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Biovolume and biomass estimates of key diatoms in the Southern Ocean

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ABSTRACT: Linear measurements of 31 Southern Ocean diatom species or genus groupings are presented and used in the derivation of species-specific biovolume, biomass and surface to volume ratios. Species measurements are in tune with summarised values in the literature and range from 2.6 to 2296 µm in length and 8.5 to 140 µm in diameter. Average cell volume ranged from 63 to 1.43 × 10^5 µm^3 and biomass from 10 to 3686 pg C cell^{-1}, the values being smallest in pennate shaped species and greatest in cylindrical centrics. The 31 species can be divided into 7 small, 12 intermediate and 12 large biomass contributors based on their cell volume and/or their surface to volume ratio. Carbon biomass estimates from biovolume equations are discussed and suggest that future work including large Southern Ocean species is warranted. Species-specific biomass values reported here should serve as a baseline for future analyses of major diatom carbon contributors in the generally high nutrient, low chlorophyll Southern Ocean.

KEY WORDS: Diatoms · Size measurements · Cell biovolume · Carbon biomass · Kerguelen Plateau

INTRODUCTION

Diatoms are a dominant group of the Southern Ocean phytoplankton community and marine ecosystem (Hasle 1969, Jacques et al. 1979, Kopczynska et al. 1986, El-Sayed & Fryxell 1993) and their carbon biomass (in both absolute and relative terms) is a fundamental parameter in determining their quantitative role in marine biogeochemical, carbon and silica budgets. The most widely used measurement for estimating phytoplankton biomass is that of *in situ* chlorophyll fluorescence or the fluorometric measurement of extracted chlorophyll (e.g. Garibotti et al. 2003). These methods provide poor information on the community structure and relative contribution in terms of carbon biomass for the different phytoplanktonic groups and even less so for the species in these groups (Havskum et al. 2004). Analyses of phytosynthetic and photoprotective pigments, called marker pigments, enable the identification and quantification of the major microalgae classes or genera (e.g. *Prochlorococcus*), but do not differentiate the phytoplankton to species level. Determination of the pigment marker fucoxanthin is used to define 'diatoms' in such analyses, but also includes the presence of pyremnesiophytes, chrysophytes, raphidophytes and certain dinoflagellates (Jeffrey & Hallegraeff 1980, 1987, Klein & Sournia 1987, Wright et al. 1991, Jeffrey et al. 2005). The counting of cells by microscopy provides the most comprehensive inventory of a sample's taxa. However, diatoms demonstrate a wide range of shapes and sizes, thus cell counts exclusively are an inadequate measure of relative diatom biomass and conversion to biovolume is necessary (Mullin et al. 1966, Strathmann 1967).

Phytoplankton biovolume and/or biomass for Southern Ocean species are rarely reported (Kang & Fryxell 1993, Ahn et al. 1997, Agustí & Duarte 2000, Moro et al. 2000, Kang et al. 2001, Pakhomov et al. 2001). More frequently, biomass is summarised as a pooled phytoplankton value and placed in comparison with species abundance data for various study sites or regions (e.g. Bathmann et al. 1997, Kopczynska & Fiala 2003, Gari-

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botti et al. 2005, Krell et al. 2005). Such assessments fall short of attributing the major carbon biomass contributors by confounding dominant relative abundance contributions irrespective of size and, therefore, carbon contribution.

The objective of the present study was to estimate the cell carbon biomass from the majority of Permanently Open Ocean Zone diatoms in the vicinity of Kerguelen Island, in the Indian sector of the Southern Ocean (Fig. 1). Studies in, around and from the sediments of the Kerguelen Plateau have shown little indication of regionalised diatom endemism in this chlorophyll productivity hot-spot (Sullivan et al. 1993), with the exception of a coastal benthic community linked to the islands themselves that stands apart from the open ocean community (from O'Meara 1877 and Manguin 1954, to recent studies of Blain et al. 2001, Riaux-Gobin & Romero 2003, Crosta et al. 2005, and L. K. Armand et al. unpubl.). The accuracy of the biomass estimate is essential for the assessment of the diatom carbon contribution in the surface waters in and around the naturally iron-fertilized Kerguelen region (Blain & Quéguiner 2005, Blain et al. 2007). Here we document microscopic size measurements, their conversion to cell biovolumes and subsequent translation to carbon biomass and surface to volume ratios. The methodology and results presented during our study will be useful for future Southern Ocean diatom analysis both from a general taxonomic perspective and also as a baseline for future biogeochemical investigations requiring specific and realistic biomass estimates based on specific taxa.

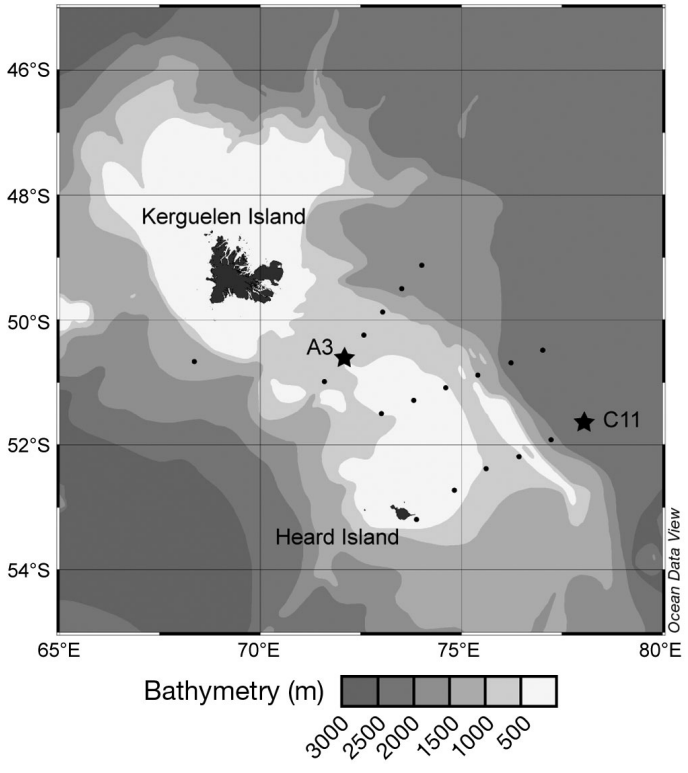

Fig. 1. Position of KEOPS (KErguelen Ocean and Plateau compared Study) Stns A3 and C11 (★). Small black dots represent other sites in the KEOPS program not discussed in this study. Table 1 details the locations and environmental conditions of each site over sampling times. Plotted using ODV (Ocean Data View, see http://odv.awi.de)

MATERIALS AND METHODS

Sample collection. Samples for analyses of phytoplankton abundance and biomass were collected as part of the KEOPS (KErguelen Ocean and Plateau compared Study) research program during the austral summer (January to February 2005) over the Kerguelen Plateau in the Southern Ocean (Blain & Quéguiner 2005, Blain et al. 2007). Two representative stations (A3, within the plateau bloom region; and C11, out of bloom region) were investigated in detail and represent the data presented in this study (Fig. 1). The stations were repeatedly visited, 4 and 3 times, respectively, over a month long period. The samples are considered to have captured the same station populations at various stages of bloom and cell division cycles. Visits to Stns A3 and C11 were set, and then subsequently tracked, based on daily MODIS satellite imagery of the chlorophyll *a* bloom at Stn A3 and the lack of a bloom at Stn C11. The physical oceanographic analysis of the study is found in Y. H. Park et al. (unpubl.) and indicates that the same water masses were sampled respectively at each site. Both have different sources and are assumed to retain clearly different evolving populations. General environmental parameters support the differing sites and conditions (Table 1). Environmental conditions and the evolving diatom communities are discussed in L. K. Armand et al. (unpubl.).

Discrete water samples were taken at various depths within the upper 150 m of the water column from 24 Niskin bottles on a rosette frame equipped with a Sea Bird SBE-911 plus CTD sensor. Aliquots of 125 ml were preserved with acid Lugol's iodine solution (final concentration of 0.32%) and stored in coloured glass bottles, in the dark and at room temperature, until their analysis on return to the laboratory.

Diatom evaluation. Diatoms were identified to the lowest possible taxonomic level, enumerated, and their linear dimensions documented under a Nikon Eclipse TE2000-E inverted microscope equipped with phase-contrast, a long distance condenser and a 12 V, 100 W halogen light source. The video system consisted of a Nikon DS-U1 camera control unit and a Nikon DS-5Mc

Table 1. Sample locations and mean physical values in surface waters from Stns A3 and C11, sampled by CTD on multiple occasions (indicated by the number after the station identifier). Sources: mean sea-surface temperature and salinity and photosynthetically available radiation (PAR) from KEOPS community data; mean chlorophyll *a* and fucoxanthin (Fuco.) data from J. Uitz et al. (unpubl.)

Stn	Sample no.	Date (d/mo/yr)	Lat. (° S)	Long. (° E)	Sea-surface temp. (°C)	Sea-surface salinity	Total chl *a* (µg l^{-1})	Fuco. (µg l^{-1})	1% PAR depth (m)
A3-1	CTD 007	19/1/05	50° 37.80′	72° 04.60′	3.5	33.56	0.94	0.56	41.8
A3-3	CTD 031	24/1/05	50° 41.30′	71° 59.90′	3.68	33.86	0.97	0.63	39.9
A3-4	CTD 076	4/2/05	50° 39.50′	72° 04.00′	3.58	33.86	1.34	0.51	46.0
A3-5	CTD 112	12/2/05	50° 37.79′	72° 05.29′	3.84	33.88	1.09	0.59	43.8
C11-1	CTD 040	26/1/05	51° 37.50′	77° 57.40′	1.91	33.80	0.22	0.10	97.5
C11-2	CTD 045	28/1/05	51° 38.80′	78° 00.10′	1.72	33.79	0.17	0.09	97.5
C11-3	CTD 082	6/2/05	51° 39.00′	78° 00.00′	1.91	33.80	0.16	0.07	122.9

cooled camera head. Diatoms were enumerated from a 10 ml sub-sample after settling for 24 h in an Utermöhl style counting chamber. Counts were made from the entire chamber following the Utermöhl methodology (Hasle 1978). This data set is discussed in detail elsewhere (Blain et al. 2007, L. K. Armand et al. unpubl. a). Taxonomy followed major modern concepts detailed in Hasle & Syvertsen (1997). Additional taxonomic references used are detailed in Appendix 1 (available as Supplementary Material online at www.int-res.com/articles/suppl/a048p295_app.pdf). Several taxa groupings are made due to the difficulty in differentiating some species in their natural state. We grouped all small *Chaetoceros Hyalochaetae* species together although the dominant contributor was *Chaetoceros socialis*. *Chaetoceros Hyalochaetae* resting spores are poorly known to species level and so grouped. The *Chaetoceros bulbosum* complex (Ehrenberg) Heiden includes all synonyms of *C. atlanticus* Cleve, *C. atlanticus* var. *neapolitana* (Schroder) Hustedt and *C. bulbosum* Ehrenberg. *Fragilariopsis rhombica* and *F. separanda* could not be separated in living material and so were grouped. *Membraneis* spp. represent a genus that was often undergoing division in our material, making exact species identification difficult. Species in this category are represented largely by *Membraneis imposter* and *M. challengeri*. *Navicula directa* and a smaller unidentified *Navicula* species represent the category *Navicula* spp. The genus *Pseudo-nitzschia* was divided into 2 categories based on the shape and perceived width of the transapical axis above and below 5 µm. Specimens with a transapical axis >5 µm are dominated by the species *P. heimii*, whereas species encountered in the <5 µm category represent *P. lineola*, *P. turgidula* and *P. subcurvata.* Chained pennates predominately in girdle view are classified as 'other pennates'

For each sample, cells assumed to be alive when collected were measured from random transects scanned across the counting chamber, at 100×, 200× or 400× magnification, according to cell size and until 20 to >100 specimens had been measured for each species. Rare species (i.e. <20 specimens observed per species) were measured, but are not detailed in this study. Measurements were made from the monitor images with the image analysis software LUCIA-G version 5 (Laboratory Imaging); the precision of measurement was determined to be generally less than 0.5 µm for measurements between 5 and 100 µm.

Volume, biomass and surface to volume ratio estimates. Biovolume estimates were made from the mean of linear dimensions using the appropriate geometric formulae reflecting the shape of the cell (Hillebrand et al. 1999). We determined the coefficient of variance percentages (CV% = SD/mean × 100) on cell volume to provide an indication of the population variability for volume, where a low percentage indicates small differences between calculated volumes and vice versa. The carbon content of diatoms was calculated from cellular biovolume according to the corrected equation of Eppley et al. (1970; corrected in Anonymous 1974, Smayda 1978):

$$\log_{10}\text{C (pg)} = 0.76 \log_{10} [\text{cell volume } (\mu m^3)] - 0.352 \quad (1)$$

Other carbon to volume relationships have been established and are presented elsewhere (Parsons et al. 1961, Mullin et al. 1966, Moal et al. 1987, Montagnes et al. 1994), but these methods mix several groups of phytoplankton and do not consider diatoms alone. Menden-Deuer & Lessard (2000) combined data from Strathmann (1967) and diatom data from the authors cited above, thus determining new conversion factors for volume to carbon biomass for diatoms both above and below a biovolume value of 3000 μm^3 (hereafter referred to as the MDL equations). For reasons divulged in the discussion, we did not follow the MDL equations for carbon biomass estimation in this work, which in some cases will result in an overestimation of a larger-celled species biomass under the Eppley et al. (1970) equation due to their decreased carbon density.

We did not correct for inert cell structures, such as vacuoles (Sicko-Goad et al. 1984, Snoeijs et al. 2002), in our biovolume estimates, as the proportions of a vacuole differ phylogenetically and physiologically (Hillebrand et al. 1999). The fact that the vacuole is simply not a box within a box (Sicko-Goad et al. 1984) means that the accuracy of vacuole volume can only be achieved when the proportions for every species of every sample are sampled. Additional complications in the estimation of cell volume result from the type and duration of fixation (Menden-Deuer et al. 2001). This presented a considerable complication to our study, taking into account the intrinsic errors of successive steps: counts, linear measurements and cell shape designation. Thus, this extra work in defining vacuole size and absolute cell volume specimen by specimen was not undertaken and presents an acknowledged assumption in our biomass calculations.

Mean surface to volume ratios (S/V ratio) were calculated using the Biovol program of Kirschtel (1992 and BIOVOL Ver. 2.1, available at www.msu.edu/~kirschte/biovol/index.html) with the exception of the rectangular forms. The S/V ratio for a rectangular form is thus determined from these calculations:

$$S = 2ab + 2bc + 2ac \text{ and } V = abc \quad (2)$$

where a, b and c are, respectively, apical, transapical and pervalvar sections.

RESULTS

Linear measurements

All data presented here are based on size measurements performed on cells from KEOPS process stations A3 and C11. A total of 31 species or taxa groups among the 50 identified in this larger study were measured. Linear measurements (the range and mean of diameter, pervalvar, apical, and transapical axes, where appropriate) for 31 diatom species or categories are presented in Table 2. The largest centric diatoms encountered in the present study were *Asteromphalus hookeri* (140 µm diameter) and *Thalassiosira lentiginosa* (129 µm diameter), although rare *Thalassiosira tumida* and *Coscinodiscus* spp. (not reported here) did obtain diameters of 170 and 134 µm, respectively. The longest diatom was *Thalassio-thrix antarctica* at 2296 µm, although chains of *Eucampia antarctica* v. *antarctica* and *Pseudo-nitzschia* spp. were observed as equally long in many samples. The smallest diatom encountered was *Fragilariopsis pseudonana*, with a mean size of 3.2, 6.6 and 3.8 µm for the pervalvar, apical and transapical axes, respectively.

Measuring the third dimension of a diatom is a problem under light microscopy due to the nature of diatom cells lying in a single, commonly valvar, plane. In general, we could not determine all 3 dimensions from the same cell, and obtaining a mean value for the missing dimension via the literature proved difficult as only range values are documented. To estimate the second dimension in centric diatoms with a discoid shape, e.g. *Azpeitia* spp., *Asteromphalus* spp., *Thalassiosira* spp., we determined a mean pervalvar axis to mean diameter ratio on 14 *Thalassiosira gracilis* specimens (result 0.68) and confirmed the ratio values against measurements in Kang et al. (2001). For pennate diatoms a subset of *Fragilariopsis kerguelensis* and *Fragilariopsis pseudonana* specimens were measured in valve view and in broad girdle view (Table 3). We determined the mean ratio of pervalvar to transapical axis and used this ratio (0.9) to estimate the third dimension in volume calculations for other elliptic or elongate pennates.

Cell volume, carbon content and surface to volume ratios

Biovolume and biomass calculations for each major species or taxa grouping are reported in Table 2. Species-specific average cell volume ranged from 63 to 1.43×10^5 µm^3 and biomass from 10 to 3686 pg C cell^{-1}. Minimum carbon biomass estimates were obtained from the pennate diatoms *Fragilariopsis pseudonana* (63 µm^3 and 10 pg C cell^{-1}) and *Cylindrotheca closterium* (125 µm^3 and 17 pg C cell^{-1}). Maximum carbon values were observed in the centric diatom *Proboscia alata* (1.43×10^5 µm^3 and 3686 pg C cell^{-1}), whereas the pennate diatoms *Thalassiothrix antarctica* and *Membraneis* spp. also attained elevated carbon values of 3556 and 3225 pg C cell^{-1}, respectively. The 3 smallest species encountered in our samples were calculated with the 3 largest S/V ratios (*Cylindrotheca closterium*, 2.214; *Fragilariopsis pseudonana*, 1.481; and *Thalassionema nitzschioides* v. *nitzschioides*, 1.261). Unsurprisingly, larger species dominated the smallest ratio values, with *Thalassiosira lentiginosa* being the smallest recorded (0.116, Table 2). The average S/V ratio for the 31 major species is 0.53; however, approximately $^2/_3$ of the species documented here have S/V ratios less than this mean, and in the majority of these cases their ratios fall between 0.1 and 0.3.

The coefficients of variation (CV) for biovolume range between 15.7 and 116.2%; this heterogeneity is in accordance with the study of Menden-Deuer et al. (2001), who reported a volume CV for Lugol's fixed cells between 5 and 122%. Of the 31 species and taxa groups observed, the majority of %CV values were <60%, with the exception of *Thalassiosira lentiginosa,*

Table 2. Range and mean (mean in parentheses when given together) values of linear measurements, biovolume, carbon biomass, cell surface (S) and surface/volume (S/V) ratio of major diatom species in the Southern Ocean. n = number of observations; D = diameter; P = pervalvar axis; A = apical axis; T = transapical axis; vol. = cell volume; CV = coefficient of variation. Shapes (Sh) were used to estimate volume from linear dimensions: B = rectangular box; C = cylinder; EP = prism on elliptic base; PP = prism on parallelogram base; PS = prolate spheroid

Species and genera groupings	n	D (µm)	P (µm)	A (µm)	T (µm)	Sh	Mean vol. (µm^3)	CV (%)	Mean cell carbon (pg cell^{-1})	Mean S (µm^2)	S/V
Asteromphalus hookeri	33	25–140 (48.5)				C	61042	90.8	1928	8729	0.143
Asteromphalus hyalinus	16	12–37 (23.4)				C	6834	54.9	365	2028	0.297
Azpeitia tabularis	24	28–100 (47.1)				C	55910	62.1	1803	8234	0.147
Chaetoceros bulbosum complex	35		9–22 (14.1)	10–30 (17)		EP	3545	32.1	222	1298	0.366
Chaetoceros Hyalochaetae resting spores	38			6.5–17 (10.2)	4.5–8.5 (6.2)	EP	277	35.5	32	247	0.893
Chaetoceros Hyalochaetae small spp.	172		4.5–13.5 (6.7)	8–22 (13.2)	4.5–11.5 (7.6)	EP	522	38.5	52	382	0.731
Corethron inerme	194	11.5–37 (20.5)	45–191 (88.4)			C	29060	53.7	1097	6335	0.218
Cylindrotheca closterium	215			24.5–150 (52.6)	1.5 - 3.5 (2.1)	PS	125	55.2	17	277	2.214
Dactyliosolen antarctica	165	9.2-47 (18.9)	Up to 226 (61.2)			C	14817		657	3615	0.244
Eucampia antarctica v. *antarctica*	296		13–58.5 (29.9)	15–60 (24.6)	7–19 (14)	EP	8113	40.5	416	2424	0.299
Fragilariopsis kerguelensis	975		5.2–14.6 (8.4)	11–104 (36)	5–14.6 (9.5)	EP	2265	40.5	158	1239	0.547
Fragilariopsis rhombica/ separanda	252			11–54 (21.7)	7–15 (10.6)	EP	1726	51.9	128	874	0.506
Fragilariopsis pseudonana	261		2–6.1 (3.2)	4–14 (6.6)	2.6–6.3 (3.8)	EP	63	39.7	10	94	1.481
Guinardia cylindrus	267	9.1–24.6 (15.2)	32–113 (56.1)			C	10190	37.4	495	3043	0.299
Haslea trompii	66			55–130 (95.6)	8–17 (11.9)	EP	9504	49.5	469	4065	0.428
Leptocylindrus danicus	117	3.2–10.5 (6.9)	33–231 (76.6)			C	2865	51.3	189	1735	0.606
Membraneis spp.	69			62–295 (161.7)	29–74.8 (47.3)	EP	120130	43.3	3225	19499	0.162
Navicula spp.	307			23–90 (41.2)	5–12 (7.6)	EP	1691	53.8	126	1131	0.669
Nitzschia sicula v. *rostrata*	29			41–90 (60.3)	6–10 (8)	PP	1825	15.7	134	607	0.332
Odontella weissflogii	30		32.6–76 (48.2)	28.4–58 (37.4)		EP	61495	37	1939	8718	0.142
Proboscia alata	37	9.2–35.7 (19.2)	140–830 (495.6)			C	143209	53.7	3686	30444	0, 213
Proboscia inermis	20	14.5–21.1 (17.9)	249–644 (394.6)			C	99631	46.7	2798	22732	0, 228
Pseudo-nitzschia spp. (<5 µm)	251			50.2–125 (90)	1.6–4.9 (3.3)	PP	449	44.1	46	367	0.817
Pseudo-nitzschia spp. (>5 µm)	222			68–157 (94.9)	3.9–8.9 (6.3)	PP	1705	35.1	127	735	0.431
Rhizosolenia chunii	93	15.1–54.2 (24.1)	32–170.6 (86.6)			C	39401	116.2	1382	7458	0.189
Thalassionema nitzschioides v. *nitzschioides*	243			10–25 (21.5)	2–4.6 (3.6)	B	253	51	30	319	1.261
Thalassionema nitzschioides f. *lanceolata*	26			30–124 (56.5)	2.2–9.5 (6.3)	B	2010	58.7	144	1421	0.707
Thalassiosira gracilis	52	8.5–23.6 (13.5)				C	1136	55.3	93	622	0.548
Thalassiosira lentiginosa	57	26–129 (59.9)				C	114956	81.9	3119	13314	0.116
Thalassiothrix antarctica	26			845–2296 (1439.3)	7.4–16 (10.4)	B	136631	46.1	3556	55830	0.409
Other pennates	263			10.9–94 (24.4)	4–10 (6.2)	EP	674	94.8	63	554	0.823

Table 3. *Fragilariopsis kerguelensis and F. pseudonana*. Average linear dimensions and determination of the pervalvar to transapical ratio (P:T) in pennate diatoms based on multiple measurements from *F. kerguelensis* and *F. pseudonana*. n = number of observations

Species	Transapical axis (µm)	Pervalvar axis (µm)	P:T	n
F. kerguelensis	9.91	8.75	0.88	128
F. pseudonana	3.66	3.29	0.90	50

Asteromphalus hookeri, 'other pennates' and *Rhizosolenia chunii,* for which %CVs were 81.9, 90.8, 94.8 and 116.2%, respectively (Table 2).

DISCUSSION

Linear measurements

We compared our linear measurements with data from the most recent and comprehensive documentation of cell dimensions found in Hasle & Syverstsen (1997) (Table 4). Our data were in good general agreement with these data and include new axis measurements for several genera or taxa groupings, specifically *Chaetoceros*, *Eucampia*, *Leptocylindrus*, *Membraneis*, *Odontella* and *Proboscia*. Nevertheless, some species showed smaller or larger variations in sizes than the data summarised in the literature. The most notable differences being as follows: (1) The diameter of *Asteromphalus hookeri* ranged between 25 and 140 µm in our study and is reported as much smaller (25 to 60 µm); however, only 10% of the diameters measured in our study exceeded 60 µm. (2) *Corethron inerme* has a minimal diameter measurement of 11.5 µm, whereas the minimal value previously cited is 30 µm. (3) *Eucampia antarctica* v. *antarctica* cells have small apical axis values, with 10% being less than the cited minimum of 18 µm. (4) Of the *Fragilariopsis kerguelensis* specimens, 1.5% have an apical axis greater than the maximum cited value of 76 µm; the maximum value observed in this study being 104 µm. Recent data from initial cell formation in *F. kerguelensis* indicate a greatest apical axis length of between 76 and 90 µm for this species (Assmy et al. 2006). (5) Of *Membraneis* spp., 82% have an apical axis greater than the maximum cited value of 125 µm. The maximum value observed in this study being 295 µm. (6) Of the *Rhizosolenia chunii* specimens, 38% have maximal diameters >28 µm (largest observed 54.2 µm) while 26% have a maximal pervalvar axis >94 µm (longest observed 170.6 µm), compared with data in Hasle & Syvertsen (1997). (7) Of *Thalassionema nitzschioides* v. *nitzschioides*, 72% have an apical axis >10 µm compared with measurements listed in Moreno-Ruiz & Licea (1995). (8) All *Thalassiothrix antarctica* specimens measured in this study have a transapical axis wider than data reported in the literature.

Overall, basic combined linear measurements for each species did not indicate large departures from previous summed observations. Variations may be regional and also heavily influenced by the cell cycle phase evident during bloom decline at our repeat sampling stations.

Carbon calculations

We compared our carbon biomass values calculated according to the Eppley et al. (1970) equation with results obtained with C:Vol regressions from the MDL equations; the results differed from 0.4% (*Odontella weissflogii*) to 24% (*Asteromphalus hyalinus*) (Table 5). These new data predicted 16 to 24% less C for diatoms with biovolumes between 7000 and 14 800 µm^3 (5 diatoms species in our study: *Dactyliosolen antarctica*, *Eucampia antarctica*, *Haslea trompii*, *Guanardia cylindrus*, *Asteromphalus hyalinus*) and also the minute diatom *Fragilariopsis pseudonana*, and predicted 7.5 to 10.4% more C for 4 large diatoms (>100 000 µm^3: *Membraneis* spp., *Proboscia alata, Thalassiosira lentiginosa, Thalassiothrix antarctica*). Differences were minor for the other species.

Although Menden-Deuer & Lessard (2000) differentiated diatoms on the basis of large biovolumes >3000 µm^3, this division was defined from comparison with other non-diatom phytoplankton groups where biomass could not be extracted from a single all-encompassing equation. The larger biovolume diatom cells were considered less dense and thus subjected to an alternative equation that decreased their C content. In Fig. 2 we show that a difference in the C biomass estimates is strikingly obtained when a species' volume is greater than 65 000 µm^3 and not at 3000 µm^3 as presented by Menden-Deuer & Lessard (2000).

The species used to date in determining such C biomass equations rarely represent those observed in our samples (i.e. *Chaetoceros* spp.). In all the studies mentioned thus far (see 'Materials and methods') the largest species identified (>65 000 µm^3) fall into the taxa *Coscinodiscus* spp. and *C. concinnus*, *Ditylum brightwellii* and *Rhizosolenia setigera*, whereas we encounter large biovolume species in the genera *Membraneis, Proboscia, Thalassiosira* and *Thalassiothrix* (Table 2).

Due to the need for additional comparative work and integration of Southern Ocean species in such equations and the additional fact that we wished to compare

Table 4. Comparison of observed linear measurements (ranges in µm; see Table 2 for definitions) with data from Hasle & Syvertsen (H&S) (1997). n = number of observations

Species and genera groupings	n	Present study				Hasle & Syvertsen (1997)			
		D	P	A	T	D	P	A	T
Asteromphalus hookeri	33	25–140				25–60			
Asteromphalus hyalinus	16	12–37				15–32			
Chaetoceros bulbosum complex	35		9–22	10–30				10–40	
Chaetoceros Hyalochaetae resting spores	38			6.5–17	4.5–8.5		2.5–20[a]	5.5–20.5[a]	
Chaetoceros Hyalochaetae small spp.	172		4.5–13.5	8–22	4.5–11.5			7–30	
Corethron inerme	194	11.5–37	45–191			30–40[b]	40–350		
Cylindrotheca closterium	215			24.5–150	1.5–3.5			30–400	2.5–8
Dactyliosolen antarctica	165	9.2–47	Up to 226			13–90	Up to 140		
Eucampia antarctica v. *antarctica*	296		13–58.5	15–60	7–19			18–92[c]	
Fragilariopsis kerguelensis	975		5.2–14.6	11–104	5 -14.6			10–76	5–11
Fragilariopsis rhombica/ separanda	252			11–54	7–15			8–53/10–33	7–13/8–13
Fragilariopsis pseudonana	261		2–6.1	4–14	2.6–6.3			4–20	3.5–5
Guinardia cylindrus	267	9.1–24.6	32–113			8–50	Up to 300		
Haslea trompii	66			55–130	8–17			70–160	10–14
Leptocylindrus danicus	117	3.2–10.5	33–231			5–16			
Membraneis spp.	69			62–295	29–74.8			80–125/85—125[d]	
Navicula spp.	307			23–90	5–12			53–120	7–12
Nitzschia sicula v. *rostrata*	29			41–90	6–10			50–90	5–8
Odontella weissflogii	30		32.6–76	28.4–58				60–84	
Proboscia alata	37	9.2–35.7	140–830			2.5–42[e]			
Proboscia inermis	20	14.5–21.1	249–643.7			10–19[e]			
Pseudo-nitzschia spp. (< 5 µm)	251			50.2–125	1.6–4.9			56–112/30–80	1.8–2.7/2.5–3.5
Pseudo-nitzschia spp. (> 5 µm)	222			68–157	3.9–8.9			67–120	4–6
Rhizosolenia chunii	93	15.1–54.2	32.2–170.6			20–28[f,g]	70–94[g]		
Thalassionema nitzschioides v. *nitzschioides*	243			10–25	2–4.6			5– <10[h]	2.3–4[h]
Thalassionema nitzschioides f. *lanceolata*	26			30–124	2.2–9.5			26–117[h]	3.5–8.7[h]
Thalassiosira gracilis	52	8.5–23.6				5–28/7–15			
Thalassiosira lentiginosa	57	26–129				47–95			
Thalassiothrix antarctica	26			845–2296	7.4–16			420–5680	1.5–6

[a]Measurements on similar species *Coronodiscus collaris* (Suto 2004) No other published sizes encountered
[b]Data cited in H&S as Hendy (1937) (*Corethron* spp.)
[c]Data cited in H&S as Syvertsen & Hasle (1983) (*Eucampia* spp.)
[d]Data cited in H&S as Paddock (1988)
[e]Jordan et al. (1991)
[f]Priddle et al. (1990)
[g]Karsten (1905)
[h]Moreno-Ruiz & Licea (1995)

Table 5. Biomass estimation comparison between the corrected equation of Eppley et al. (1970) (corrected in Smayda 1978) and the equations of Menden-Deuer & Lessard (2000) (MDL). Percent variation is the difference of Eppley–MDL over the corrected Eppley et al. (1970) equation

Species and genera groupings	Biovolume (μm^3)	Eppley (pg C $cell^{-1}$)	MDL diatom <3000 μm^3 (pg C $cell^{-1}$)	MDL diatom >3000 μm^3 (pg C $cell^{-1}$)	Variation (%)
Asteromphalus hookeri	61 042	1928		1919	0.4
Asteromphalus hyalinus	6834	365		279	23.6
Azpeitia tabularis	55 910	1803		1776	1.5
Chaetoceros bulbosum complex	345	38	33		12.8
Chaetoceros Hyalochaetae resting spores	277	32	28		13.8
Chaetoceros Hyalochaetae small spp.	522	52	46		11.0
Corethron inerme	29 060	1097		998	9.0
Cylindrotheca closterium	125	17	14		17.2
Dactyliosolen antarctica	14 817	657		551	16.1
Eucampia antarctica	8113	416		324	22.0
Fragilariopsis kerguelensis	2265	158	151		4.0
Fragilariopsis rhombica/separanda	1726	128	121		5.4
Fragilariopsis pseudonana	63	10	8		20.1
Guinardia cylindrus	10 190	495		396	19.8
Haslea trompii	9504	469		373	20.5
Leptocylindrus danicus	2865	189	183		2.9
Membraneis spp.	120 130	3225		3485	−8.1
Navicula spp.	1691	126	119		5.5
Nitzschia sicula v. *rostrata*	1825	134	127		5.1
Odontella weissflogii	61 495	1939		1932	0.4
Proboscia alata	143 209	3686		4068	−10.4
Proboscia inermis	99 631	2798		2955	−5.6
Pseudo-nitzschia spp. (<5 µm)	449	46	41		11.6
Pseudo-nitzschia spp. (>5 µm)	1705	127	120		5.4
Rhizosolenia chunii	39 401	1382		1305	5.6
Thalassionema nitzschioides v. *nitzschioides*	253	30	26		14.2
Thalassionema nitzschioides f. *lanceolata*	2010	144	137		4.6
Thalassiosira gracilis	1136	93	86		7.4
Thalassiosira lentiginosa	114 956	3119		3352	−7.5
Thalassiothrix antarctica	136 631	3556		3903	−9.7
Other pennates	674	63	57		9.8

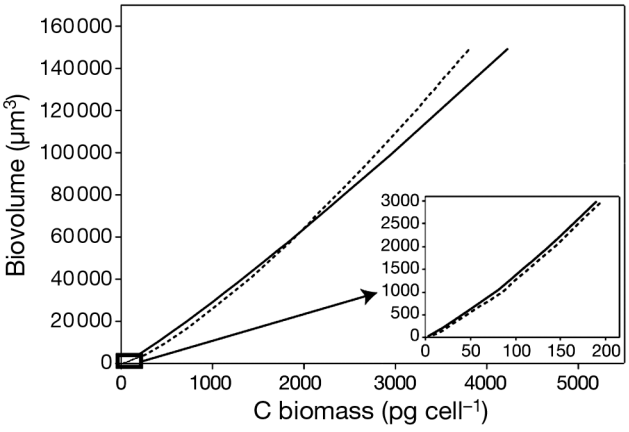

Fig. 2. Plot of diatom biomass estimates using the corrected equation of Eppley et al. (1970) (corrected in Smayda 1978) (dashed line) and the 2 equations of Menden-Deuer & Lessard (2000) (MDL; solid line). Biomass estimates are derived from arbitrary biovolumes between 0 and 150 000 μm^3, covering the range of biovolumes encountered in our study. The inset specifically reveals estimates of biovolumes ≤3000 μm^3, which separates the use of 2 MDL equations

our results with those currently published from the Southern Ocean (i.e. Moro et al. 2000 and Kang et al. 2001) we decided to continue use of the corrected Eppley et al. (1970) equation to predict C content in this study. It would seem appropriate that additional modification of current C:Vol equations are required to capture Southern Ocean diatom variability. We did not undertake this extension in this study.

Cell volume, carbon content and surface to volume ratios

Biovolume and carbon biomass results were compared principally against the sea ice or ice-edge community studies of Moro et al. (2000) and Kang et al. (2001) (Table 6). Moro et al. (2000) present biovolume measurements from Wood Bay, Ross Sea, whereas Kang et al. (2001) represent research around the northern tip of the Antarctic Peninsula in the Weddell Sea.

Table 6. Species-specific comparison of mean cell biovolume and mean cell carbon biomass with results from Moro et al. (2000) and Kang et al. (2001). Pennate results from Kang et al. (2001) recalculated with equivalent geometric shapes of this study in parentheses. Vol. = cell volume; Shapes (Sh) were used to estimate volume from linear dimensions: C = cylinder; EP = prism on elliptic base; PP = prism on parallelogram base; PS = prolate spheroid; B = rectangular box

Species and genera groupings	Present study			Moro et al. (2000)	Kang et al. (2001)		
	Sh	Vol. (μm^3)	Cell carbon (pg $cell^{-1}$)	Vol. (μm^3)	Sh	Vol. (μm^3)	Cell carbon (pg $cell^{-1}$)
Azpeitia tabularis	C	55 910	1803		C	13 451	611
Chaetoceros bulbosum complex	EP	3545	222	4568			
Chaetoceros Hyalochaetae resting spores	EP	246	29		EP (B)	118	17
Chaetoceros Hyalochaetae small spp.	EP	522	52		EP (B)	257	30
Corethron inerme[a]	C	29 060	1097	68 427	C	41 720	1444
Cylindrotheca closterium	PS	125	17	663	PS	268	31
Eucampia antarctica v. *antarctica*	EP	8113	416	111 182	EP (B)	50 377	1666
Fragilariopsis kerguelensis	EP	2265	158		EP (B)	1483	114
Fragilariopsis rhombica/separanda	EP	1726	128	2364/1942	EP (B)	827/2356	73/162
Fragilariopsis pseudonana	EP	63	10		EP (B)	177	23
Guanardia cylindrus	C	10 190	495	1346			
Haslea trompii	EP	9504	469		EP (B)	8207	420
Navicula spp.[b]	EP	1691	126	5715	EP (B)	3727	230
Odontella weissflogii[c]	EP	61 495	1939	190 806	EP (B)	88 008	2546
Proboscia alata	C	143 209	3686	10 911	C	40 886	1422
Proboscia inermis	C	99 631	2798		C	29 824	1119
Pseudo-nitzschia spp. (<5 µm)[d]	PP	449	46	132	PP (PS)	510	51
Pseudo-nitzschia spp. (>5 µm)[e]	PP	1705	127		PP (PS)	922	77
Thalassiosira gracilis	C	1136	93		C	2633	177
Thalassiosira lentiginosa	C	114 956	3119		C	88 856	2564

[a]*Corethron criophilum* Castracane, in Moro et al. (2000) and in Kang et al. (2001) studies
[b]*Navicula directa* (Wm Smith) Ralfs, in Moro et al.'s (2000) study
[c]*Odontella* sp. in Moro et al.'s (2000) study
[d]*Pseudo-nitzschia lineola* Cleve/ *turgiduloides* Hasle, in Kang et al.'s (2001) study and *Pseudo-nitzschia turgiduloides* Hasle, in Moro et al.'s (2000) study
[e]*Pseudo-nitzschia hemii* Manguin, in Kang et al.'s (2001) study

Differences for 10 species between the 3 studies reveal cell biovolumes that vary considerably. *Guinardia cylindrus*, *Proboscia alata* and *Pseudo-nitzschia* spp. (<5 µm) all reveal the smallest biovolumes in the Ross Sea study, while the remainder of the common species have the largest biovolumes of any of the 3 studies. We believe that sea-surface temperatures play an important role in the environmental preference and thus size and frustule structure of a species as is often reported in the literature (eg. Villareal & Fryxell 1983, Smith et al. 1994, Suzuki & Takahashi 1995, Montagnes & Franklin 2001, Atkinson et al. 2003). Other environment linked variables such as light and nutrient supply cannot be excluded either (e.g. Fiala & Oriol 1990, Stapleford & Smith 1996, Stramski et al. 2002); however, explicit Southern Ocean diatom ecology or life cycle research is depauperate in the literature, resulting in generalised hypotheses on any cause and response for any single species.

Alternatively, differences in biovolume measurements can be attributed to valid taxonomic differences within a species, such as forms or varieties. This explanation can be applied to the case of *Eucampia antarctica* biovolume measurements in Table 6, where the Moro et al. (2000) and Kang et al. (2001) studies show *E. antarctica* biovolumes 13.7 and 6.2 times larger, respectively, to the specimens we report around Kerguelen. It is evident that the Ross and Weddell Sea forms encountered in the comparative papers represent the flat ribbon chained *E. antarctica* var. *recta*, and in our survey, the spiralling chained form of *E. antarctica* var. *antarctica* (form descriptions in Fryxell & Prasad 1990). We cannot discount the fact that species identified as *Corethron criophilum* by the previous studies (see footnotes in Tables 3 & 4) and *Corethron inerme* in the present study account for the differences observed in biovolume and biomass estimates, although it is highly likely, and thus rigorous taxonomic treatment employing the taxonomic differences reported in Crawford et al. (1998) will assist in future definitions of species contributions to the carbon cycle.

An important point to consider in comparing biovolumes is the use of shape equations to determine these values. The Kang et al. (2001) study did not correct for vacuole size, but employed alternative pennate-shape equations (i.e. rectangular and prolate spheroid) to resolve their biovolume values, against the Hillebrand et al. (1999) standardized genera equations we apply here. We recalculate their specific volumes and subsequent biomass contributions in Table 6 in order to make comparison possible between our studies. The comparison of biovolume and biomass estimates of individual species in our study against those in more southerly waters evoke a biogeographic delineation dependent on a species generally reported habitat, such that greater values of either estimate for that species follow suite. For example *Thalassiosira lentiginosa*, *Azpeitia tabularis*, *Fragilariopsis kerguelensis and Pseudo-nitzschia* (>5 µm category), which have larger biovolume and biomass estimates in our study, are known to thrive in open-ocean regions (Hasle & Syvertsen 1997, Crosta et al. 2005). In contrast, *Cylindrotheca closterium*, *Fragilariopsis pseudonana* and *Thalassiosira gracilis* are reported with larger biovolume and biomass estimates in the marginal sea-ice to ice-affected studies, where they are dominantly observed (Kang & Fryxell 1993, Hasle & Syvertsen 1997, Garibotti et al. 2003). The implication with this comparison of biovolumes is to highlight the need for a standardized species-specific approach in future research, which we propose rests with the genus determined equations of Hillebrand et al. (1999).

Cell volume estimates have also been subjected to an arbitrary definition, discriminating small and large diatoms by a delimiting cell volume of 1000 µm^3 (Snoeijs et al. 2002). Employing this definition to our Southern Ocean species indicates that 7 taxa (*Chaetoceros Hyalochaetae* species and resting spores, *Cylindrotheca closterium*, *Fragilariopsis pseudonana*, *Pseudo-nitzschia* (<5 µm category), *Thalassionema nitzschioides* v. *nitzschioides*, and 'other pennates') could be considered as small diatoms (<1000 µm^3 = <85 pg C cell^{-1}), whereas the remaining 24 taxa could be defined as large diatoms (Table 2). We believe this arbitrary classification can be divided into a further division, which we identify as intermediate between small and large diatoms. We define intermediate diatoms as those with a cell volume between 1000 and 10 000 µm^3 (equivalent to $85 > x > 488$ pg C cell^{-1}), thus delimiting large diatoms as those with volumes greater than 10 000 µm^3. Under this definition the 24 remaining taxa can be divided into 12 intermediate sized diatoms and 12 large diatom species (Table 7). This size defining application could be employed in future modelling studies or carbon budget calculations that wish to differentiate carbon contributions from large, intermediate and small diatoms in terms of biomass rather than by bulk size-fractionated assessments based on filter mesh sizes and generalised definitions of pico- (0.2 to 2 µm), nano- (2 to 20 µm) and

Table 7. KEOPS species and taxa groupings divided into small, intermediate and large diatom contributors based on volume definitions of Snoeijs et al. (2002) and this work in comparison with derived *S*/*V* ratios and mean cellular carbon contributions

Diatom size category Species and genera groupings	Mean cell vol. (µm^3)	*S*/*V*	Mean carbon (pg C cell^{-1})
Small (<1000 µm^3)			
Fragilariopsis pseudonana	63	1.481	10
Cylindrotheca closterium	125	2.214	17
Thalassionema nitzschioides v. *nitzschioides*	253	1.261	30
Chaetoceros Hyalochaetae resting spores	277	0.893	32
Pseudo-nitzschia spp. (<5 µm)	449	0.817	46
Chaetoceros Hyalochaetae small spp.	522	0.731	52
Other pennates	674	0.823	63
Intermediate (>1000, <10 000 µm^3)			
Thalassiosira gracilis	1136	0.548	93
Navicula spp.	1691	0.669	126
Pseudo-nitzschia spp. (>5 µm)	1705	0.431	127
Fragilariopsis rhombica/separanda	1726	0.506	128
Nitzschia sicula v. *rostrata*	1825	0.332	134
Thalassionema nitzschioides f. *lanceolata*	2010	0.707	144
Fragilariopsis kerguelensis	2265	0.547	158
Leptocylindrus danicus	2865	0.606	189
Chaetoceros bulbosum complex	3545	0.366	222
Asteromphalus hyalinus	6834	0.297	365
Eucampia antarctica v. *antarctica*	8113	0.299	416
Haslea trompii	9504	0.428	469
Large (>10 000 µm^3)			
Guinardia cylindrus	10 190	0.299	495
Dactyliosolen antarctica	14 817	0.244	n/a
Corethron inerme	29 060	0.218	1097
Rhizosolenia chunii	39 401	0.189	1382
Azpeitia tabularis	55 910	0.147	1803
Asteromphalus hookeri	61 042	0.143	1928
Odontella weissflogii	61 495	0.142	1939
Proboscia inermis	99 631	0.228	2798
Thalassiosira lentiginosa	114 956	0.116	3119
Membraneis spp.	120 130	0.162	3225
Thalassiothrix antarctica	136 631	0.409	3556
Proboscia alata	143 209	0.213	3686

microplankton (20 to 200 µm) contributions that do not resemble the diversity of shapes found in diatoms and thus respective biomass contributions.

Although mean cell volumes are used here to indicate a mean species value, the variation, as illustrated by the %CV values, is equally important in assessing the variation within the population. In this case, the small %CV values associated with a given mean volume provide a measure of size dispersion in the given volume and subsequent biomass estimates. In our study the majority of %CV range between 32 and 62%. We cannot say at this time whether this represents a normal species variability range outside of the Menden-Deuer et al. (2001) study, since there are no other studies in this fashion. In our study, measured cells are derived from 2 different stations, within and exterior to the bloom, taken at 2 different times; therefore, cells of one species could differ in size dependent on various life cycle stages observed (e.g. vegetative stages observed at the first visit compared to resting stages as the bloom ended, or large cells at one site compared with small cells at another site). So it is not surprising that %CV tend to be mid-large in value when size is variable over time and space. One distinction we are able to decipher with one of the large %CV values (*Rhizosolenia chunii*, 116.2%) is that sizes are smaller in samples from Stn A3 (bloom conditions) compared with samples from Stn C11 (high nutrient low chlorophyll, HNLC). Separated by station, *Rhizosolenia chunii* mean biovolume is 14 734 µm^3 (%CV = 27.2) at Stn A3 and 106 436 µm^3 (%CV = 24.9) in samples from Stn C11 (Fig. 3).

It would appear that the combination of the 2 stations and differing species populations may result in %CV values >60% (Table 2). However, the same did not hold true for *Thalassiosira lentiginosa* with an 81%CV, as Stn A3 samples with a smaller biovolume of 34 382 µm^3 compared with the biovolume of 132 275 µm^3 at Stn C11 both show large %CV values (43.9 and 73.3%, respectively), suggesting that the populations at both sites have heterogeneous size ranges.

In theory, diatoms can adapt to low nutrient concentrations by reducing their size through successive vegetative division; small cells have greater *S*/*V* ratio, which increases the exchanges of solutes across the cell surface (Morel et al. 1991). For both *Rhizosolenia chunii* and *Thalassiosira lentiginosa* this hypothesis may support our observations of declining bloom conditions (Blain et al. 2007) at Stn A3 with the smaller biovolume and larger *S*/*V* estimates of these species than estimated for the population in the HNLC region at Stn C11 (*R. chunii S*/*V* = 0.262 at Stn A3 and 0.136 at Stn C11; *T. lentiginosa S*/*V* = 0.173 at Stn A3 and 0.111 at Stn C11). However, it is most likely that size diminution of *R. chunii* and *T. lentiginosa* at Stn A3 is a result of faster vegetative division in the previously nutrient rich Stn A3 waters compared to the nutrient-limited populations at Stn C11.

S/*V* ratios for 4 species — *Cylindrotheca closterium* (2.68), *Leptocylindrus danicus* (0.67), *Proboscia alata* (0.62) and *Thalassionema nitzschioides* (1.03) — were reported from the Baltic Sea by Snoeijs et al. (2002) and form the basis of possible comparisons with our study. In all cases, the *S*/*V* ratios are strikingly similar, with the exception of the value for *P. alata* for which the *S*/*V* ratio is much smaller in our South Ocean species (0.213). This discrepancy could be related to several factors, not the least of which life cycle stage and actual taxonomic differences are likely candidates.

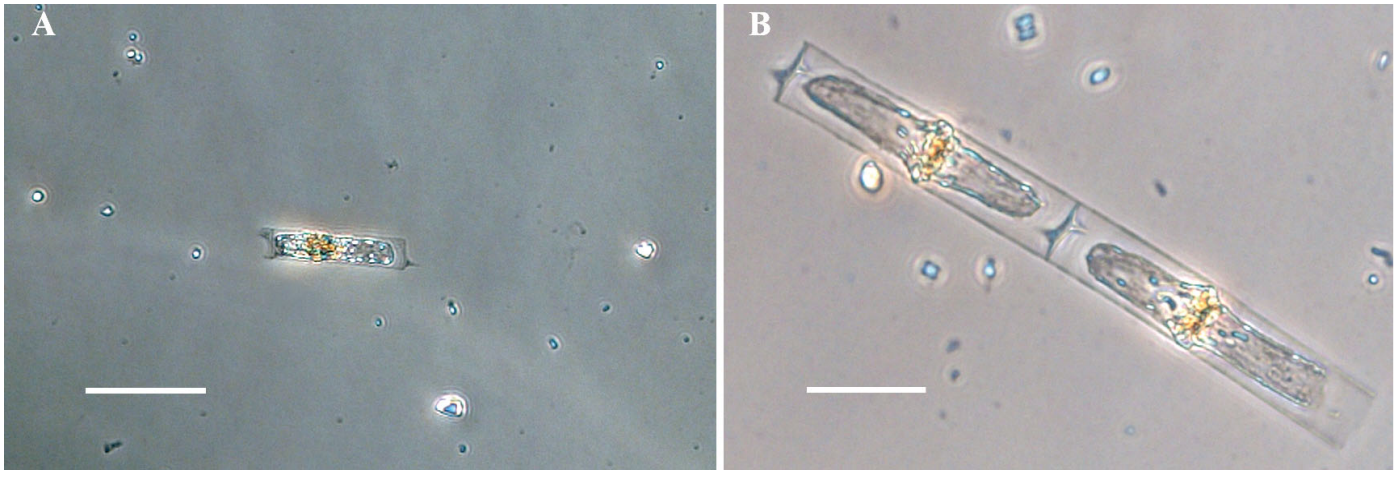

Fig. 3. *Rhizosolenia chunii* at (A) Stn A3 within the plateau bloom region and (B) Stn C11 out of bloom region, over the Kerguelen Plateau in the Southern Ocean. Scale bars = 50 µm

A theory driven by Smetacek and colleagues in recent years (Verity & Smetacek 1996, Smetacek et al. 2002, 2004, Hamm et al. 2003) in assessing phytoplankton biomass success has resulted in a hypothesis of mortality adaptation as an explanation for biomass accumulation of larger phytoplankton in the open-ocean environment; via defensive changes to the frustule such as increased size/length, highly silicified cells and defence mechanisms such as spines, protrusions and barbs. This mortality adaptation is considered costly to faster division, improved nutrient uptake and thinner frustules, which would ordinarily allow greater biomass accumulation in a high-nutrient, low-predation environment. The biomass accumulation of larger or heavily protected species in a community also suggests that limiting nutrient sources (such as iron or silica) are realised from the regeneration pool of the smaller taxa (Smetacek et al. 2002). In general, high *S/V* ratios are associated with small cell size and in this sense would represent uptake specialist diatoms; conversely, small *S/V* ratios linked to larger cells represent predation defence specialists. The majority of our species reveal small *S/V* ratios (i.e. <0.3), which would suggest that the Kerguelen community is predation defensive (Tables 2 & 7).

Our categorised diatom size contributors derived from uncorrected cell volumes against a species *S/V* ratio indicate that small diatoms in our samples have *S/V* ratios of >0.7, intermediate diatoms have an *S/V* ratio range between 0.2 and 0.7, whereas large diatoms have an *S/V* ratio of <0.2. The sole exception to this relation is that observed with *Thalassiothrix antarctica*, for which biovolume values suggest that the species can be considered a large cell whereas the calculated *S/V* ratio is 0.4. We assume this discrepancy is related to sample methodology, where we were more likely to have encountered smaller specimens of *T. antarctica* in our CTD sampling of the water column.

CONCLUSIONS

Our study is the first to describe the carbon content of major diatom species in the open ocean region of the Southern Ocean. These values are determined from multiple linear measurements of specimens in 2 neighbouring, yet biogeochemically contrasting, regions over a month long period at the end of the summer bloom period southeast of Kerguelen Island. Our linear measurements show minimal discrepancies from measurements previously encountered and summarised in the literature. We expect that some of the observed variation is derived from the vegetative phase of reproduction observed as a result of the bloom conditions. We believe that this variation in size of a species population is seen in the values provided by %CV. However, we are relatively uncertain, given that this represents the first time such measurements have been given for these species, whether such values indicate a normal range of size dispersion in bloom affected cells, variation in biogeochemically differentiated populations of the same species or other unidentified factors.

Biovolume and subsequent biomass measurements varied from 63 μm^3 and 10 pg C $cell^{-1}$ in *Fragilariopsis pseudonana* to 1.43×10^5 μm^3 and 3686 pg C $cell^{-1}$ in *Proboscia alata*. We suggest that future biomass determinations follow the Hillebrand et al. (1999) genus-specific geometric equations to enable comparison between studies. The use of a C:Vol equation, as represented either by the corrected Eppley et al. (1970) or biovolume differentiated MDL equations, is not an easy choice given that neither takes into account taxa that are generally dominant in the Southern Ocean to determine their equations, particularly those with larger biovolume estimates. We choose out of comparison convenience to use the corrected Eppley et al. (1970) equation, noting that in comparison to the MDL equations only when biovolume was exceptionally large did major discrepancies between estimates occur. Obviously, the next step would be to define new modified MDL type equations that take into account Southern Ocean diatom size variations along with new studies on carbon contents of the same taxa.

The need to assess vacuole size in diatoms is a difficult and time intensive task, most unlikely to be assessed for sometime. This measure remains the largest uncertainty in our study and we accept that our biomass estimates lack this correction as should all future studies. We employed and extended the biovolume definition of Snoeijs et al. (2002) to designate cell size and subsequent carbon contributor status to the diatoms encountered in our samples. This simple definition presents a more useful description of a diatom community, with respect to any one of the 3 biovolume-derived measurements in Table 7, than presented to date by generalised size definitions of phytoplankton communities (pico-, nano- and microplankton). We expect improvements on the definitions and Table 7 with time and additional significant studies of phytoplankton in the ocean. The definition of mean biomass contribution here with abundance data (L. K. Armand et al. unpubl.) will lead to a more meaningful assessment of the carbon contribution of phytoplankton within the oceanic carbon cycle as has been initiated in the KEOPS program.

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