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Cell volumes of marine phytoplankton from globally distributed coastal data sets

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ABSTRACT

Globally there are numerous long-term time series measuring phytoplanton abundance. With appropriate conversion factors, numerical species abundance can be expressed as biovolume and then converted to phytoplankton carbon. To-date there has been no attempt to analyze globally distributed phytoplankton data sets to determine the most appropriate species-specific mean cell volume. We have determined phytoplankton cell volumes for 214 of the most common species found in globally distributed coastal time series. The cell volume, carbon/cell and cell density of large diatoms is 200,000, 20,000 and 0.1 times respectively, compared to small diatoms. The cell volume, carbon/cell and cell density of large dinoflagellates is 1500, 1000 and 0.7 times respectively, compared to small dinoflagellates. The range in diatom biovolumes is 100 times greater than across dinoflagellates (i.e. >200,000 vs. 1500 times) and within any diatom species, the range in biovolume is up to 10-fold. Variation in diatom cell volumes are the single largest source of uncertainty in community phytoplankton carbon estimates and greatly exceeds the uncertainty associated with the different volume to carbon estimates. Small diatoms have 10 times more carbon density than large diatoms and small dinoflagellates have 1.5 times more carbon density than large cells. However, carbon density varies relatively little compared to biovolume. We recommend that monthly biovolumes should be determined on field samples, at least for the most important species in each study area, since these measurements will incorporate the effects of variations in light, temperature, nutrients and life cycles. Since biovolumes of diatoms are particularly variable, the use of size classes will help to capture the percentage of large and small cells for each species at certain times of the year. This summary of global datasets of phytoplankton biovolumes is useful in order to evaluate where locally determined biovolumes lie within the global spectrum of spatial and temporal variations and may be used as a species cell volume reference where no locally determined volume estimates are available. There is a need to adopt standard protocols for measuring biovolumes and documenting the accompanying metadata which would improve inter-comparability among time series data sets.

1. Introduction

There is considerable concern about the long-term changes that are occurring in coastal ecosystems, leading to the development of

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management strategies and mitigation procedures to deal with current and future anthropogenic stressors and climatic changes. One way to capture this long-term variability in phytoplankton is to set up time series sampling stations and document the variations in abundance and species composition in relation to changes of environmental variables (Zingone et al., 2010). Two of the most important variables in phytoplankton time series are the estimates of the carbon biomass as a common currency, and the abundance of different species since they shape the planktonic food web and determine the productivity of the whole pelagic ecosystem. Chl *a* as a proxy for determining phytoplankton carbon is frequently used, but there are large variations in the C/Chl *a* ratio among and within a species due to environmental factors such as seasonal changes in temperature and limitations in nutrients and light (Taylor et al., 1997). More importantly, when bulk measures such as Chl *a* are used, no information is obtained on the amount of carbon that is contributed by individual species.

For various ecosystem applications and modeling, it is necessary to convert phytoplankton cell counts into a common currency such as wet weight, carbon or nitrogen, because a large number of small cells are equivalent to a few very large cells in terms of carbon biomass that is utilized as food for the next trophic level. To convert cell numbers to carbon biomass for primary producers, it is necessary to know the cell volume of the various species in the sample, and the carbon per cell volume (carbon density) multipliers for each species (Verity et al., 1992; Montagnes et al., 1994; Menden-Deuer and Lessard, 2000).

There are several ways to calculate cell volumes. The 'gold standard' is to determine the geometrical shape that approximates the shape of the cell and then make measurements of the dimensions to enter into the formula for that particular geometrical shape (Mullin et al., 1966; Strathmann, 1967; Eppley et al., 1970; Taguchi, 1976; Wheeler, 1999). Some of the challenges in this approach are that different investigators may choose a different geometric shape than the recommended shape (Hillebrand et al., 1999; Sun and Liu, 2003) for the same species, especially for cells with a complex shape. For small cells, it may be difficult to measure the dimensions accurately due to the 'halo effect' around a small cell under the light microscope. In addition, the 'hidden dimension' (i.e. the depth dimension) is difficult to measure since cells are viewed in two dimensions under the microscope. Yet the use of microscopically determined cell volumes is the only way to resolve C biomass estimates at the species level (Montagnes et al., 1994; Menden-Deurer and Lessard, 2000). Alternatively, there are several automated or semi-automated methods for estimating cell volume include the Coulter counter (Boyd and Johnson, 1995), image analysis (FlowCAM) (Sieracki et al., 1998; Jakobsen and Carstensen, 2011), and flow cytometry (Olson et al., 1985), although they all have some limitations. A recent improvement is the direct measurement of a biovolume in 3D confocal microscopy, which however has been tested for only a few selected species (Roselli et al., 2015).

Under the influence of seasonally varying environmental factors, the cell volume of diatoms often varies during the season with different size classes occurring for a species (Olenina et al., 2006; Jakobsen et al., 2015). When cells become nutrient (N, P or Fe) limited, they are usually smaller (Harrison et al., 1990; Davidson et al., 2002; Timmermans and van der Wagt, 2010). In contrast, diatoms become larger under silicate limitation because there is not enough silicate for the two daughter cells to complete the siliceous valves between them and therefore they form a biprotoplastic cell (Harrison et al., 1977). Under light limitation, cells are usually smaller (Thompson et al., 1991). There is no consistent trend with temperature since cell volume has been reported to decrease (Montagnes and Franklin, 2001) or increase with increasing temperatures (Thompson et al., 1992). Under a range of salinities from 5 to 25 in an Indian estuary, Mitra et al. (2012) found that cells were smaller at higher salinities.

In addition to environmental factors, cell size varies during life cycles. The importance of asexual and sexual reproduction in diatom life cycles and the relation to variations in cell size is well documented (von Dassow et al., 2006; D'Alelio et al., 2010). Sexual reproduction can be induced by environmental stresses such as nutrient limitation since sexual reproduction is more readily inducible in small cells (Harrison et al., 1976; Costello and Chisholm, 1981; Edlund and Stoermer, 1997; von Dassow et al., 2006). One of the advantages of sexual reproduction for diatoms is that the return to a large cell volume usually coincides with a much higher growth rate (i.e. a reinvigoration or rejuvenation of the cell's physiological processes) (Harrison et al., 1976; Costello and Chisholm, 1981; Saravanan and Godhe, 2010) and surprisingly, a lower sinking rate for new larger post-auxospore cells of *Ditylum* (Waite and Harrison, 1992). Sexual reproduction may occur at various times, but at least in diatoms, there is a tendency for sex to occur in the autumn when cells are smaller probably due to summer nutrient limitation (Mizuno and Okuba, 1985; Waite and Harrison, 1992; Koester et al., 2007; D'Alelio et al., 2010; von Dassow and Montresor, 2011). An abrupt increase in cell volume may also occur vegetatively and is termed vegetative enlargement (Gallagher, 1983; Nagai et al., 1995).

Diatom cell sizes range from a few microns up to 2 mm (i.e. 1000x) and consequently their biovolumes can span about 9 orders of magnitude. Therefore, it is necessary to be able to convert cell abundance into cellular carbon, especially for trophic models. Because determining biovolume microscopically is tedious and time consuming, it is not surprising that there are only a few data sets available, even for ecologically important species associated with time series programs. Furthermore, few of these data have ever been published.

Many time series have abundance data but they lack the species-specific cell volume data to convert abundance into carbon biomass. Hence, there is a need for a reference list of biovolumes for a large number of species from different coastal sites. The objective of this study was to collect and analyze biovolume data for the most common (i.e. occur >5 times) phytoplankton species found in globally distributed coastal time series data sets. Biovolumes have been determined for Baltic Sea phytoplankton (Olenina et al., 2006) and for some diatoms (Leblanc et al., 2012), but to-date there has been no attempt to analyze global data sets to determine the variation in cell volume for a large number of phytoplankton species from various coastal oceans.

2. Methods

2.1. The data sets

We obtained 40 published and unpublished cell volume data sets from various coastal regions around the world that were often produced in conjunction with time series monitoring programs. The several datasets from northern San Francisco Bay and from Chesapeake Bay were merged into one data set for each area to avoid duplication, making a total of 36 sites (Table 1). The data sets were cleaned up by merging synonyms, correcting spelling mistakes, removing non-relevant species and up-dating the nomenclature using WoRMS (World Registry of Marine Species; (https://marinespecies.org)). This important process was by far the most laborious step to harmonize and aggregate these 36 data sets into one data base (Table 2). ALGAEBASE (http://www.algaebase.org/) was used for additional nomenclatural validation and up-dating and in some cases, more recent literature not yet incorporated