Giulia Ghedini, Martino E. Malerba, Dustin J. Marshall – "How to estimate community energy flux? A comparison of approaches reveals that size-abundance trade-offs alter the scaling of community energy flux" *Proceedings of the Royal Society B*, doi:10.1098/rspb.2020.0995

Supplementary Information

Table S1. Summary of the steps taken to reconstruct community metabolism and net production for each approach.

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Mean rates per cell
Community energy flux can be predicted from the average cell energy use among species (\overline{E}_{cell}) and the total abundance of cells (N):
$\overline{E}_{\rm com} = \overline{E}_{\rm cell} (\overline{E}_{\rm cell sp1}, \overline{E}_{\rm cell sp2}, \dots, \overline{E}_{\rm cell spn}) \times N$
 Calculate the mean metabolic and photosynthetic rate per-cell among species (population rate/n of cells for each species, averaged across species) using independent data (i.e. Malerba et al. 2017).
2. Multiply average cell metabolism $(4.68 \times 10^{-9} \mu \text{mol } O_2 \text{min}^{-1} \text{cell}^{-1})$ or photosynthesis (1.23 $\times 10^{-8} \mu \text{mol } O_2 \text{min}^{-1} \text{cell}^{-1})$ by the total abundance of cells (number of cells in 500ml) for each community at each sampling time.
3. Convert community oxygen consumption rates (μ mol O ₂ min ⁻¹) to energy rates (J d ⁻¹) assuming 24h of darkness for metabolism and a 16L:8D photoperiod for net production.
Mean biomass-specific (biovolume-specific) rates per cell
Community energy flux can be predicted from the average energy use per unit biomass (biovolume) of cells among species (\overline{E}_{bio}) and the total community biomass (biovolume, B):
$\overline{E}_{\rm com} = \overline{E}_{\rm bio} (\overline{E}_{\rm bio sp1}, \overline{E}_{\rm bio sp2}, \ldots, \overline{E}_{\rm bio spn}) \times { m B}$
1. Calculate the mean metabolic or photosynthetic rate per unit biovolume across species (per-cell rate/cell biovolume for each species, averaged across species) using independent data (Malerba et al. 2017).
2. Multiply average biovolume-specific metabolism or photosynthesis $(1.47 \times 10^{-11} \text{ and } 4.17 \times 10^{-11} \mu \text{mol } O_2 \text{ min}^{-1} \mu \text{m}^{-3}$ respectively) by total community biovolume (μm^3 in 500ml) for each community at each sampling time.
 Convert community rates in µmol O₂ min⁻¹ to Joules d⁻¹ assuming 24h of darkness for metabolism and a 16L:8D photoperiod for net production.
Size-dependent rates across species
Community energy flux can be predicted as the sum of cell energy use of each species (\overline{E}_{celli}) which can be calculated from interspecific scaling relationship estimating the average effects of size on energy use (β):
$\overline{E}_{com} = \sum_{i=1}^{S} (\overline{E}_{celli} \times N_i)$ where $\log_{10}(\overline{E}_{celli}) = \alpha + \beta \times \log_{10}(\overline{S}_i)$
1. Calculate the daily cell metabolism and net production for each species in the community from its average size (biovolume) using the common coefficient and intercept from interspecific scaling relationships that quantify the common size-dependence of cell energy use across species (Malerba et al. 2017):

 Log_{10} (cell metabolism J d⁻¹ cell⁻¹) = $0.71 \times log_{10}$ (mean cell volume) - 7.32 Log_{10} (cell net production J d⁻¹ cell⁻¹) = $0.63 \times log_{10}$ (mean cell volume) - 6.89 2. Multiply cell rates of each species (\overline{E}_{celli}) by their species abundance measured in the experimental communities (N_i) to calculate population rates (J d⁻¹ µl⁻¹) and sum across species to obtain community rates (J d⁻¹ for a total community volume of 500mL).

Size- and density-dependent rates across species

As above, but including both the size- (β) and density-dependence (δ) of cell energy use among species (\overline{E}_{celli}) as a function of the species size (\overline{S}_i) and population biomass density (D_i):

 $\overline{E}_{com} = \sum_{i=1}^{s} (\overline{E}_{celli} \times N_i)$ where $\log_{10}(\overline{E}_{celli}) = \alpha + \beta \times \log_{10}(\overline{S}_i) + \delta \times D_i$

1. Convert the cell density of each species (cells μ l⁻¹) in the experimental communities to their biomass density concentration equivalent (D*i*, i.e. optical density expressed in %) using the equations below from data of Malerba et al. 2017:

Amphidinium	Concentration (Di) = $1.421 \times 10^{-14} + 5.098 \times 10^{-2} \times \text{cell density}$
Dunaliella	Concentration = $1.421 \times 10^{-14} + 2.315 \times 10^{-2} \times \text{cell density}$
Amphora	Concentration = $1.421 \times 10^{-14} + 4.167 \times 10^{-1} \times \text{cell density}$
Tetraselmis	Concentration = $4.450 \times 10^{-9} + 7.231 \times 10^{-2} \times$ cell density
Synechococcus	Concentration = $1.851 \times 10^{-9} + 3.008 \times 10^{-3} \times cell$ density
Tisochrysis	Concentration = $-5.868 \times 10^{-10} + 9.536 \times 10^{-3} \times \text{cell density}$

2. Calculate the daily cell metabolism and net production using interspecific scaling relationships that quantify the common size- and density-dependence of cell energy use across species (Malerba et al. 2017):

 Log_{10} (cell metabolism J d⁻¹ cell⁻¹) = 0.71 × log_{10} (mean cell vol) – 0.004 × Concentration – 7.32 Log_{10} (cell net production J d⁻¹ cell⁻¹) = 0.63 × log_{10} (mean cell vol) – 0.004 × Concentration – 6.89

using the mean volume and concentration of each species as measured in the experimental communities at each sampling time.

3. Multiply cell rates of each species by their population abundance in the experimental communities (N_i) to calculate population rates (J d⁻¹ μ l⁻¹) and sum across species to obtain community rates (J d⁻¹ for a total community volume of 500mL).

Average individual species rates

Community energy flux can be predicted as the sum of the average cell energy use of each species $(\overline{E}_{cell sps})$ multiplied by the abundance of that species (N_{sps}):

$$\overline{E}_{\rm com} = \sum_{k=1}^{s} ((\overline{E}_{\rm cell \, sp1} \times N_{\rm sp1}) + (\overline{E}_{\rm cell \, sp2} \times N_{\rm sp2}) + \dots + (\overline{E}_{\rm cell \, sps} \times N_{\rm sps}))$$

- 1. Calculate the average energy use per cell of each species individually based on their population rates from an independent dataset (i.e. $\overline{E}_{cell sps}$ = measured population rate of species s divided by n cells of species s). If measured for a range of different densities and light intensities take the average energy use per cell among these different conditions for each species.
- Calculate the cell metabolism of each species over a 24h dark period and net production for a 16L:8D cycle. Convert rates of oxygen consumption (µmol O₂ day⁻¹ cell⁻¹) to J day⁻¹. The average rates of the species in the experimental communities are:

Species	Cell metabolism (J d ⁻¹)	Cell net production (J d ⁻¹)
Amphidinium	$2.95 imes10^{-6}$	$2.86 imes10^{-6}$
Dunaliella	$2.03 imes 10^{-7}$	$6.1 imes 10^{-7}$
Amphora	$1.26 imes 10^{-5}$	$1.89 imes10^{-5}$
Tetraselmis	$5.94 imes10^{-6}$	$4.53 imes10^{-6}$
Synechococcus	$3.58 imes 10^{-8}$	$7.09 imes10^{-8}$
Tisochrysis	$2.08 imes10^{-7}$	$6.09 imes10^{-7}$

3. Multiply the average cell metabolism or net production rate of each species ($\overline{E}_{cell sps}$) by the total abundance of cells of that species in the community at each sampling time (N_{sps}, cells μ l⁻¹). Sum across species to obtain total community rates.

Density-dependent individual species rates

Community energy flux can be predicted from the density-dependence of cell energy use (\overline{E}_{spk}) parametrized for each species individually (δ_k) as a function of their population biomass density (D_k) .

 $\overline{E}_{com} = \sum_{k=1}^{s} (\overline{E}_{spk} \times N_{spk})$ where $\log_{10}(\overline{E}_{spk}) = \alpha_k + \delta_k \times \log_{10}(D_k)$

1. For each species, estimate the density-dependence of cell metabolism and photosynthesis $(\mu \text{mol } O_2 \text{ min}^{-1} \text{ cell}^{-1})$ as a function of population biomass concentration (D_k, i.e. optical density expressed in % (Fig. S1) using independent data (Malerba et al. 2017):

Amphidinium	\log_{10} cell metabolism = $-7.726 - 0.453 \times \log_{10}$ Conc
Dunaliella	\log_{10} cell metabolism = $-9.762 + 0.156 \times \log_{10}$ Conc
Amphora	\log_{10} cell metabolism = $-7.123 - 0.437 \times \log_{10}$ Conc
Tetraselmis	\log_{10} cell metabolism = $-6.949 - 0.832 \times \log_{10}$ Conc
Synechococcus	\log_{10} cell metabolism = $-10.228 - 0.064 \times \log_{10}$ Conc
Tisochrysis	\log_{10} cell metabolism = $-9.152 - 0.298 \times \log_{10}$ Conc

Amphidinium	\log_{10} cell photosynt. = $-7.525 - 0.443 \times \log_{10}$ Conc + 0.0004 × light
Dunaliella	\log_{10} cell photosynt. = $-8.914 - 0.190 \times \log_{10}$ Conc + $0.002 \times $ light
Amphora	\log_{10} cell photosynt. = $-6.815 - 0.369 \times \log_{10}$ Conc $-0.00005 \times $ light
Tetraselmis	\log_{10} cell photosynt. = $-7.274 - 0.377 \times \log_{10}$ Conc - 0.0001 × light
Synechococcus	\log_{10} cell photosynt. = $-9.351 - 0.453 \times \log_{10}$ Conc + 0.001 × light
Tisochrysis	\log_{10} cell photosynt. = $-8.705 - 0.244 \times \log_{10}$ Conc + $0.001 \times$ light

- 2. Using the equations above, calculate cell metabolism or cell photosynthesis for each species based on their population biomass concentration in each community at each sampling time (calculated for approach 4 "Size- and density-dependent rats across species").
- 3. Multiply cell rates by each species' density $(N_{spk}, cells \mu l^{-1})$ to calculate population rates $(\mu mol O_2 \min^{-1} \mu l^{-1})$ and sum across species to obtain community rates of metabolism and photosynthesis.
- 4. Convert community oxygen rates to energy rates for a total community volume of 500mL (J d⁻¹). Calculate community metabolic rate assuming 24h darkness, and community net production as the difference between 16h of photosynthesis and 8h of metabolism.

Reference

Malerba, M. E., et al. (2017). "Phytoplankton size-scaling of net-energy flux across light and biomass gradients." Ecology 98(12): 3106-3115. https://doi.org/10.1002/ecy.2032

Table S2. Summary of the square-root of the mean square error (RMSE) for each approach standardized by the best approach within each run (RMSE = 1). The approaches are ranked from best to worse based on their average accuracy (RMSE). Values in bold indicate the best approach within each run.

Approach	Metabolism		Net proc	luction		
	Run 1	Run 2	Run 1	Run 2	Average RMSE (± SE)	Rank
Mean biomass-specific rates	1.00	1.00	1.10	1.03	$1.03 (\pm 0.02)$	1
Density-dependent individual species rates (species density)	1.45	1.03	1.00	1.00	1.12 (± 0.11)	2
Density-dependent individual species rates (community density)	1.26	1.16	1.35	1.25	1.26 (± 0.04)	3
Size and density-dependent rates across species (species density)	1.42	1.14	1.72	1.06	1.34 (± 0.15)	4
Size-dependent rates across species	1.51	1.07	2.27	1.58	1.61 (± 0.25)	5
Size and density-dependent rates across species (community density)	1.87	1.52	1.92	1.28	1.65 (± 0.15)	6
Average individual species rates	1.96	2.00	1.30	1.59	1.71 (± 0.17)	7
Mean rates per cell	44.5	26.6	38.6	29.3	34.8 (± 4.13)	8

Table S3. Mean estimates and 95% Wald confidence intervals for the intercept and slope of the relationship between observed and predicted community metabolism and net production (J d⁻¹) from each approach, ranked in order of complexity (Fig. 1). Results are based on mixed models including community as a random effect and using Satterthwaite's approximation for degrees of freedom. For each approach, we report the R² from the model as a measure of precision, the bias (calculated as 1 – observed slope) and the square root of the mean square error (RMSE) standardised by the approach with the lowest RMSE within each run (RMSE = 1 indicates the most accurate approach and higher values indicate progressively worse accuracy). Values in bold indicate the best performing models with each run for precision (R²), bias or accuracy (RMSE). Significance: *** p < 0.0001, ** p < 0.001, * p < 0.05.

Metabolism									
Run 1	Intercept	Slope	df	F	p	R ²	Bias	RMSE	
Mean rates per cell	1232 (1053, 1410)	-0.002 (-0.008, 0.004)	96	0.39	0.53	0.004	1.002	44.5	
Mean biomass-specific rates	502 (364, 641)	0.63 (0.52, 0.74)	98	130	***	0.57	0.37	1	
Size-dependence across species	790 (596, 984)	0.34 (0.22, 0.47)	97	28	***	0.22	0.66	1.51	
Size and density-dependence across species (species density)	780 (540, 1020)	0.48 (0.26, 0.70)	96	18.5	***	0.15	0.52	1.42	
Size and density-dependence across species (community density)	464 (122, 806)	1.27 (0.73, 1.82)	98	21.21	***	0.17	-0.27	1.87	
Average individual species rates	668 (560, 776)	0.36 (0.31, 0.42)	65	152	***	0.61	0.64	1.96	
Density-dependent individual species rates (species density)	27 (-343, 398)	0.73 (0.52, 0.94)	94	46.4	***	0.28	0.27	1.45	
Density-dependent individual species rates (community density)	-91 (-271, 88)	1.63 (1.41, 1.84)	77	224	***	0.69	-0.63	1.26	
Run 2	Intercept	Slope	df	F	p	R ²	Bias	RMSE	
Mean rates per cell	1170 (1019, 1313)	0.004 (-0.007, 0.014)	67	0.59	0.44	0.006	0.99	26.7	
Mean biomass-specific rates	605 (442, 767)	0.56 (0.44, 0.68)	98	83.8	***	0.45	0.44	1	
Size-dependence across species	622 (430, 814)	0.54 (0.40, 0.68)	98	58.4	***	0.37	0.46	1.07	
Size and density-dependence across species (species density)	498 (280, 716)	0.85 (0.63, 1.06)	98	58.1	***	0.36	0.15	1.14	
Size and density-dependence across species (community density)	289 (-8.21, 587)	1.52 (1.08, 1.95)	97	46.74	***	0.31	-0.52	1.52	
Average individual species rates	906 (784, 1028)	0.24 (0.17, 0.31)	98	44	***	0.31	0.76	2.00	
Density-dependent individual species rates (species density)	-290 (-594, 13)	0.96 (0.77, 1.14)	98	102.4	***	0.51	0.04	1.03	

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Density-dependent individual species rates (community	229 (30, 430)	1.28 (1.04, 1.52)	97	109	***	0.52	-0.28	1.16		
Net production										
Run 1	p	R ²	Bias	RMSE						
Mean rates per cell	2072	-0.005	95	1.29	0.26	0.01	1.01	38.6		
Mean biomass-specific rates	745 (435, 1057)	0.71 (0.58, 0.85)	98	106	***	0.52	0.29	1.10		
Size-dependence across species	1583 (1184, 1982)	0.18 (0.06, 0.29)	97	8.77	**	0.08	0.82	2.27		
Size and density-dependence across species (species density)	1645 (1183, 2106)	0.21 (0.04, 0.41)	95	4.01	*	0.03	0.79	1.72		
Size and density-dependence across species (community density)	1550 (938, 2162)	0.40 (-0.07, 0.88)	96	2.74	0.1	0.02	0.60	1.92		
Average individual species rates	865 (594, 1136)	0.53 (0.44, 0.63)	95	115	***	0.55	0.47	1.30		
Density-dependent individual species rates (species density)	454 (97, 811)	0.82 (0.66, 0.98)	97	106.2	***	0.52	0.18	1		
Density-dependent individual species rates (community density)	371 (73, 670)	1.25 (1.06, 1.44)	92	167	***	0.65	-0.25	1.35		
Run 2	Intercept	Slope	df	F	p	R ²	Bias	RMSE		
Mean rates per cell	1593 (1369, 1817)	0.004 (-0.006, 0.013)	88	0.49	0.49	0.005	0.99	29.3		
Mean biomass-specific rates	753 (545, 962)	0.53 (0.44, 0.62)	96	131	***	0.55	0.47	1.03		
Size-dependence across species	853 (580, 1125)	0.39 (0.29, 0.48)	97	63.03	***	0.37	0.61	1.58		
Size and density-dependence across species (species density)	757 (453, 1061)	0.56 (0.41, 0.72)	97	51.7	***	0.33	0.44	1.06		
Size and density-dependence across species (community density)	701 (288, 1115)	0.83 (0.51, 1.14)	98	26	***	0.20	0.17	1.28		
Average individual species rates	1071 (887, 1255)	0.35 (0.27, 0.42)	97	83.9	***	0.45	0.65	1.59		
Density-dependent individual species rates (species density)	805 (590, 1019)	0.57 (0.45, 0.68)	97	96.6	***	0.48	0.43	1		
Density-dependent individual species rates (community density)	807 (599, 1017)	0.81 (0.65, 0.97)	97	100	***	0.49	0.19	1.25		

Table S4. Mean estimates and 95% Wald confidence intervals for the intercept and slope from linear mixed models (including community as a random effect) estimating the relationship between cell size and (1) cell abundance, (2) cell metabolism or net production, (3) community metabolism or net production, and the relationship between (4) community metabolism or net production and community biovolume. All data are log_{10} transformed and data from sampling 0 has been removed because at the start of the experiment cell abundance and cell size were experimentally manipulated. Significance: *** p < 0.0001, ** p < 0.001, * p < 0.05.

Relationship	Run	Intercept	Slope	F (df)	R ²						
Cell abundance	Run 1	5.33 (5.15, 5.50)	-1.02 (-1.1, -0.94)	592 (83)***	0.84						
~ cell size	Run 2	5.01 (4.84, 5.19)	-0.84 (-0.93, -0.75)	335 (88)***	0.78						
Metabolism											
Cell metabolism	Run 1	-8.10 (-8.21, -7.98)	1.10 (1.04, 1.16)	1186 (87)***	0.93						
~ cell size	Run 2	-7.99 (-8.13, -7.84)	1.04 (0.97, 1.12)	684 (88)***	0.89						
Community	Run 1	2.92 (2.79, 3.06)	0.08 (0.02, 0.15)	6.28 (84)*	0.05						
cell size	Run 2	2.76 (2.62, 2.90)	0.18 (0.11, 0.26)	22.33 (82)***	0.21						
Community	Run 1	-3.11 (-4.46, -1.76)	0.56 (0.44, 0.69)	80.6 (53)***	0.48						
community biovolume	Run 2	-3.18 (-4.80, -1.56)	0.57 (0.42, 0.72)	57.4 (87)***	0.40						
		Net prod	uction	<u> </u>							
Cell net	Run 1	-7.94 (-8.05, -7.82)	1.12 (1.07, 1.18)	1425 (85)***	0.94						
production ~ cell size	Run 2	-7.8 (-7.94, -7.66)	1.02 (0.94, 1.09)	744 (88)***	0.89						
Community net production ~ cell size	Run 1	3.09 (2.94, 3.24)	0.1 (0.04, 0.18)	8.9 (83)**	0.07						
	Run 2	2.92 (2.78, 3.05)	0.17 (0.1, 0.24)	21.2 (88)***	0.19						
Community net	Run 1	-3.47 (-4.96, -1.98)	0.61 (0.48, 0.75)	79.1 (81)***	0.49						
community biovolume	Run 2	-2.88 (-4.30, -1.46)	0.55 (0.43, 0.68)	70.8 (88)***	0.43						



Figure S1. Density-dependence of cell metabolism (top) and cell photosynthesis across light intensities (bottom) as a function of population biomass density (%) for each of the six species in the communities.



Figure S2. Relationship between observed rates of community metabolism and rates estimated from mean metabolism per cell among species (a & b), mean mass-specific metabolism among species (c &

d), size-dependent cell metabolism across species (e & f), size- and density-dependent cell metabolism across species (g & h), average cell metabolism for individual species (i & j) and densitydependent cell metabolism for individual species (k & l). Each graph reports the square root of the mean square error (RMSE) standardised by the most accurate approach within that run (RMSE = 1 indicates the most accurate approach, values larger than 1 indicate progressively larger errors). In both runs community metabolism was best predicted from the average biomass-specific metabolism among species. The solid line represents estimates of community metabolism from linear mixed models with 95% confidence intervals. Broken lines are 1:1 lines for comparison. Lighter colours indicate older communities.



Figure S3. Relationship between observed community net production and rates estimated from mean net production per cell among species (a & b), mean biomass-specific net production among species

(c & d), size-dependent cell net production across species (e & f), size- and density-dependent net production across species (g & h), average cell net production for individual species (i & j) and density-dependent cell net production for individual species (k & l). Each graph reports the square root of the mean square error (RMSE) standardised by the most accurate approach (RMSE = 1). Community net production was best predicted by the approach based on the density-dependence of individual species rates. The solid line represents estimates of community net production from linear mixed models with 95% confidence intervals. Broken lines are 1:1 lines for comparison. Lighter colours indicate older communities.



Figure S4. Comparison of community metabolism calculated from the size- and density-dependence of cell metabolism across species (top) or density-dependent individual species metabolic rates (bottom) using either community biomass density (red) or individual species biomass density (blue). The density of conspecifics (blue) explains most of the variation in community metabolism for both approaches, and leads to the greater accuracy, except for predictions based on individual species rates in run 1 (see also Table S2).



Figure S5. Comparison of community net production calculated from the size- and densitydependence of cell net production across species (top) or the density-dependence of net production rates for individual species (bottom) using either community biomass density (red) or individual species biomass density (blue). The density of conspecifics (blue) explains most of the variation in community productivity for both approaches and always increases accuracy (see also Table S2).



Figure S6. Plot of the squared errors (log₁₀-transformed) calculated for each approach against observed community metabolism (top) and net production (bottom). The larger the errors on the y-axis, the larger the bias of the approach. Regression lines with a negative slope indicate lower accuracy for smaller values of community energy flux, while those with postive slopes indicate lower accuracy for larger values of community energy flux. Errors for the two approaches that account for density-dependence (across species and individual species rates) are based on predictions using species density as they were usually more accurate than those based on community density (see Table S2, and Figure S4 and S5 for comparison).



Figure S7. Over time, average cell net production (a) increased nearly isometrically with average cell size in communities (slope = 1.12, 95% CI = 1.07, 1.18), but total cell abundance declined with average size with an almost inverse slope (b; slope = -1.02, 95% CI = -1.1, -0.94). The reciprocal size-scaling of cell energy flux and abundance means that total community net production is (almost) independent of mean cell size in the community (c; slope = 0.1, 95% CI = 0.04, 0.18) and mostly driven by total biovolume (d; slope = 0.61, 95% CI = 0.48, 0.75). All data are log_{10} -transformed. Here shown for net production in run 1 (see Fig. 3 for metabolism for run 1 and Fig S8 for run 2).



Figure S8. Over the 9 weeks of the experiment, the average metabolism (a) and net production (e) of cells within communities increased with average cell size with an isometric slope (slope = 1.04, 95% CI = 0.97, 1.12; and 1.02, 95% CI = 0.94, 1.09, respectively), but total cell abundance declined with average size with an almost inverse slope (b or f, slope = -0.84, 95% CI = -0.93, -0.75). The almost reciprocal scaling of cell size with cell energy flux and abundance meant that total community energy flux was (almost) independent of size (metabolism (c): slope = 0.18, 95% CI = 0.11, 0.26; net production (g): slope = 0.17, 95% CI = 0.1, 0.24), and mostly driven by biovolume (metabolism (d): slope = 0.57, 95% CI = 0.42, 0.72; net production (h): slope = 0.55, 95% CI = 0.43, 0.68). Data are log₁₀-transformed. Here shown for run 2, see Fig. 3 and S7 for run 1 and Table S4 for analyses.



Figure S9. When taken individually, most species did not show a clear relationship between population abundance and cell size, either within (coloured lines) or across (thick black line) sampling times (weeks).



Figure S10. Weekly changes in the total biovolume of communities over time.



Figure S11. Plot of observed community metabolism (a & b for run 1 and 2 repectively) or net production (c & d for run 1 and 2 repectively) against estimates of community rates from the mean biomass-specific energy flux of cells among species. This approach based on biomass-specific rates consistently overestimates community rates (values fall below the 1:1 broken line) where large cells (size of circle) occur at their relative highest densities (lighter colours), suggesting that density-dependence of cell energy use becomes increasingly important under these conditions.