears: planktonic protozoans are thought to achieve higher GGE than do planktonic metazoans. Modelers are quite aware of high protozoan GGE (sensu Caron et al. 1990*a*) and usually use protozoan GGE ≥40% in their models. On the other hand, the conclusion of Calow (1977)—that "Metazoa can achive the best possible levels of efficiency predicted by theory and may, in this respect, be more efficient than isolated bacterial and protozoan cells"—is ignored. This generalization has been (possibly uncritically) applied by, among others, Fasham (1985) using a protozoan GGE of 40% vs. a metazoan GGE of 15%; Vézina and Platt (1988) 10–60 vs. 0–40%; Weisse et al. (1990), 40 vs. 25%; Nielsen and Kiørboe (1991), 40 vs. 33%; Leakey et al. (1992), 40 vs. 25%; Lignell et al. (1993), 40–50 vs. 25%; Nielsen et al. (1993), 40 vs. 33%; and Stone et al. (1993), 40–50 vs. 20%. The assumed taxon specificity is the only generalization on GGE of planktonic organisms used in these models. Individual studies have shown that GGE will depend on food concentration (Verity 1985; Urabe 1991), temperature (Sherr et al. 1983; Rassoulzadegan 1982), and food quality. One aspect of food quality, the effect of relative prey size on GGE, has not yet been addressed systematically in individual studies. However, pelagic predators are well known for their size-selective feeding behavior (Hansen et al. 1994). Furthermore, the dependence of GGE on relative prey size plays a crucial role in models on the trophic transfer efficiency along size gradients (Borgmann 1982; Gaedke 1993). Another important aspect of food quality is the biochemical composition of the food (Checkley 1980; Nakano 1994; Sterner and Hessen 1994). Unfortunately, lack of data prevents further analysis of the effect of biochemical prey composition on GGE.

The purpose of this contribution is twofold. First, the experimental evidence for taxon-specific GGE of planktonic consumers is reexamined. Second, the dependence of GGE on food concentration, ambient temperature, and predator–prey weight ratios is analyzed to provide a new and critical basis for the use of GGE in models.

Methods

Database—The literature was examined for laboratory studies of the GGE of planktonic nano- and microflagellates,

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dinoflagellates, ciliates, rotifers, cladocerans, and copepods. In total, 687 observations from 52 sources were evaluated (*see Fig. 1* for references) that either reported GGE directly or that allowed its calculation directly. Only GGE <100% were considered. A complete dataset with information on food concentration (F), temperature (T), predator and prey weight (w_2 and w_1, respectively), and with GGE measurements based on carbon, dry weight, or energy could be obtained for 520 observations from 32 sources. When necessary, F, w_2, and w_1 were standardized in units of carbon using the conversion factors listed in Table 1. F is expressed as mg C liter^{-1}, w_1 and w_2 as pg C ind.$^{-1}$, and T as °C. The weight ratio between predator and prey was calculated as (w_2/w_1).

Regression analysis—F and w_2/w_1 were $\log_{10}$-transformed to meet the requirements of least-squares regression analysis, i.e. normality and equal variance. It has already been reported in the literature that GGE is probably not a linear function of either T (Sherr et al. 1983) or F (Verity 1985). Additionally, feeding preferences of planktonic consumers point toward an optimum predator–prey size ratio (Hansen et al. 1994), suggesting that GGE might not be a linear function of (w_2/w_1). To accommodate for these nonlinearities I introduced quadratic terms for $\log(F)$, T, and $\log(w_2/w_1)$ within multivariate regression statistics. The data were analyzed with the regression procedure of SAS (SAS Institute 1988). The basic model used was

$$\mathrm{GGE} = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n + \epsilon,$$

where β_i terms are parameters for the independent variables X_i [$\log(F)$, $[\log(F)]^2$, $\log(w_1/w_2)$, $[\log(w_1/w_2]^2$, T, and T^2]. I used a stepwise selection model (significance level to enter the model, 0.05; significance level to stay, 0.05) to search for important independent variables (SAS Institute 1988).

Results

Present findings are restricted to and depend on the range of conditions for which experimental evidence is available, which I now briefly describe (*see Fig. 1*). The weight of pelagic predators considered in this study differed by eight orders of magnitude, ranging from nanoflagellates with a body weight of 0.3 pg C ind.$^{-1}$ to copepods with a body weight of 90 μg C ind.$^{-1}$ (Fig. 1a). Body weight of nano/microflagellate prey differed sharply from the weight of the prey organisms offered to the other groups (Fig. 1b). Dinoflagellates and copepods were grown on a broad range of prey weights, whereas the prey of rotifers and cladocerans used in the experiments covered only very narrow weight ranges. With the exception of four observations with roughly equal predator and prey weights (Caron et al. 1986), predators were always larger than their prey. Strong differences in $\log(w_2/w_1)$ existed between the taxonomic groups (Fig. 1c). $\mathrm{Log}(w_2/w_1)$ was smallest for dinoflagellates, being on average only one to two orders of magnitude larger than their prey. Dinoflagellates were followed by nano/microflagellates, ciliates, rotifers, and copepods. Filter-feeding cladocerans had the largest $\log(w_2/w_1)$, being on average more than five orders of magnitude larger than their prey. Variability

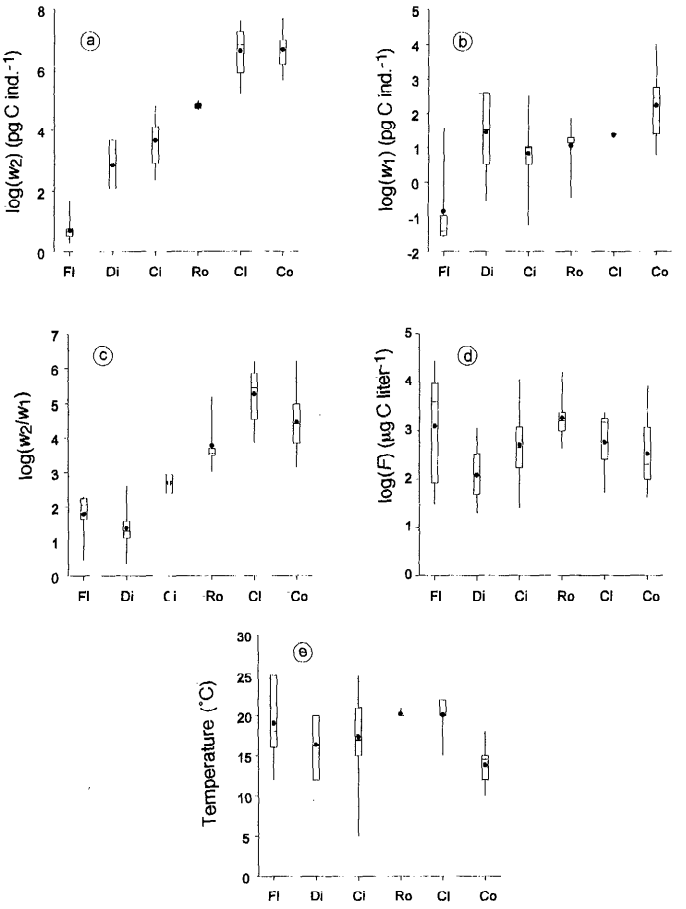

Fig. 1. Plots of experimental conditions of single observations [nano/microflagellates (Fl), dinoflagellates (Di), ciliates (Ci), rotifers (Ro), cladocerans (Cl), and copepods (Co)]. Dots represent the mean value, the central line of the box is the median of the distributions, and the box limits the 25% and 75% quartiles of the data. The whiskers include all data within the 5–95 percentile of the distribution. (a) Weight of predators [$\log(w_2)$], (b) size of prey [$\log(w_1)$], (c) predator–prey size ratio [$\log(w_2/w_1)$], (d) food concentration [$\log(F)$], and (e) ambient temperature.

Data source for nano/microflagellates: Kopylov et al. 1980; Fenchel 1982; Sherr et al. 1983; Stoecker and Evans 1985; Caron et al. 1986; Børsheim and Bratbak 1987; Geider and Leadbetter 1988; Caron 1990; Caron et al. 1990*a*; Grover 1990; Caron et al. 1991; Holen and Boraas 1991; Hochstädter 1993; Gonzáles et al. 1994; Nakano 1994; Jürgens 1995. Data source for dinoflagellates: Strom 1991; Hansen 1992; Nakamura et al. 1992; Strom and Buskey 1993; Buskey et al. 1994. Data source for ciliates: Rubin and Lee 1976; Rassoulzadegan 1982; Scott 1985; Taniguchi and Kawakami 1985; Verity 1985; Jonsson 1986; Stoecker and Evans 1986; Turley et al. 1986; Caron et al. 1991; Müller 1991; Ohman and Snyder 1991; Hochstädter 1993. Data source for rotifers: Doohan 1973; Pilarska 1977; Leimeroth 1980; Scott 1980; Schlüter et al. 1987; Rothhaupt 1993; Walz 1993. Data source for cladocerans: Richman 1958; Buikema 1975; Sharma and Pant 1984; Urabe 1991, Urabe and Watanabe 1991. Data source for copepods: Mullin and Brooks 1970; Gaudy 1974; Harris and Paffenhöfer 1976; Paffenhöfer 1976; Checkley 1980; Copping and Lorenzen 1980; Abou Debs 1984; Kiørboe et al. 1985; Hamburger and Boëtius 1987; Sauter and Van den Bosch 1994.

Table 1. Conversion factors of original data to units of C.

Crustaceans	C (pg)=0.5 × dw (pg)	Berberovic 1990
Rotifers	C (pg)=0.5 × dw (pg)	Latja and Salonen 1978
Phytoplankton	C (pg)=0.11 × cell vol. (μm^3)	Rocha and Duncan 1985
Bacteria	C (pg)=0.09 × cell vol.$^{0.59}$ (μm^3)	Simon and Azam 1989
Nano/microflagellates	C (pg)=0.22 × cell vol. (μm^3)	Børsheim and Bratbak 1987
Ciliates	C (pg)=0.154 × cell vol. (μm^3)	Müller and Geller 1993

in $\log(w_2/w_1)$ was largest for cladocerans and copepods and low for rotifers. Food concentrations offered were highest for rotifers and nano/microflagellates (Fig. 1d). The range of food concentrations was high for nano/microflagellates and low for rotifers. Nano/microflagellates, dinoflagellates, and ciliates were studied under broad ranges of temperatures, whereas experiments with rotifers, cladocerans, and copepods covered only a narrow temperature range (Fig. 1e).

In contrast to the differences in $\log(F)$ and $\log(w_2/w_1)$ between taxa, GGE varied less between taxa, but greatly within taxa (Fig. 2). For all taxa, GGE as low as a few percent were reported as well as values reaching up to 60 and 80% or more. The ranges between the 25 and 75% quartiles amounted to 13–35%. They were particularly large for ciliates and cladocerans and relatively small for dinoflagellates and rotifers. Mean and median GGE of all taxa scattered around 20–30%. Nano/microflagellates showed highest GGE (mean GGE, 32%; median GGE, 28%), followed by ciliates (30%, 30%), cladocerans (27%, 28%), dinoflagellates (26%, 26%), copepods (26%, 22%), and rotifers (24%, 23%). Protozoan GGE (30%, 28%) were slightly higher than metazoan GGE (26%, 23%).

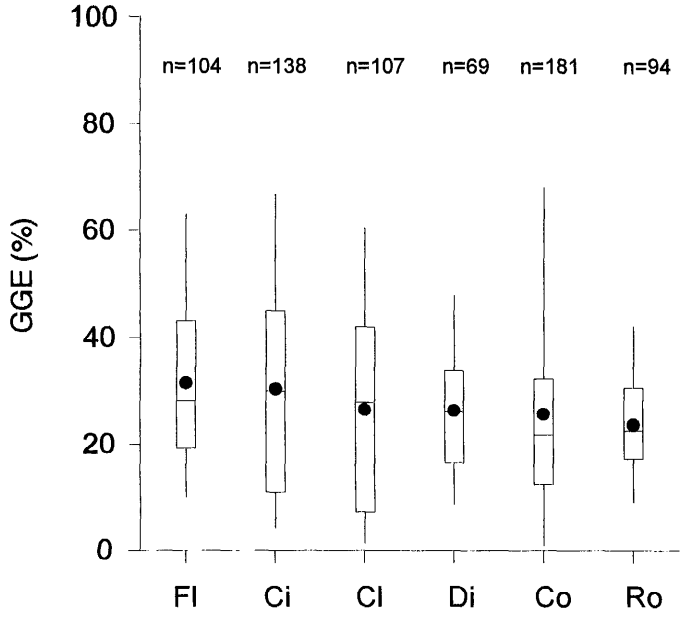

Fig. 2. Plots for GGE of nano/microflagellates (Fl), ciliates (Ci), cladocerans (Cl), dinoflagellates (Di), copepods (Co), and rotifers (Ro). Dots represent the mean value, the central line of the box is the median of the distributions, and the box limits the 25% and 75% quartiles of the data. The whiskers cover the 5–95 percentiles of the data.

The high variability in GGE could partially be attributed to the variability in the independent variables (Tables 2, 3; Figs. 3, 4). GGE was negatively correlated with food concentrations within ciliates, rotifers, and cladocerans but positively within nano/microflagellates and copepods (Table 2). An inverse relationship between GGE and $\log(w_2/w_1)$ was found within nano/microflagellates, dinoflagellates, ciliates, and cladocerans. GGE of nano/microflagellates and dinoflagellates increased and GGE of ciliates and copepods decreased with temperature (Table 2). Exploratory data analysis suggested that GGE depends strongly on the specific experimental setup and assumptions used in the individual studies when calculating GGE. To explore these dependencies, multiple stepwise regressions were run for the full dataset of each taxon and for various subsets that were formed by excluding one study at any one time. The latter are called exclusion datasets in the following. This procedure resulted in 38 different datasets, i.e. 6 datasets that included all sources of the respective 6 taxa and 32 exclusion datasets (Table 3).

The variability of GGE explained by multivariate models was highest for ciliate and cladoceran multivariate models (Table 3) (R^2 on average 0.62 and 0.59, respectively) and differed not much between individual models (0.47–0.74 for ciliates and 0.44–0.73 for cladocerans). That is, the dataset for these taxa was rather homogeneous and the rather high R^2 did not depend on the exclusion or consideration of one particular study. In contrast, models of copepods had mostly low but highly variable R^2 (on average 0.16 with a range of 0.06–0.39). Models for nano/microflagellates, dinoflagellates, and rotifers had intermediate R^2 and differed moderately in their explanatory power. These differences in explanatory power between taxa were not caused by the number of independent variables selected into the models. Models with all six independent variables exhibited similar differences of R^2 between taxa.

The decrease of GGE at high food concentrations was the most reliable relationship between GGE and any independent variable in the multivariate models (Table 3). GGE decreases at high food concentrations in 25 models (Table 3), i.e. almost all models of nano/microflagellates, ciliates, and rotifers, and in some models of the other groups. Nineteen models selected both $\log(F)$ and $[\log(F)]^2$ as significant variables. In all these cases GGE was correlated positively with $\log(F)$ and negatively with $[\log(F)]^2$, reflecting an initial increase of GGE with food concentration and subsequent decline of GGE at high food concentrations. Two exclusion datasets (i.e. nano/microflagellate dataset M5 and copepod dataset M34) yielded a positive relationship between GGE and food concentration.

Table 2. Pearson correlation coefficients between GGE and independent variables [log(F), log(w_2/w_1), T] for different taxa (NS—not significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

	log(F)	log(w_2/w_1)	T
Nano/microflagellates (n=63)	0.45**	−0.27*	0.33**
Dinoflagellates (n=62)	−0.18 NS	−0.52***	0.49***
Ciliates (n=74)	−0.58***	−0.25*	−0.53***
Rotifers (n=92)	−0.26*	−0.07 NS	−0.11 NS
Cladocerans (n=107)	−0.49***	−0.64***	0.01 NS
Copepods (n=122)	0.25**	−0.12 NS	−0.33**

GGE of nano/microflagellates, rotifers, and ciliates was highest at food concentrations of about 1 mg C liter^{-1}, 1 mg C liter^{-1} and 100 μg C liter^{-1}, respectively (Fig. 3a, d, c). However, the statistical significance of this pattern, i.e. positive correlation with log(F) and negative correlation with log(F)^2, depended on single sources, e.g. observation of Jürgens (1995) and Nakano (1994) for nano/microflagellates; M5 and M9 in Table 3), Verity (1985) for ciliates (M17), and Rothhaupt (1993) and Pilarska (1977) for rotifers (M25 and M26). Regarding rotifers, the observations from Rothhaupt (1993) did not fit with the overall trend because they indicated an increase in GGE with increasing food concentrations (Fig. 3d), but food quality during his experiments probably was low (Rothhaupt pers. comm.). Excluding data from Rothhaupt (1993) (Table 3, M25) doubles the R^2 compared to the all sources regression model for rotifers (Table 3, M21).

Multivariate models of cladoceran GGE (Table 3) suggested a negative relationship between log(w_2/w_1) and GGE. Additionally, within four out of six cladoceran models log(w_2/w_1) and [log(w_2/w_1)]^2 were considered significant, reflecting decreases in GGE at very small and very large log(w_2/w_1). Remarkably, a broad range of log(w_2/w_1) covering at least three orders of magnitude allowed rather high GGE (>30%) in all taxa (Fig. 4). Maximum achievable GGE tended to decrease at extreme values of log(w_2/w_1) and highest GGE of ciliates and copepods were restricted to rather narrow ranges of log(w_2/w_1) of 10^2–10^3 for ciliates and 10^4–10^5 for copepods.

Temperature was also frequently, but not consistently, selected into the multivariate models. Within dinoflagellate models, GGE increased with increasing temperature, whereas ciliate GGE decreased with increasing temperature. Within the copepod models, the behavior of GGE with respect to temperature differed between exclusion models (Table 3). The increase of GGE at high temperatures within three cladoceran models was most probably a result of the observations of Sharma and Pant (1984). These authors measured rather high GGE of a tropical cladoceran at high temperatures.

Discussion

GGE can be expressed as the product of net growth efficiency [NGE = growth/(growth + respiration)] and assimilation efficiency [AE = (growth + respiration)/ingestion]—GGE = NGE × AE. The maximum NGE of heterothermic organisms was estimated at 70–80% by Calow (1977) and 82–88% by Schroeder (1981) based on biochemical reasoning. Measured AE was shown to reach values of >80%, sometimes approaching 100% (Porter et al. 1982; Verity 1985). Hence, maximum GGE can be expected to be as a first approximation at least 60–80%. All taxa considered in this study are able to achieve approximately theoretically maximum GGEs. However, these high GGEs are not typical for any of these groups. Mean and median values for all taxa scatter between 20 and 30%, which does not support the conclusion of Caron et al. (1990*b*) that GGEs of 30–60% are typical for protozoa. Considering the high variability and the difficulties in measuring and calculating GGE, it is questionable if the small differences in GGE between protozoans and metazoans or between different taxonomic groups in this dataset are ecologically relevant and robust against methodological artifacts. Thus, the use of taxon-specific GGEs in models is not supported by empirical data.

The second important result besides the similarity of mean GGE across planktonic taxa is the large variability of GGEs which could only partially and with differing success between taxa be traced back to differences in independent variables. Models for all taxa were sensitive to the exclusion or consideration of single sources. The most consistent results were obtained for ciliates and cladocerans, the groups with the largest variability in GGE (Fig. 2). Only within these groups did multivariate regression analysis yield results partly insensitive to the exclusion of single sources. Within all multivariate models (Table 3) cladoceran GGE was negatively correlated with log(w_2/w_1) and ciliate GGE was negatively correlated with log(F). However, the positive correlation of ciliate GGE with log(F) and the negative correlation of ciliate GGE with temperature, for example, depend on the consideration of Verity (1985) within the multivariate models (compare M17 with other multivariate models for ciliate GGE). The dependency on single sources is especially evident for taxa where the explanatory power of the predictive variables is low (e.g. copepods). Exclusion of single sources may even reverse the relationship between GGE and independent variables. Excluding observations of Hamburger and Boëtius (1987) results in a positive relationship between GGE and food concentration, whereas excluding either Santer and van den Bosch (1994) or Harris and Paffenhöfer (1976) results in a negative relationship. Santer and van den Bosch (1994) measured rather high GGE for *Cyclops vicinus* at high algal food concentrations. They demonstrated that this copepod, usually considered as a carnivorous species at least during the late copepodid and adult stages, could be reared with a pure algal diet, however at high concentrations. Within their high concentrations, Santer and van den Bosch (1994) reported a significant decline of

Table 3. Impact of individual studies on the selection of independent variables [log(F), [log(F)]^2, log(w_2/w_1), [log(w_2/w_1)]^2, T, T^2] for different sets and subsets of nano/microflagellate, dinoflagellate, ciliate, rotifer, cladoceran, and copepod data by means of stepwise multiple regression (significance for model entry, 0.05; significance for model stay, 0.05). An increase of GGE with an increase of the independent variable is shown as +, and an inverse relationship as −.

	Log(F)	[Log(F)]^2	Log (w_2/w_1)	[Log (w_2/w_1)]^2	T	T^2	R^2
Nano/microflagellates							
M1 (n=63): all sources	+	−					0.29
M2 (n=55): excl. of Sherr et al. 1983	+	−					0.40
M3 (n=59): excl. of Caron et al. 1986	+	−					0.25
M4 (n=61): excl. of Holan and Boraas 1991	+	−					0.25
M5 (n=48): excl. of Nakano 1994	+						0.29
M6 (n=61): excl. of Gonzáles et al. 1993	+	−					0.29
M7 (n=62): excl. of Børsheim and Bratbak 1987	+	−					0.27
M8 (n=59): excl. of Hochstädter 1993	+	−					0.18
M9 (n=36): excl. of Jürgens 1995	No variables selected						—
Dinoflagellates							
M10 (n=62): all sources				−			0.28
M11 (n=34): excl. of Strom 1991		−					0.23
M12 (n=48): excl. of Strom and Buskey 1993			−				0.36
M13 (n=42): excl. of Buskey et al. 1994			−				0.25
Ciliates							
M14 (n=74): all sources	+	−				−	0.64
M15 (n=72): excl. of Turley et al. 1986	+	−				−	0.66
M16 (n=71): excl. of Stoecker and Evans 1986	+	−				−	0.65
M17 (n=27): excl. of Verity 1985		−					0.47
M18 (n=65): excl. of Taniguchi and Kawakami 1985	+	−				−	0.74
M19 (n=63): excl. of Scott 1985	+	−	−		−		0.58
M20 (n=72): excl. of Hochstädter 1993	+	−				−	0.62
Rotifers							
M21 (n=92): all sources	+	−					0.16
M22 (n=89): excl. of Leimeroth 1980	+	−					0.15
M23 (n=74): excl. of Walz 1993	+	−					0.18
M24 (n=72): excl. of Scott 1980	+	−					0.20
M25 (n=51): excl. of Rothhaupt 1993		−					0.32
M26 (n=82): excl. of Pilarska 1977	No variables selected						—
Cladocerans							
M27 (n=107): all sources			+	−			0.46
M28 (n=99): excl. of Richman 1958			+	−			0.44
M29 (n=75): excl. of Urabe and Watanabe 1991			−		−	+	0.73
M30 (n=81): excl. of Urabe 1991		−	+	−	−	+	0.62
M31 (n=92): excl. of Sharma and Pant 1984	+	−		−	−		0.68
M32 (n=81): excl. of Buikema 1975	+	−	+	−	−	+	0.51
Copepods							
M33 (n=122): all sources						−	0.11
M34 (n=107): excl. of Hamburger and Boëtius 1987	+						0.18
M35 (n=87): excl. of Paffenhöfer 1976						−	0.06
M36 (n=104): excl. of Mullin and Brooks 1970					−	+	0.39
M37 (n=92): excl. of Santer and van de Bosch 1994		−					0.06
M38 (n=98): excl. of Harris and Paffenhöfer 1976		−			+	−	0.33

GGE with increasing food concentration. The dataset of copepods comprises cyclopoid and calanoid copepods from freshwater and marine environments and may be too heterogeneous to allow any generalizations about a general copepod GGE.

With the exception of ciliates and cladocerans the explanatory power of the multivariate models was weak. What are the reasons for this limited potential to identify regularities? First, both ingestion and growth rates are difficult to measure, which results in great uncertainty of G/I = GGE. Second, researchers use different methods and units to measure ingestion and growth rates, which are not fully comparable. Peters and Downing (1984), for example, demonstrated effects of experiment duration and container volume on the measurement of zooplankton ingestion rates. Ingestion rates based on the uptake of radioisotopes are lower than ingestion

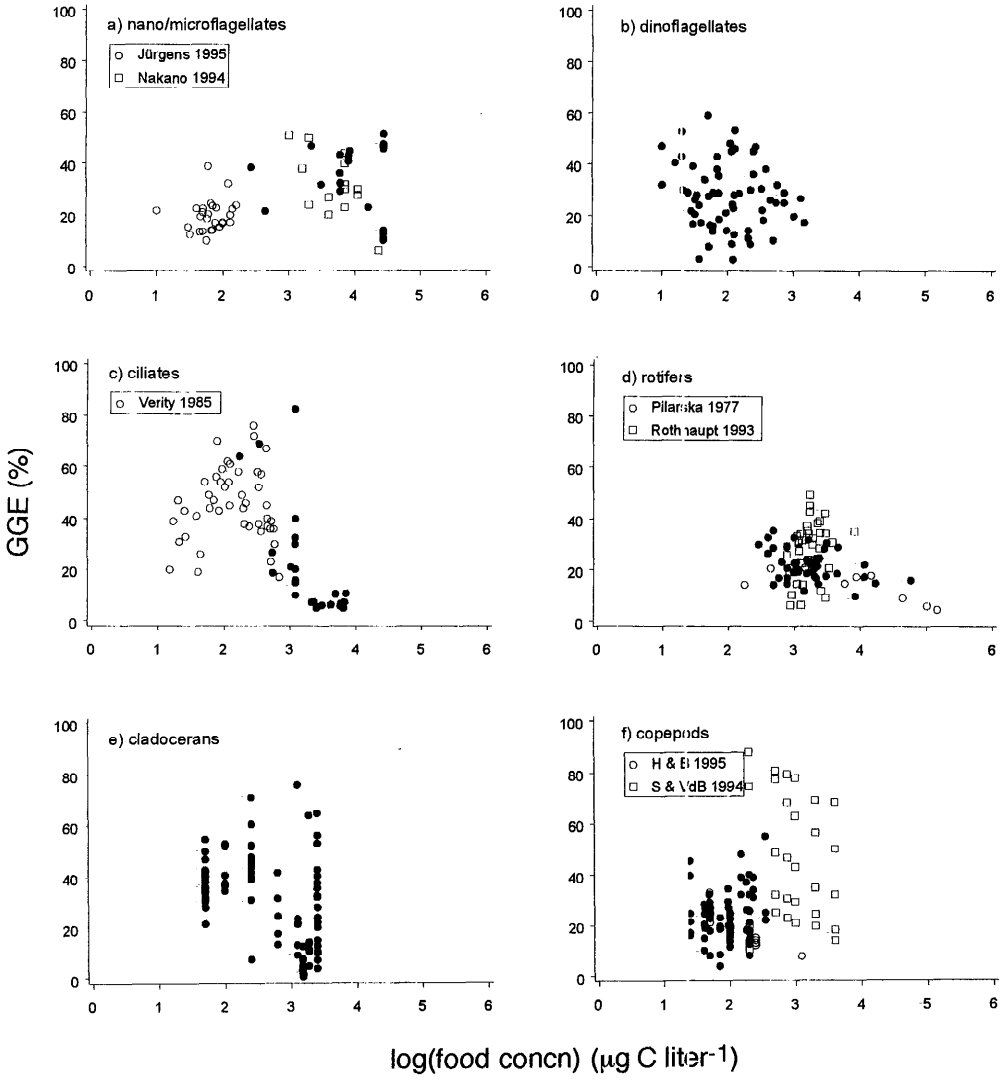

Fig. 3. Relationship between GGE and log(F) for the different taxa. Studies that influence regression statistics regarding the selection of log(F) or [log(F)]^2 into the models are especially marked, other observations are represented by black dots. Only observations that reported carbon, dry weight, or energy-specific GGE are shown (*see Table 3* for data sources). S&VdB refers to Santer and Van den Bosch (1994) and H&B refers to Hamburger and Boëtius (1987).

rates measured with other techniques (Peters and Downing 1984). Estimates of GGE based on the uptake of radioisotopes will thus result, other things being equal, in a relatively high GGE.

The effect of the methodological protocol is presumably small as compared to the impact of different techniques required to study the GGE of organisms, which differ in weight by orders of magnitude. Furthermore, the increase in body weight results in a change of the study object. For small and fast-growing protozoans usually GGE of population growth is calculated, whereas the long development times of crustaceans make it feasible to establish their GGE during individual development. If we compare protozoan and crustacean GGEs, for example, we must be aware that taxonomic and methodological effects on GGE are intertwined. Different methods will also influence the relationship of GGE with environmental factors. For example, protozoan GGE is mostly determined by studying the growth and ingestion rates of populations in batch cultures (Sherr et al. 1983; Verity 1985; Müller 1991). Growth is determined as increase in protozoan biomass and ingestion as decrease in food biomass. This implies that the food concentration is not constant and that the protozoans experience abundant food at the start of the experiment and low food concentrations at the end. On the other hand, growth of larger sized metazoans usually is monitored over longer intervals that usually involves transferring the animals daily to new research vessels with distinct food concentrations and measuring their ingestion rate during short-term experiments, which allow food concentrations to be kept rather constant. Differences in size between protozoan and metazoan plankton may also affect the units chosen for the calculation of GGE. Whereas

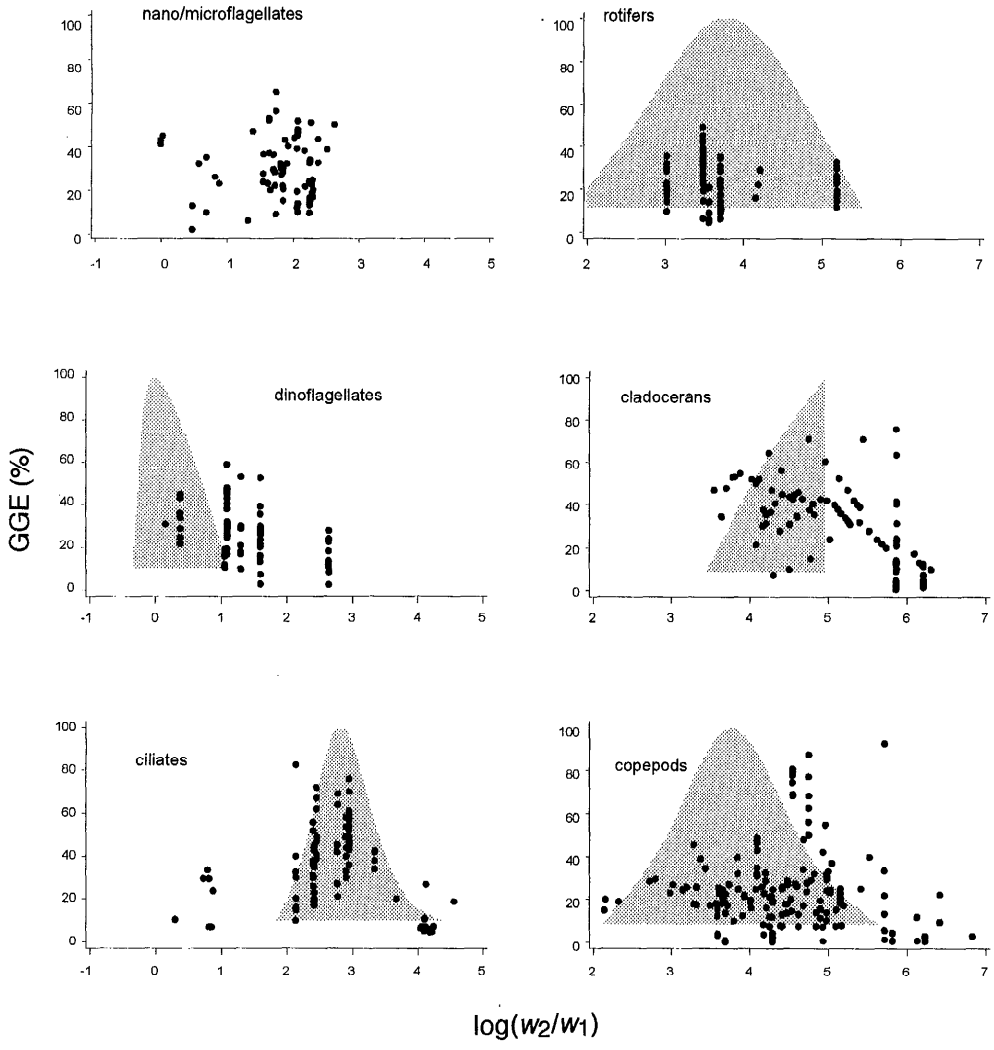

Fig. 4. Relationship between GGE and $\log(w_2/w_1)$ for the different taxa. Shaded areas represent optimum clearance spectra according to Hansen et al. (1994). See text for further explanation.

metazoan GGE is based on carbon or dry weight measurements, protozoan GGE is often expressed as volume specific. However, volume-to-carbon conversion factors of predator and prey may neither be equal nor constant. Consequently volume-specific and carbon-specific GGE may differ considerably. For example, Ohman and Snyder (1991) calculated GGE of the ciliate *Strombidium* based on both volume and carbon measurements: volume-specific GGE exceeded carbon-specific GGE by a factor of four (82 vs. 20%). To reduce the impact of different units on model results, only studies that reported carbon, dry-weight, or energy-specific GGE were included in the regression models.

Another reason for additional residual variability is the neglect of other potentially relevant independent variables, e.g. the nutritional quality of the food. A simplified aspect of nutritional quality is the elemental ratio of the food organisms (Sterner and Hessen 1994). For example, the C:P ratios of algae are known to be highly variable [e.g. for *Scenedesmus* it varies between 2,000 and 150 on an atomic basis (mol/mol) (Sterner et al. 1993)], whereas daphnids have a rather constant C:P ratio of ~90. Daphnids supplied with algae with 2,000 mol C/mol P can at most incorporate 90/2,000, or 4.5% of the carbon ingested. Using P-saturated algae a GGE of 60% would be possible. The dependence of GGE of the marine copepod *Paracalanus parvus* on the C:N ratio of various algal species was demonstrated by Checkley (1980). Feeding on *Peridinium trochoideum* (C:N = 3 mol C/mol N), the copepod was able to produce eggs with a GGE of 44.5%. Feeding on *Gonyaulax polyedra* (C:N = 9.6), a GGE of only 13% was achieved; that is, an increase in the relative N content by a factor of 9.6/3(=3.2) resulted in an increase of GGE by a factor of 44.5/13(=3.4). This clearly demonstrates the potential impact of prey nutrient composition on the GGE of consumers. Besides methodological factors and the lack of data on the nutrient composition of the prey, unexplained variability may also be caused by species-specific differences in GGE. For example, typical K-strategists may achieve higher GGE than typical r-strategists (Odum 1969). Given these shortcomings it is remarkable that food concentration and predator–prey weight

ratio could explain a considerable portion of the variability in GGE for some taxa. The remaining discussion will focus on the effects of these two variables on GGE.

On average, investigations of GGE considered for this study were conducted with prey organisms that allow optimum clearance rates. According to Hansen et al. (1994) dinoflagellates exhibit optimum clearance rates at predator–prey–equivalent spherical diameter (ESD) ratios of 1 : 1, other flagellates at 3 : 1, ciliates at 8 : 1, rotifers at 17 : 1, copepods at 18 : 1, and cladocerans at 45 : 1. Conversion of ESD to volume results in log(predator volume/prey volume) of 0 (dinoflagellates), 1.4 (other flagellates), 2.7 (ciliates), 3.7 (rotifers), 3.8 (copepods), and 5 (cladocerans). These values correspond closely to the median and mean values of carbon-specific $\log(w_2/w_1)$ shown in Fig. 1c [except for dinoflagellates, however, the only value may not be representative (Hansen 1992)]. Hence, the selection of prey species by the authors of the individual studies reflects the taxon-specific differences in size-selective feeding behavior.

There is no close match between preferred prey size and GGE; that is, food items that could be cleared with low efficiency according to Hansen et al. (1994) are still able to support growth of planktonic organisms with rather high GGE in most taxa. Size-selectivity spectra for the different taxonomic groups (Hansen et al. 1994) are shown as hatched areas in Fig. 4 in order to facilitate a comparison between the optimal $\log(w_2/w_1)$ with respect to clearance rates and GGE. GGE of nano/microflagellates, dinoflagellates, ciliates, and cladocerans was negatively correlated with $\log(w_2/w_1)$. However, after accounting for the effect of food concentration within the multivariate models for nano/microflagellates and ciliates, $\log(w_2/w_1)$ was not able to explain a significant fraction of the residual variability of GGE. Only within dinoflagellates and cladocerans did $\log(w_2/w_1)$ play an important role in the multivariate models. The importance of prey size for the growth of dinoflagellates was demonstrated by Jeong and Latz (1994) for two *Protoperidinium* species. Highest growth rates were achieved at log(predator volume/prey volume) of 0.7 and 0.9, respectively, which approximately equals $\log(w_2/w_1)$ at maximum GGE in this study (Fig. 4b). With increasing log(predator volume/prey volume), growth rates of both *Protoperidinium* species declined (Jeong and Latz 1994).

The large variability of $\log(w_2/w_1)$ for cladocerans (Fig. 1c) is not a result of examining GGE with prey of different size but of measuring GGE of organisms during ontogenetic growth fed with one prey species. Changes in GGE during ontogenetic growth have been reported in various studies of cladoceran and copepod GGE (Paffenhöfer 1976; Santer and van den Bosch 1994; Urabe and Watanabe 1991). Mechanisms underlying these changes in GGE during development are not understood. Ontogenetic differences in NGE of *Calanus pacificus* may reflect differences in size-specific rates of anabolic and catabolic processes (Vidal 1980), and the decrease in GGE with increasing age may be caused by metabolic changes resulting from the initiation of reproductive activity (Urabe and Watanabe 1991). So far, ontogenetic changes in GGE were not attributed to changes in $\log(w_2/w_1)$ and the dependence of cladoceran GGE on $\log(w_2/w_1)$ found in this survey (Table 3) may be coincidental. This is supported by the paradox that $\log(w_2/w_1)$ was most important for cladocerans, which are well known for their broad food size range. However, studies are needed that explore the relationship between GGE and $\log(w_2/w_1)$ in more detail. Future studies of GGE during ontogenetic growth should consider that culturing daphnids or copepods growing two orders of magnitude (in carbon units) with a single algal species presupposes that they are able to cope efficiently with a predator–prey weight ratio spanning at least two orders of magnitude [i.e. such studies should analyze whether the observed ontogenetic changes of GGE are attributable to changes in $\log(w_2/w_1)$].

Both NGE and AE are influenced by the ambient food concentration, resulting in a complex relationship between GGE and food concentration. NGE of planktonic crustaceans was shown to increase hyperbolically with increasing food concentration leveling off at some critical value, which will depend on the differential partitioning between maintenance metabolism and growth (Dagg 1976; Lampert 1977; Vidal 1980). In contrast to the positive correlation between food concentration and NGE, AE drops with increasing food concentrations. The synergistic effect on GGE is reflected in a positive correlation of GGE with $\log(F)$ and a negative correlation of GGE with $[\log(F)]^2$ in 19 of the 32 models listed in Table 3, which mirrors the optimum function expected from theoretical considerations.

The relationship between AE and food concentration has been discussed since Beklemsihev (1962) introduced the theory of superfluous feeding. The importance of superfluous feeding has been questioned by various authors and Conover (1966) stated that "it is difficult to see what selective advantage this mechanism could have for the zooplankton." Nevertheless, declining assimilation efficiencies with increasing food concentrations were found in many studies of metazoan zooplankton (Richman 1958; Schindler 1968; Pilarska 1977; Sharma and Pant 1984; Hamburger; and Boëtius 1987; Urabe and Watanabe 1991). Santer and van den Bosch (1994) observed shorter gut retention times with increasing food concentration, leading to less complete digestion and lower AE. *Calanus pacificus,* adapted to low food concentrations, reached AE up to 85% compared to 68% at higher food concentrations (Landry et al. 1984). Fecal pellets of copepods became more robust with increasing food concentrations, indicating decreasing AE (Dagg and Walser 1986; Butler and Dam 1994). Data on AE of protozoans are sparse. Verity (1985) could not find a dependence of AE on food concentration, whereas other observations are available that support the negative correlation between AE and food concentration for ciliates: Taniguchi and Kawakami (1985) reported higher vacuole turnover rates and incomplete digestion at higher food concentrations, and Stoecker and Evans (1985) observed undigested algal cells within the fecal pellets of ciliates at high food concentrations. Much experimental evidence therefore supports the concepts of low AE and incomplete digestion when food is abundant.

What are the adaptive reasons for incomplete digestion? One way for organisms to maximize their fitness is to maximize their energy input, i.e. their absolute assimilation and not AE. By applying reactor theory to animal digestion, Jumars et al. (1989) showed that maximum assimilation is in-

deed achieved with lower AE when food abundance is not limiting. They predicted maximum uptake of digestive products along the gut or vacuole walls (i.e. maximum assimilation rates at high food concentrations) with high feeding rates and low AE. Low AE at high food concentrations is thus no sign for nonoptimality, but rather an adaptation to reach maximum assimilation rates.

Implications for the use of GGE in models—Laboratory studies suggest that planktonic protozoans and metazoans are able to achieve maximum carbon-specific GGE predicted by theory. However, average GGE for all taxa scatter around 20–30%, i.e. maximum GGE are neither typical for planktonic protozoans nor metazoans. This is acknowledged in model studies for metazoans but often not for protozoans. One-fourth of the measured GGE of ciliates and dinoflagellates yields values below 11%, respectively 16% in the present dataset. If the grazing impact of protozoans is estimated by measuring their growth rates and assuming a rather high GGE of 40% (Weisse et al. 1990; Lignell et al. 1993), for example, the grazing impact is likely to be underestimated, especially during blooms. Ciliates and dinoflagellates are important grazers during phytoplankton blooms (Gaedke and Straile 1994; Neuer and Cowles 1994), providing abundant food for herbivores. Considering the dependency of GGE on food concentrations, a rather low GGE of ~10–20% may be more appropriate under such conditions (Jumars et al. 1989), which increases the estimate of protozoan grazing by a factor 2–4 and may lead to different conclusions with respect to the importance of different grazers and the fate of primary production.

Nutrient composition of prey items could play an important role in determining GGE, and differences in the ability to feed on nutrient-rich prey might result in taxa-specific differences in GGE under conditions of nutrient limitation. For example, the ability to feed efficiently on small nutrient-rich bacteria may allow higher GGE compared to consumers that are not able to use bacteria as additional source of nutrients. In contrast to the effects of food quantity and quality on GGE, the dependency of GGE on temperature and $\log(w_2/w_1)$ is less clear. The selection of temperature into some regression models should not be overemphasized. Organisms are generally adapted to ambient temperatures and no strong dependency of GGE on temperature is to be expected in situ. Predation is known to shift the size structure of potential prey organisms (Jürgens et al. 1994), which might have consequences for the GGE of the predator. However, for most taxa relatively high GGE were achieved over a large range of $\log(w_2/w_1)$. Further studies are warranted that address the dependency of GGE on $\log(w_2/w_1)$ explicitly.

This survey of empirical data on GGE provided no empirical evidence for the general assumption of taxon-specific GGE. The independent variables considered in this study were able to explain up to 50% of the variability of GGE in some taxa. Food concentration, i.e. $\log(F)$ and $\log(F)^2$, was the most important and reliable factor explaining variability in GGE. Methodological problems are likely to obscure stronger generalizations on factors that influence GGE. Future consideration of elemental ratios of consumer and prey organisms might considerably decrease the unexplained variability in GGE across studies. Models on carbon flow should consider the dependency of GGE on food quantity and quality instead of using constant but taxon-specific GGE.

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