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Photosynthesis and respiration in marine phytoplankton: Relationship with cell size, taxonomic affiliation, and growth phase

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ABSTRACT

We determined the rates of photosynthesis and respiration in batch cultures of 22 marine phytoplankton species from five phyla covering a range of 7 orders of magnitude in cell size. Rates were determined during the exponential growth phase and also during the stationary phase, when cell growth was limited by nitrogen availability. We observed, in all growth phases, a curvature in the size scaling of carbon fixation, such that the relationship between carbon-specific photosynthesis and cell size was unimodal, with the highest rates being measured in intermediate-size species. The log–log relationship between individual metabolic rates and cell size showed an overall lineal pattern with a slope equal or near 1, irrespective of whether volume or carbon is used as a metric for cell size. Thus, our results demonstrate that when small species (<50 μm^3 cell diameter) are considered together with intermediate- and large-sized species phytoplankton metabolism does not follow Kleiber's 3/4-power rule. Considering all species together, respiration losses represented on average 9% and 22% of total carbon fixation during the exponential growth and stationary phases, respectively. Carbon-specific respiration was largely independent of cell size and growth phase, but tended to take higher values in the dinoflagellates. During the stationary growth phase, and contrary to other groups, most diatoms were able to maintain carbon fixation rates similar to those measured during exponential growth. Our results highlight the ability of intermediate-to-large size species to sustain high metabolic rates in spite of their cell size, which helps to explain why they dominate phytoplankton blooms in the ocean.

1. Introduction

The basic observation that small organisms tend to have higher growth rates and biomass-specific metabolic rates than larger organisms has driven the search for universal scaling laws that could explain the flux of energy through individuals and, by extension, communities and ecosystems (Brown et al., 2004). Size-scaling relationships can be represented using power functions such as:

$$R = aM^b \quad (1)$$

where R is an individual metabolic rate, M is body size (mass or volume), b is the size-scaling exponent and a is a coefficient. After taking logarithms, Eq. (1) can also be written as:

$$\log R = \log a + b \log M \quad (2)$$

where b is the slope of the linear function. Since Kleiber first reported that metabolic rates in birds and mammals scale with body mass with a b value of 3/4 (Kleiber, 1932), this allometric relationship has proven to be applicable to a wide range of organisms, from unicells to multicellular organisms including large plants and animals (Savage et al., 2004).

Phytoplankton cell size, which ranges over more than 9 orders of magnitude, from <1 μm^3 in the smallest cyanobacteria to >10^9 μm^3 in the largest diatoms, can have a large effect on different metabolic rates (Chisholm, 1992; Finkel et al., 2010). It is unclear, however, to which extent Kleiber's rule can be applied to phytoplankton. While several studies have confirmed the applicability of the 3/4-power rule for phytoplankton carbon fixation (Blasco et al., 1982; López-Urrutia et al., 2006; Taguchi, 1976) and respiration (Blasco et al., 1982; Laws, 1975), some others have found size-scaling relationships with b values that deviate significantly from 3/4. In some cases, the values of b obtained were lower than 3/4, which implied a stronger decrease of metabolic rates with increasing cell size (Finkel et al., 2004), whereas in other studies b was higher than 3/4, indicating a smaller degree of size-dependence (Banse, 1976; Lewis, 1989). Recently, field-based studies have reported b values not significantly different from 1 (Huete-Ortega et al., 2012; Marañón, 2008; Marañón et al., 2007).

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These isometric size-scaling relationships mean that individual metabolic rates are directly proportional to cell size, and therefore that biomass-specific metabolic rates in phytoplankton are independent of cell size. However, there are methodological uncertainties involved in the determination of size-dependent metabolic rates in natural assemblages. For instance, one possibility is that a stronger grazing pressure upon smaller cells during experimental incubations may bias the slope values of the resulting size-scaling relationships.

The different results obtained in previous studies may have been due to variability in experimental methods, the use of different ranges in cell size, the presence of sub-optimal growth conditions, or the fact that the species studied belonged to a single taxonomic group and/or covered a relatively narrow range in cell size. This uncertainty over the size-scaling of phytoplankton metabolism and growth is particularly relevant, since ocean ecological models often require the representation of size-dependent physiological traits of phytoplankton (Armstrong, 1994; Irwin et al., 2006; Ward et al., 2012) but rely on the use of size-scaling parameters obtained from literature reviews (Litchman et al., 2007; López-Urrutia et al., 2006). While undoubtedly useful to provide general patterns, these literature-based studies, however, suffer from the lack of methodological consistency among studies and the disparate growth conditions of the cultures used, which often results in noisy size-scaling relationships with a large amount of unexplained variance.

Elucidating whether or not the size-scaling of phytoplankton metabolism follows the general allometric rule is necessary not only to verify if broad macroecological patterns are valid across all domains of life (DeLong et al., 2012) but also to identify the ultimate mechanisms that control the spatial and temporal variability of phytoplankton size structure in the sea (Chisholm, 1992; Kiørboe, 1993). Since cell size is a key functional trait in phytoplankton, understanding its relationship with growth and metabolism is crucial to define the ecological strategies of different functional groups and how environmental forcing controls the assembly of communities in the ocean (Litchman et al., 2007).

We have studied the growth, biochemical composition, and carbon and nitrogen metabolism of 22 phytoplankton species grown in batch cultures. All cultures had the same conditions and all measurements were performed using the same protocol, thus avoiding methodological differences that may influence the results. Recently we have shown that phytoplankton metabolism does not follow Kleiber's power rule when cells are growing exponentially under optimal conditions (López-Sandoval et al., 2013; Marañón et al., 2013). Here we aim to determine if the same result holds for different growth phases, particularly when cells are experiencing nutrient deficiency, a situation that is often encountered in nature. In addition, we analyze the differences between taxonomic groups in terms of growth and carbon metabolism. Our results provide general patterns regarding the taxon- and cell size-dependence of metabolic rates, which has implications to understand the dynamics of phytoplankton community structure in the sea.

2. Methods

2.1. Phytoplankton cultures

A detailed description of culture conditions and the determination of cell abundance, size, and biomass have been given previously (López-Sandoval et al., 2013; Marañón et al., 2013). Briefly, the 22 phytoplankton species used for this study (Table 1) were grown in batch cultures at 18 ± 0.5 °C under an irradiance of 250 μmol photons m^{-2} s^{-1} provided by white light fluorescent tubes with a light:dark cycle of 12:12 h. Growth media were prepared with autoclaved, 0.2-μm filtered seawater collected from the Ría de Vigo (Spain). We used the f/4 medium for most species, K/2 medium for *Ostreococcus tauri* and *Micromonas pusilla*, and PCR-SC11/2 for *Prochlorococcus* sp. In all cases, nitrogen concentrations were modified so that the N/P molar ratio was ca. 6 and nitrogen limitation was ensured during the stationary growth phase. Cultures were acclimated to the temperature and irradiance conditions and to the growth medium for at least three transfers before the beginning of each experiment.

During the last growth cycle, daily samples were taken for determination of cell abundance, in vivo fluorescence, chlorophyll *a* concentration, biovolume, the photosystem II maximum photochemical efficiency

Table 1
Mean cell biovolume and biomass, photosystem II maximum quantum efficiency (F_v/F_m), carbon-specific total photosynthesis (P^C) and respiration (R^C), and the respiration to photosynthesis ratio (R:P) for each species during the exponential growth (Exp), and stationary (Sta) phases. P^C is also given for the intermediate (Int) phase. R:P is computed as $100 \times R^C / P^C$. Biomass data correspond to the mean value measured during all growth phases. NA, data not available.

Class	Species	Culture medium, NO^{3-}/NH_4^+	Biovolume (μm³)	Biomass (pgC cell^{-1})	F_v/F_m		P^C (h^{-1})			R^C (h^{-1})		R:P	
					Exp	Sta	Exp	Int	Sta	Exp	Sta	Exp	Sta
Bacillariophyceae	*Skeletonema costatum*	f/4, f/16[a]	242	22	NA	NA	0.14	0.13	0.16	0.004	0.007	2.5	4.3
Bacillariophyceae	*Thalassiosira rotula*	f/8, f/32[a]	2597	203	0.62	0.53	0.07	0.09	0.1	0.003	0.006	4	6
Bacillariophyceae	*Phaeodactylum tricornutum*	f/4, f/16[a]	93	5	0.63	0.33	0.2	0.15	0.03	0.003	0.002	1.3	7
Bacillariophyceae	*Thalassiosira weissflogii*	f/4, f/16[a]	1163	54	0.69	0.52	0.12	0.12	0.06	0.003	0.002	2.2	2.6
Bacillariophyceae	*Melosira nummuloides*	f/4, f/16[a]	2285	317	0.62	0.52	NA	NA	0.08	0.002	0.002	NA	2.6
Bacillariophyceae	*Coscinodiscus radiatus*	f/4, f/16[a]	81,955	3983	0.65	0.63	0.02	0.02	0.03	0.003	0.004	11.9	11
Bacillariophyceae	*Coscinodiscus wailesii*	f/4, f/16[a]	2,498,458	77,720	0.71	0.72	0.05	0.02	0.03	0.005	0.001	9.8	4.9
Bacillariophyceae	*Ditylum brightwellii*	f/4, f/16[a]	75,827	2551	0.6	0.6	0.05	0.05	0.04	0.003	0.004	9.5	9.9
Peridinea	*Protoceratium reticulatum*	L/2, L/8[b]	23,823	983	0.61	0.55	0.05	0.04	0.02	0.004	0.005	8.1	26.1
Peridinea	*Akashiwo sanguinea*	L/2, L/8[b]	47,349	2746	0.5	0.47	0.05	0.01	0.01	0.008	0.004	17.6	60.2
Peridinea	*Alexandrium minutum*	L/2, L/8[b]	5575	895	0.6	0.44	0.03	0.02	0.02	0.007	0.005	24.3	26.9
Peridinea	*Alexandrium tamarense*	L/2, L/8[b]	88,836	1435	0.57	0.47	0.04	0.03	0.02	0.01	0.008	26.6	49.6
Prymnesiophyceae	*Gephyrocapsa oceanica*	f/4, f/16[a]	82	12	0.66	0.62	0.17	0.08	0.03	0.005	0.005	3	17.2
Prymnesiophyceae	*Emiliania huxleyi*	f/4, f/16[a]	158	7.8	0.64	0.64	0.12	0.11	0.11	0.004	0.003	3.1	2.3
Prymnesiophyceae	*Calcidiscus leptoporus*	f/4, f/16[a]	51	4.2	0.67	0.53	NA	0.16	0.13	0.003	0.003	NA	2.6
Prymnesiophyceae	*Isochrysis galbana*	f/8, f/32[a]	64	4.6	0.68	0.55	0.1	0.05	0.03	0.007	0.004	6.6	12.2
Pavlovophyceae	*Pavlova lutheri*	f/4, f/16[a]	45	5.1	0.62	0.57	0.14	0.1	0.06	0.007	ND	5.4	NA
Eustigmatophyceae	*Nannochloropsis gaditana*	f/4, f/16[a]	8.6	2	0.57	0.56	0.07	0.04	0.03	0.005	0.002	7.4	8.1
Mamiellophyceae	*Micromonas pusilla*	K/2, K/8[c]	10.7	1.8	0.59	0.29	0.07	0.01	0.02	0.007	0.005	9.8	30.2
Mamiellophyceae	*Ostreococcus tauri*	K/2, K/8[c]	2.4	0.69	0.62	0.12	0.04	0.02	0.01	0.002	0.004	5.8	80.9
Cyanophyceae	*Synechococcus* sp.	f/4, f/16[a]	0.41	0.1	NA	NA	0.04	0.06	0.01	0.004	0.004	12.4	29.6
Cyanophyceae	*Prochlorococcus* sp.	PCR-S11, PCR-S11/4[d]	0.12	0.04	0.45	NA	0.02	0.01	0	0.002	0.003	11.9	67

[a] Guillard (1975).
[b] Guillard and Hargraves (1993).
[c] Keller and Guillard (1985).
[d] Roscoff Culture Collection's recipe.