

Carbon sequestration and stoichiometry of motile and nonmotile green algae

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Abstract

Actively motile, flagellated phytoplankton taxa often exploit vertical gradients in the availability of light and nutrients. The ability to move actively usually goes along with low investment in structural carbon components and should entail costs in terms of increased energy expenditure. This should be reflected in higher metabolic rates and higher light requirements for growth and, consequently, in lower light-dependent specific production rates, carrying capacities, and carbon-to-phosphorus (C:P) ratios (during phosphorus limitation) of flagellated compared to nonmotile taxa. Laboratory experiments with four flagellated and five nonmotile species of green algae, performed over a light gradient, corroborated these expectations. Parameter fits to short-term production-irradiance measurements suggest that flagellated taxa had higher respiration rates and higher light requirements for growth than nonmotile taxa. Accordingly, both short-term photosynthetic rates and longer-term (14 d) biomass accrual were lower for flagellated than for nonmotile taxa. While most of the variance in algal C:P ratios was explained by species-specific effects, there was also a tendency for algal C:P ratios to be lower in flagellated than in nonmotile taxa. Collectively, these results point at significant costs of motility, which may explain why flagellated taxa are often outcompeted by nonmotile taxa in turbulently mixed environments, where active motility is of little use.

Primary production in aquatic systems is strongly dependent on the supply with two fundamentally different kinds of essential resources: light and nutrients. While light is always supplied externally from above and decreases exponentially with depth, mineral nutrients are often scarce in the upper, illuminated water layers but abundant in deeper zones, where mineralization rates exceed uptake rates. The availabilities of light and mineral nutrients therefore frequently exhibit opposing vertical gradients (Klausmeier and Litchman 2001; Huisman et al. 2006; Jäger et al. 2008). Many phytoplankton taxa cope with this environmental challenge by influencing their vertical position in the water column through active movement or buoyancy regulation. For example, periodic vertical migrations allow motile algae to access deeper, nutrient-rich water and to adjust for optimal irradiance (Olli 1999). Hence, motile species seem to have a considerable advantage over nonmotile species, especially at low turbidity and in stratified water columns (Jones 1993; Ralston et al. 2007; Jäger et al. 2008).

The capacity to perform vertical movements is, however, of little use in deeply and well-mixed water columns, where both motile and nonmotile phytoplankton taxa are displaced passively by turbulent forces. Correspondingly, shifts from stratified to well-mixed conditions are commonly associated with shifts from flagellated or buoyant to nonmotile phytoplankton taxa (Reynolds et al. 1983; Jones and Gowen 1990; Huisman et al. 2004). The latter suggests

that there are costs to motility that play out when its potential benefits cannot be exploited. Motility should indeed involve costs in terms of energy expenditure and the provision of specific cell structures that are required for movement. While costs of motility are thus very plausible, surprisingly little is known about the nature of these costs. Theoretical considerations suggest that most planktonic protists should expend only a low (<1%) to moderate (1–10%) proportion of their total metabolic rate on motility (Raven and Richardson 1984; Crawford 1992). Intriguingly, however, empirical estimates of the cost of locomotion in rotifers amounted to 38% of total metabolism, which greatly exceeded a theoretical expectation of 1% (Epp and Lewis 1984). We are unaware of any actual measurements of the costs of motility in unicellular algae. Clearly, there is a need for more research in this area.

The uptake of dissolved inorganic nutrients and the rate of light-dependent carbon fixation by phytoplankton are not tightly coupled. For nutrients that can be effectively stored (such as phosphorus), the carbon-to-nutrient ratio in phytoplankton biomass is therefore often highly flexible and varies with environmental conditions (Sternner et al. 1997; Berger et al. 2006). For example, the carbon-to-phosphorus (C:P) ratio of phytoplankton can vary more than 20-fold as a function of the supply ratio with light and phosphorus (Urabe and Sternner 1996; Sternner et al. 1997; Striebel et al. 2008). For a number of reasons, it seems plausible to expect that actively motile and nonmotile phytoplankton taxa should, on average, differ in the flexibility and range of their biomass C:P ratios. First, in nonturbulent water columns, motile taxa can perform periodical vertical migrations between upper, illuminated, and deeper, nutrient-rich layers and should thus achieve more balanced ratios of carbon fixation to phosphorus uptake compared to nonmotile taxa. Second, everything

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else being equal, motile taxa, in particular flagellated ones, should respire more carbon and need more phosphorus than nonmotile taxa because active movement requires increased metabolism and a sufficient turnover of the phosphorus-rich molecule adenosine triphosphate (ATP). Higher metabolic rates and higher phosphorus requirements should, in turn, be reflected in lower C:P ratios of flagellated taxa. Finally, many nonmotile species of (green) algae possess cell walls containing large amounts of phosphorus-free, structural carbon compounds, such as cellulose, which shifts their C:P ratio toward higher values, especially compared to flagellated taxa.

On the basis of the previously mentioned considerations, we hypothesized that flagellated and nonmotile phytoplankton taxa should, on average, differ with respect to their energetic costs, their phosphorus requirements, and their structural carbon requirements. These differences should be reflected in on average higher metabolic rates and higher light requirements for growth and, consequently, in lower light-dependent specific production rates, carrying capacities, and C:P ratios of flagellated compared to nonmotile taxa. To test these expectations, we performed short-term production and longer-term biomass accrual experiments with four flagellated and five nonmotile phytoplankton species over a gradient of light supplies.

Methods

To minimize trait variability among the study species stemming from other sources than motility (e.g., major differences in pigment constitution), all taxa were chosen from a single taxonomic group, that is, green algae. All in all, we used nine different species: four motile, flagellated ones (*Chlamydomonas* sp., *Haematococcus pluvialis*, *Phacotus lenticularis*, and *Carteria* sp., all Chlorophyceae, order Volvocales) and five nonmotile ones (*Scenedesmus* sp. and *Golenkinia brevispicula*, both Chlorophyceae, order Chlorococcales; *Tetraedron minimum* and *Monoraphidium* sp., both Chlorophyceae, order Sphaeropleales; and *Staurastrum tetracerum*, Zygnematomyceae, order Zygnematales). We tested for group-specific differences concerning biovolume per cell ($t = 1.747$; $df = 7$; $p = 0.12$), carbon content per cell ($t = -1.25$; $df = 7$; $p = 0.25$) and per biovolume ($t = 0.597$; $df = 7$; $p = 0.57$). The t -tests revealed no significant differences between groups.

The algae were precultured over a period of several weeks prior to the experiments in a phosphorus-reduced growth medium (WC medium after Guillard and Lorenzen [1972] containing $10 \mu\text{g P L}^{-1}$). The same medium was subsequently used in all growth experiments. We established five levels of continuous incident photosynthetically active radiation: 3, 10, 20, 110, and $290 \mu\text{mol quanta m}^{-2} \text{s}^{-1}$. Each algal treatment was established with the same initial biovolume ($2 \times 10^6 \mu\text{m}^3 \text{mL}^{-1}$) and replicated three times. The treatments were arranged as semibatch cultures (10% exchange d^{-1}) in 250-mL translucent cell culture bottles in a climate chamber at 20°C . To maintain a homogeneous distribution of both algae and nutrients and

to counteract sedimentation of nonmotile species, bottles were shaken two times per day.

The growth experiments lasted for 14 d, at which point phytoplankton populations had reached the stationary phase; that is, no increase in algal biomass (as measured with an automatic particle counter) had been observed for three or more consecutive days. Particulate organic carbon and particulate phosphorus were analyzed at the start of the experiment and after 14 d of incubation. To determine particulate organic carbon and particulate phosphorus, we filtered samples from each culture bottle onto precombusted, acid-washed glass-fiber filters (Whatman GF/F). Particulate organic carbon was measured with an elemental analyzer (CE Instruments), and particulate phosphorus was measured photometrically after sulfuric acid digestion followed by molybdate reaction.

We measured specific net primary production of all nine species over the same gradient of light intensities as used in the growth experiments. We quantified primary production with the oxygen method after 4 h of incubation (Wetzel and Likens 2003). The algae were precultured, and the measurements were conducted in the same phosphorus-reduced growth medium as was used in the growth experiments. Again, each algal treatment (taxon \times light intensity combination) was started at the same initial algal biovolume and replicated three times.

The data on biomass accrual (particulate organic carbon), phytoplankton C:P ratios, and specific net primary production were all analyzed with a nested 2-way analysis of covariance with incident radiation as a continuous treatment factor, algal motility as a categorical treatment factor, and species as a random factor nested within motility. All response variables and incident radiation were log transformed prior to statistical analyses.

To quantitatively describe the dependence of specific net primary production of each species on light intensity, we used nonlinear least square regressions to fit a modified Michaelis–Menten–type model to the data from the primary production assays:

$$\text{sNPP} = y_0 + \frac{(P_{\max} \times \text{light intensity})}{(k_s + \text{light intensity})} \quad (1)$$

This allowed us to estimate light saturated specific photosynthetic rates (P_{\max}), half-saturation constants (k_s), and basal respiration rates (y_0) for each species. In addition, the intercept of the fitted net photosynthesis curves with the x-axis was used to estimate the light intensity ($\text{light}_{\text{comp}}$) at which gross photosynthesis is sufficient to compensate for respiratory losses. As an additional measure of the costs of motility, we determined the ratio of specific respiration to maximal specific production (Harris 1978).

Results

Specific net primary production—Specific net primary production in the short-term incubations increased with light availability (Fig. 1; Table 1). Equation 1 gave excellent fits to the relationships between light intensity

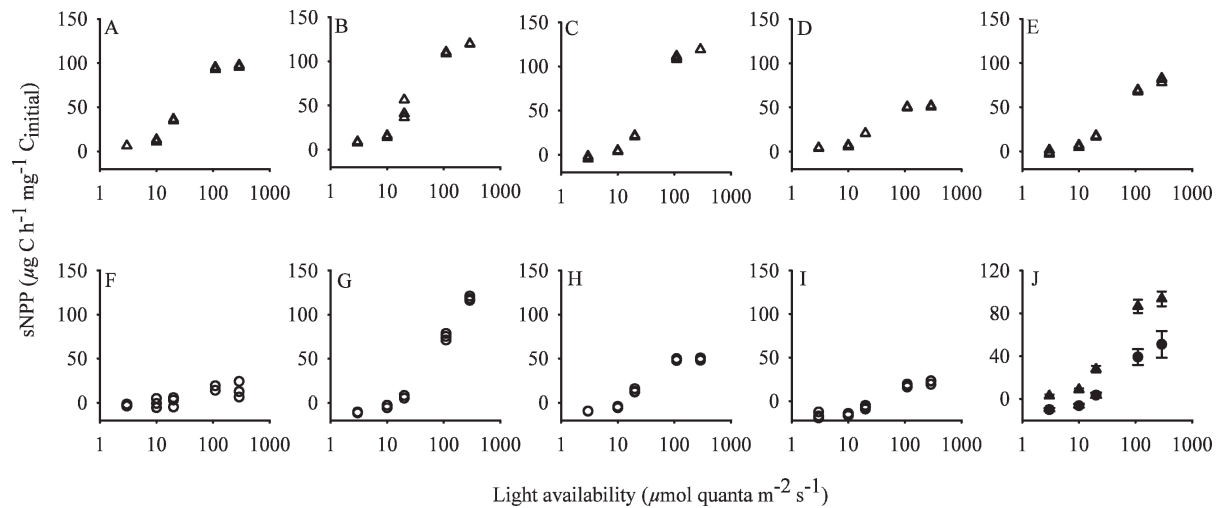


Fig. 1. Specific net primary production (μg carbon assimilation per mg initial biomass [POC] per hour) of nonmotile species—triangles; (A) *Golenkinia brevispicula*; (B) *Monoraphidium* sp.; (C) *Scenedesmus* sp.; (D) *Staurastrum tetracerum*; (E) *Tetraedron minimum*—and motile species—circles; (F) *Carteria* sp.; (G) *Chlamydomonas* sp.; (H) *Haematococcus pluvialis*; (I) *Phacotus lenticularis*—as a function of incident radiation. (J) Mean values of motile (circles) and nonmotile (triangles) species with standard errors; note different y-axis scaling.

and specific net primary production of all nine species ($R^2 \geq 0.97$ and $p < 0.0001$ for all species except *Carteria*, where $R^2 = 0.71$ and $p = 0.0006$). There was no clear difference in the estimated half-saturation constants (k_s) between motility categories (flagellated vs. nonmotile species; Table 2). In contrast, there was a trend for lower maximum photosynthetic rates (P_{\max}) and higher specific respiration rates in flagellated compared to nonmotile species (Table 2). While none of these trends was statistically significant, their combination yielded significant differences in primary production between flagellated and nonmotile taxa. In particular, flagellated species needed higher light intensities to balance respiratory losses ($\text{light}_{\text{comp}}$; Table 2) and had a higher ratio of respiration to P_{\max} (Table 2), and their specific net primary production was on average lower over the entire range of light intensities compared to nonmotile species (Fig. 1J; Table 1).

Phytoplankton biomass and C:P ratios—In agreement with the short-term primary production essays, the biomasses of all flagellated and nonmotile taxa in the stationary phase increased with increasing light availability in the longer-term experiments, reaching maximum values close to 5 mg C L^{-1} and about 3 mg C L^{-1} for the most

productive nonmotile and flagellated species, respectively (Fig. 2; Table 1). The light levels at which different species reached their maximum biomasses ranged from 20 to $290 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$. On average, flagellated species attained lower biomasses than nonmotile species, the differences being small at light intensities $\leq 10 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ but rather large at light intensities of $20 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ and above (Fig. 2J; motility \times light interaction, Table 1).

Phytoplankton C:P ratios also increased with increasing light availability, with several species reaching molar ratios of up to 1200 at light intensities of $110 \mu\text{mol quanta m}^{-2} \text{ s}^{-1}$ and above (Fig. 3; Table 1). On average, nonmotile species tended to have higher C:P ratios than flagellated ones at all but the lowest light intensity (Fig. 3J; motility \times light interaction, Table 1). Most of the variance in algal C:P ratios was, however, explained by species-specific differences within rather than between motility categories, suggesting that some species within each motility category have inherently low C:P ratios (e.g., *Tetraedron* sp., *Phacotus* sp., and *Carteria* sp.), while others attain inherently high C:P ratios (e.g., *Scenedesmus* sp., *Staurastrum* sp., and *Haematococcus pluvialis*) in high-light environments.

Table 1. Summary of nested analyses of covariance of the contributions of light availability, motility, and species (nested within motility) to the total variances in specific net primary production (sNPP), carbon biomass accrual (POC), and molar carbon-to-phosphorus ratios (C:P).

	sNPP			POC			C:P		
	SS	df	<i>p</i>	SS	df	<i>p</i>	SS	df	<i>p</i>
Light	12.86	1, 124	0.0001	3.63	1, 122	0.0001	3.58	1, 122	0.0001
Motility	3.82	1, 7	0.011	1.29	1, 7	0.175	0.33	1, 7	0.588
Motility \times light	0.15	1, 124	0.0001	0.39	1, 122	0.0001	0.13	1, 122	0.097
Species	2.26	7, 124	0.011	3.97	7, 122	0.0001	7.16	7, 122	0.0001

Table 2. Photosynthetic parameters estimated from photosynthesis–light intensity curves fitted according to Eq. 1. Shown are separate parameter estimates (with standard error in parentheses) for each species with values of the regression fits (all $p \leq 0.0006$) as well as the average parameter values (with standard errors) for motile and nonmotile species. Also shown are the p -values of t -tests comparing average parameter values of motile and nonmotile species.

	<i>Golenkinia</i> sp.	<i>Monora-</i> <i>plidium</i> sp.	<i>Scene-</i> <i>desmus</i> sp.	<i>Staura-</i> <i>strum</i> sp.	<i>Tetra-</i> <i>dron</i> sp.	Mean nonmotile species	<i>Carteria</i> sp.	<i>Chlamy-</i> <i>domonus</i> sp.	<i>Haemato-</i> <i>coccus</i> sp.	<i>Phacotus</i> sp.	Mean motile species	Comparison motile vs. nonmotile (p)
Light _{comp} (μmol photons m ⁻² s ⁻¹)	2.5	2.03	6.6	2.16	5.11	3.98 (1.01)	10.78	12.95	9.67	34.03	16.86 (5.77)	0.005
Respiration (μg C mg C _{init} ⁻¹ h ⁻¹)	8.06 (5.39)	7.48 (5.8)	19.55 (6.34)	3.94 (3.08)	9.40 (2.59)	9.69 (2.63)	5.29 (4.21)	18.05 (1.47)	19.9 (3.9)	21.43 (2.17)	16.17 (3.69)	0.25
P_{max} (μg C mg C _{init} ⁻¹ h ⁻¹)	123.99 (5.59)	149.02 (6.3)	171.64 (8.43)	64.79 (3.11)	110.25 (3.74)	123.94 (18.15)	24.29 (4.47)	197.98 (6.36)	80.24 (3.81)	52.43 (2.82)	88.74 (38.16)	0.23
k_s (μmol photons m ⁻² s ⁻¹)	35.93 (8.58)	38.38 (8.78)	51.32 (13.03)	33.26 (8.3)	54.86 (9.48)	42.75 (4.33)	38.64 (37.10)	129.04 (12.48)	29.32 (6.98)	49.23 (14.04)	61.56 (22.86)	0.51
Respiration × P_{max}^{-1}	0.07	0.05	0.11	0.06	0.09	0.08 (0.01)	0.22	0.09	0.25	0.41	0.24 (0.07)	0.031
r^2	0.98	0.98	0.98	0.97	0.99	—	0.71	0.99	0.97	0.97	—	—

Discussion

We had hypothesized that, compared to nonmotile algae, flagellated algal taxa should have higher metabolic rates and higher light requirements for growth, and, as a result, lower light-dependent specific production rates, carrying capacities, and C:P ratios. These expectations were largely fulfilled in our comparison of nonmotile and motile, flagellated green algae. While the trend for higher respiration rates of flagellated compared to nonmotile species was not statistically significant, flagellated taxa required a higher light intensity for positive net photosynthesis and attained lower photosynthetic rates at all levels of incident radiation than did nonmotile taxa. Indeed, our photosynthetic measurements corroborate earlier measurements (Harris 1978; Cushing 1989) showing that the ratio of specific respiration to maximal specific production is higher for motile than for nonmotile species.

Lower photosynthetic rates of flagellated taxa in short-term incubations were subsequently reflected in lower steady-state biomasses and C:P ratios, the differences between flagellated and nonmotile taxa being most pronounced at the highest levels of incident radiation. Specific net primary production, for example, was negative for all flagellated taxa at the lowest incident radiation but positive for nonmotile taxa. Nevertheless, longer-term biomass accrual did not differ between flagellated and nonmotile taxa at the lowest incident radiation. This suggests that compensatory physiological and/or ecological adaptations (e.g., increased mixotrophic nutrition at low light levels) may have taken place over the course of the biomass accrual experiments. It also suggests that the most important costs of motility may be in terms of a reduced capacity to effectively use a higher light supply rather than in terms of a higher basic metabolism.

The primary production measurements suggest that, at least in the short term, flagellated species needed higher minimal light intensities to have a positive carbon balance (Table 2), indicating that actively motile species needed more energy to compensate for respiration losses. Our laboratory experiment was conducted in well-mixed vessels with limited volume. Thus, significant spatial heterogeneity in resource availability was absent from our experiment, and flagellated species could not take advantage of their ability to move. The lower biomasses attained by flagellated species compared to nonmotile species therefore point at the costs and disadvantages of this strategy in a spatially homogeneous environment. In turbulent pelagic environments, where directional movement is impossible, flagellated species would thus be expected to be inferior competitors. Conversely, flagellated species would be expected to be superior competitors in stably stratified environments, where the spatial separation of high-light and high-nutrient environments is often pronounced. A recent mesocosm experiment investigating the effects of turbulence and water column depth on phytoplankton community composition is in agreement with this hypothesis. Turbulent water columns were dominated by nonmotile species such as diatoms, whereas stratified water

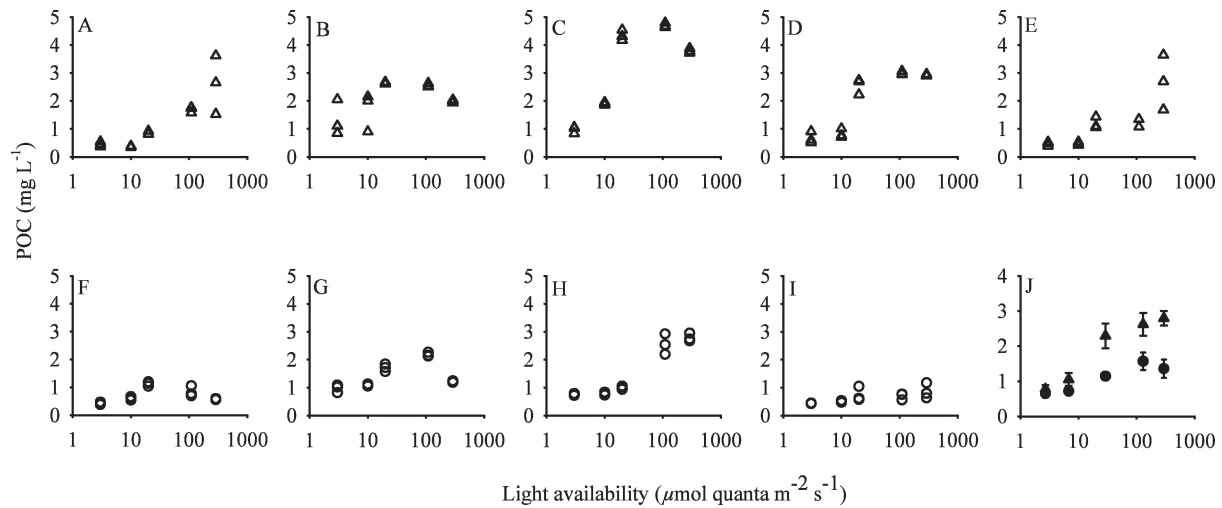


Fig. 2. Biomass, determined as particulate organic carbon at the end of the experiment (day 14), of (A–E) nonmotile (triangles) and (F–I) motile (circles) species (labeling as in Fig. 1) as a function of incident radiation. (J) Mean values of motile (circles) and nonmotile (triangles) species with standard errors; note different y-axis scaling.

columns were dominated by flagellated taxa (Jäger et al. 2008).

Nearly all flagellates use a combination of phototrophic and phagotrophic production (Raven 1997), suggesting that they might use mixotrophic nutrition as a means of gaining sufficient phosphorus for motility and growth in environments where dissolved phosphorus is scarce. Phosphorus is often several orders of magnitude more concentrated in the biomass of bacteria than in the water (Vadstein 2000). Mixotrophic algae that feed on bacteria could access this additional phosphorus source. In a study of the effect of mixotrophy on phytoplankton carbon to phosphorus stoichiometry, mixotrophic species showed indeed considerably lower C:P ratios than purely autotrophic algae (Katechakis et al. 2005). The mixotrophic species

studied by Katechakis et al. (2005) were all flagellated, while the autotrophs were all nonmotile. Thus, the question remains whether lower C:P ratios of flagellates are a consequence of motility, mixotrophic nutrition, or both. Our data suggest that motility per se may not be sufficient to explain the generally lower C:P ratios of flagellates since we found substantial variation among species within motility categories, indicating that other traits in addition to motility contribute to species-specific responses. Therefore, future research should examine the amount of mixotrophic nutrition within motile phytoplankton species and the contribution of mixotrophy and motility to phytoplankton biomass stoichiometry.

While experimental manipulations of light and phosphorus availability have frequently resulted in strong

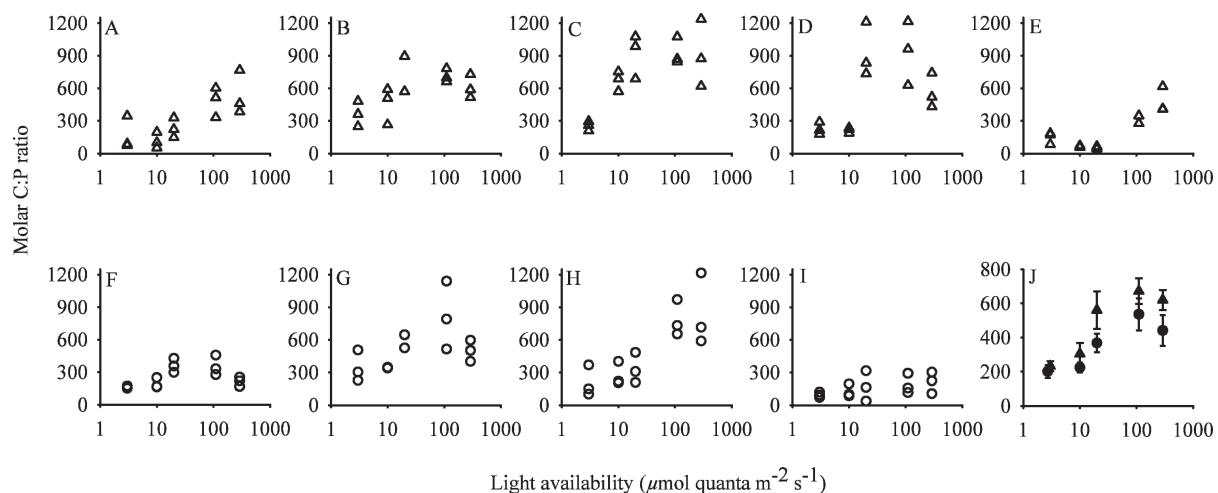


Fig. 3. Molar carbon-to-phosphorus ratios at the end of the experiment (day 14) of (A–E) nonmotile (triangles) and (F–I) motile (circles) species (labeling as in Fig. 1) as a function of incident radiation. (J) Mean values of motile (circles) and nonmotile (triangles) species with standard errors; note different y-axis scaling.

effects on the carbon-to-phosphorus stoichiometry of phytoplankton biomass (Urabe et al. 2002; Diehl et al. 2005; Striebel et al. 2008), sometimes such manipulations may induce only weak stoichiometric responses. On the basis of our data, we suggest that the relative contribution to total phytoplankton biomass by taxa with highly flexible C:P ratios (such as nonmotile green algae) vs. taxa with limited stoichiometric flexibility (such as flagellates) can explain some of the variation in phytoplankton stoichiometric responses to variations in light and nutrient supply. In line with this, Jäger et al. (2008) observed that variation in algal C:P ratios among mesocosms differing in water column depth (and thus in ratios of light to phosphorus supply) was considerably lower in stratified water columns with a high proportion of motile algae than in turbulently mixed water columns dominated by nonmotile taxa.

Shifts in biomass composition of phytoplankton communities may have consequences beyond phytoplankton ecophysiology. Phytoplankton–zooplankton interactions can be strongly influenced by phytoplankton stoichiometry (Sterner and Hessen 1994; Andersen et al. 2004; Diehl 2007). Fast-growing herbivorous zooplankton species, such as *Daphnia*, have high demands for phosphorus and therefore exhibit relatively low biomass C:P ratios. Consequently, low biomass C:P ratios and the absence of distinct cell walls can result in high assimilation efficiencies of actively motile phytoplankton taxa when grazed by *Daphnia* (Katechakis et al. 2005). The proportion of motile species within phytoplankton communities may therefore influence the transfer efficiency between phytoplankton and fast-growing zooplankton and thus potentially strongly affect pelagic ecosystem dynamics. Studies manipulating the proportion of motile species in phytoplankton communities grazed by *Daphnia* are needed to investigate this possible link between the functional composition of phytoplankton communities and herbivorous zooplankton dynamics.

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