# Functional trait variation and nitrogen use efficiency in temperate coastal phytoplankton

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### **Supplement 1**

Table S1. List of the diatom species identified by inverted microscopy counts in coastal waters of the eastern English Channel (EEC) between 2011 and 2014, and their corresponding frequency (%), average biomass ( $\mu$ gC L<sup>-1</sup>), and surface to cell volume ratio (S/V,  $\mu$ m).

	Frequency	Average biomass	S/V ratio
	%	$\mu g C L^{-1}$	$\mu m^{-1}$
Actinotychus spp.	15	0.04	0.22
Asterionellopsis glacialis	55	0.22	1.07
Bacillaria paxillifera	4	0.05	0.86
Biddulphia rhombus	15	0.27	0.12
Brockmaniella brockmanii	9	0.02	0.53
Cerataulina pelagica	19	0.48	0.77
Ceratoneis closterium	57	0.06	2.13
Chaetoceros compressus/tortissimus	30	0.23	0.79
C. curvisetus/pseudo-curvisetus/debilis	21	0.21	0.22
C. danicus	13	0.02	1.35
C. decipiens	15	0.79	0.29
C. densus/eibenii	9	0.08	0.30
C. diadema	11	0.17	0.31
C. didymus	2	0.01	1.61
C. lauderi/teres	9	0.03	0.30
C. simplex/tenuissimus	17	0.03	1.57
C. socialis	45	0.51	1.61
C. wighamii/perpusillus	21	0.13	1.57
Corethron criophilum	2	0.05	0.04
Coscinodiscus spp	4	0.13	0.02
C. radiatus	9	0.12	0.07
C. wailesii	4	2.10	0.02
Dactyliosolen fragillissimus	32	5.38	1.00
Delphineis surirella	11	0.04	0.33
Diploneis spp.	26	0.20	0.04
Ditylum brightwelli	45	5.34	0.28
Eucampia zodiacus/bicornata	4	0.02	0.07
Guinardia delicatula	70	14.90	1.25
G. flaccida	70	14.50	0.46
G. striata	51	5.91	1.08
Helicotheca tamesis	4	1.19	0.05
Lauderia annulata	13	1.33	0.86
Leptocylindrus danicus	51	26.46	2.13
L. minimus	19	0.08	3.16
Meuneria membranacea	26	0.14	0.09
Navicula sppp.	36	0.03	0.07
Nitzschia longissima	17	0.03	2.13
Odontella aurita	4	0.01	0.21

	Frequency	Average biomass	S/V ratio
	%	μgC L <sup>-1</sup>	$\mu m^{-1}$
Pseudo-nitzschia americana	32	0.09	1.96
Pseudo-nitzschia spp.	40	0.05	3.94
P. delicatissima complex	70	1.07	4.63
P. fraudulenta	36	3.94	1.09
P. pungens	23	0.08	1.34
Paralia sulcata	62	0.19	0.30
Pleurosigma spp./Gyrosigma spp.	47	2.33	0.05
Podosira stelligera	2	0.01	0.20
Raphoneis amphiceros	30	0.07	0.09
Rhizosolenia imbricata var. shrubsolei	74	17.77	1.74
R. setigera	28	0.13	0.24
R. setigera f. pungens	9	0.26	0.54
Skeletonema spp.	26	0.16	1.63
Thalassionema nitzschoides	40	0.10	0.84
Thalassiosira angulata/curviseriata	15	0.49	1.00
T. fallax	2	0.01	1.30
T. gravida	19	0.39	1.24
T. levanderi	4	0.04	1.50
T. punctigera	9	0.05	0.18
Trigonium alternans	4	0.03	0.12

#### **Supplement 2**

## Supplementary information related to photo-physiological parameters, and C/N and C/P cell content ratios.

Only published data on phytoplankton cultures grown in nutrient-replete media and at a temperature of or close to 20°C were selected. The photophysiological parameters were obtained by extracting raw data from published growth-irradiance curves using the ImageJ v.143u free software (Rasband 2006), and then by curve fitting according to the Monod equation (see Shwaderer et al. 2011) for the similarity in the photophysiological parameters values with the common Platt equation [Platt et al. 1980]:

$$\mu(I) = \frac{\mu_{\max}I}{I + \frac{\mu_{\max}}{\alpha_{\mu}}}$$

with  $I \ (\mu \text{E m}^{-2} \text{ s}^{-1})$  the irradiance,  $\mu \text{max} \ (\text{day}^{-1})$  the maximal growth rate, and  $\alpha_{\mu} \ (\mu \text{E}^{-1} \text{ m}^2 \text{ s} \text{ day}^{-1})$  the initial slope of the growth-irradiance curve. The onset of light saturation  $(E_k, (\mu \text{E m}^{-2} \text{ s}^{-1}))$  was calculated as  $\mu_{\text{max}}/\alpha_{\mu}$ .

Table S2. References for phytoplankton photo-physiological traits data ( $\alpha\mu$ ,  $E_k$ , and  $\mu$ max(Light)) and those related to nitrogen and phosphorus cell requirement (C/N and C/P cell content ratios). Each number corresponds to one publication, of which the list is given below.

	C/N ratio	C/P ratio	aµ-Ek-µmax
Coccolithophores	18,20,29,31,43,46,55	18,20,46	14,18
	(5 species, 14 data values)	(4 species, 7 data values)	(3 species, 3 data values)
Cryptophytes	2,6,8,24,32,34,42,43,47,48,50,55	6,42	4,28
	(10 species, 14 data values)	(3 species, 3 data values)	(2 species, 2 data values)
Diatoms	1,9,16,20,26,29,31,32,34,46,50 (27 species, 39 values)	9,16,20,26,42,44,46 (13 species, 18 data values)	3,7,11,12,13,17,23,25,27,35,36,37, 38,40,41,49,51,52,54 (16 species, 27 data values)
<i>P.globosa</i> diploid	22,56	22	22,39
	(2 data values)	(1 data value)	(2 data values)
<i>P.globosa</i> haploid	21	22	55
	(1 data value)	(2 data values)	(1 data value)
Picoeukaryotes	31,55	30	10,25,45,53
	(4 species, 4 data values)	(1 species, 1 data value)	(5 species, 5 data values)
Synechococcus spp.	5,15,24,31,42,55	5,19,42	33
	(6 data values)	(3 data values)	(1 data value)

1/Arrigo KR, Robinson DH, Worthen DL, Dunbar RB, DiTullio GR, VanWoert M, Lizotte MP (1999) Phytoplankton community structure and the drawdown of nutrients and CO2 in the Southern Ocean. Science 283:365–367

- 2/Augustin CB, Boersma M (2006) Effects of nitrogen stressed algae on different *Acartia* species. J Plankton Res 28:429-436
- 3/Aydýn GS, Aydin G, Kocatas A, Buyukisik B (2009) Effects of light and temperature on the growth rate of potentially harmful marine diatom: *Thalassiosira allenii* Takano (Bacillariophyceae). African J Biotechnol 8:4983-4990
- 4/Bartual A, Lubián LM, Gálvez FX (2002) Effect of irradiance on growth, photosynthesis, pigment content and nutrient consumption in dense cultures of *Rhodomonas salina* (Wislouch) (Cryptophyceae). Cienc Mar 28:381–392

- 5/Bertilsson S, Berglund O, Karl DM, Chisholm SW (2003) Elemental composition of marine *Prochlorococcus* and *Synechococcus*: Implications for the ecological stoichiometry of the sea. Limnol Oceanogr 48:1721-1731
- 6/Bi R (2013) Chemical composition of phytoplankton as the determinant of food quality. Degree Dissertation. Kiel University.
- 7/ Brand LE, Guillard RRL (1981) The effects of continuous light and light intensity on the reproduction rates of twenty-two species of marine phytoplankton. J Exp Mar Biol Ecol 50:119–132
- 8/Broglio E, Jónasdóttir SH, Calbet A, Jakobsen HH, Saiz E (2003) Effect of heterotrophic versus autotrophic food on feeding and reproduction of the calanoid copepod *Acartia tonsa*: relationship with prey fatty acid composition. Aquat Microb Ecol 31:267–278
- 9/Burkhardt S, Riebesell U, Zondervan I (1999) Stable carbon isotope fractionation by marine phytoplankton in response to daylength, growth rate, and CO2 availability. Mar Ecol Prog Ser 184:31–41
- 10/Cochlan WP (1989) Nitrogen uptake by marine phytoplankton: the effects of irradiance, nitrogen supply and diel periodicity. Doctoral Thesis. University of British Columbia, 238 pp.
- 11/Cullen JJ, Lewis MR (1988) The kinetic of algal photoadaptation in the context of vertical mixing. J Plankton Res 10:1039-1063
- 12/Falkowski PG, Dubinsky Z, Wyman K (1985) Growth-irradiance relationships in phytoplankton. Limnol. Oceanogr. 30:311-321
- 13/Falkowski PG, Owens TG (1980) Light—shade adaptation two strategies in marine phytoplankton. Plant Physiol 66:592–595
- 14/Fielding SR (2014) *Emiliania huxleyi* population growth rate response to light and temperature: a synthesis. Aquat Microb Ecol 73:163–170
- 15/Fu FX, Warner ME, Zhang Y, Feng Y, Hutchins DA (2007) Effects of increased temperature and CO2 on photosynthesis, growth, and elemental ratios in marine *Synechococcus* and *Prochlorococcus* (Cyanobacteria). J Phycol 43:485-496
- 16/Goldman JC, Sell DAA, Ennett MR (1992) Chemical characterization of 3 large oceanic diatoms-Potential impact on water column chemistry. Mar Ecol Prog Ser 88:257-270
- 17/Guillard RR, Ryther JH (1962) Studies of marine planktonic diatoms :I.Cyclotella nana (Hustedt), and Detonula confervacea (Cleve) gran. Can J microbiol 8:229-239
- 18/Heinle M (2013) The effects of light, temperature and nutrients on coccolithophores and implications for biogeochemical models. Doctoral thesis. University of East Anglia.
- 19/Heldal M, Scanlan DJ, Norland S, Thingstad F, Mann NH (2003) Elemental composition of single cells of various strains of marine *Prochlorococcus* and *Synechococcus* using X-ray microanalysis. Limnol Oceanogr 48:1732-1743
- 20/Ho TY, Quigg A, Finkel ZV, Milligan AJ, Wyman K, Falkowski PG, Morel FMM

(2003) The Elemental Composition of Some Marine Phytoplankton. J Phycol 39:1145–1159

- 21/Hoogstraten A, Peters M, Timmermans KR, de Baar HJW (2012) Combined effects of inorganic carbon and light on *Phaeocystis globosa* Scherffel (Prymnesiophyceae). Biogeosciences 9:1885–1896
- 22/Jahnke J (1989) The light and temperature dependence of growth rate and elemental composition of *Phaeocystis globosa* Scherffel and *P. pouchetii* (Har.) Lagerh. in batch cultures. Neth J Sea Res 23:15–21
- 23/Kaeriyama H, Katsuki E, Otsubo M, Yamada M, Ichimi K, Tada K, Harrison PJ (2011) Effects of temperature and irradiance on growth of strains belonging to seven *Skeletonema* species isolated from Dokai Bay, southern Japan. Eur J Phycol 46:113–124

- 24/Koski M, Klein Breteler W, Schogt N, Gonzalez S, Jakobsen HH (2006) Life-stage-specific differences in exploitation of food mixtures: diet mixing enhances copepod egg production but not juvenile development. J Plankton Res 28:919-936
- 25/Kulk G, de Poll WHV, Visser RJW, Buma AGJ (2011) Distinct differences in photoacclimation potential between prokaryotic and eukaryotic oceanic phytoplankton. J Exp Mar Biol Ecol 398:63–72
- 26/La Roche J, Geider RJ, Graziano LM, Murray H, Lewis K (1993) Induction of specific protein in eukaryotic algae grown under iron-, phosphorus-, or nitrogen-deficient conditions. J Phycol 29:767– 77
- 27/Laws EA, Bannister TT (1980) Nutrient-and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. Limnol Oceanogr 25:457–473
- 28/Lewitus AJ, Caron DA (1990) Relative effects of nitrogen or phosphorus depletion and light intensity on the pigmentation, chemical composition, and volume of *Pyrenomonas salina* (Cryptophyceae). Mar Ecol Prog Ser 61:171–181
- 29/Llewellyn CA, Gibb SW (2000) Intra-class variability in the carbon, pigment and biomineral content of prymnesiophytes and diatoms. Mar Ecol Prog Ser 193:33-44
- 30/ Maat DS, Crawfurd KJ, Timmermans KR, Brussaard CP (2014) Elevated CO2 and phosphate limitation favor *Micromonas pusilla* through stimulated growth and reduced viral impact. Appl Environ Microb 80:3119-27
- 31/Marañón E, Cermeño P, López-Sandoval DC, Rodríguez-Ramos T, Sobrino C, Huete-Ortega M, Blanco JM, Rodríguez J (2013) Unimodal size scaling of phytoplankton growth and the size dependence of nutrient uptake and use. Ecol Lett 16:371–379
- 32/Moal J, Martin-Jezequel V, Harris RP, Samain JF, Poulet SA (1987) Interspecific and intraspecific variability of the chemical-composition of marine-phytoplankton. Oceanol acta 10:339-346
- 33/Morris I, Glover H (1981) Physiology of photosynthesis by marine coccoid cyanobacteria—Some ecological implications. Limnol Oceanogr 26:957–961
- 34/Nejstgaard JC, Båmstedt U, Bagøien E, Solberg PT (1995) Algal constraints on copepod grazing. Growth state, toxicity, cell size, and season as regulating factors. ICES J Mar Sci 52:347-357
- 35/Nelson DM, D'Elia CF, Guillard RR (1979) Growth and competition of the marine diatoms *Phaeodactylum tricornutum* and *Thalassiosira pseudonana*. II. Light limitation. Mar Biol 50:313–318
- 36/Nishikawa T, Yamaguchi M (2006) Effect of temperature on light-limited growth of the harmful diatom *Eucampia zodiacus* Ehrenberg, a causative organism in the discoloration of *Porphyra thalli*. Harmful Algae 5:141-147
- 37/Nishikawa T, Yamaguchi M (2008) Effect of temperature on light-limited growth of the harmful diatom *Coscinodiscus wailesii*, a causative organism in the bleaching of aquacultured *Porphyra thalli*. Harmful Algae 7:561-566
- 38/Paasche E (1968) Marine Plankton Algae Grown with Light-Dark Cycles. Physiol Plantarum 21:66-77
- 39/Peperzak L (1993) Daily irradiance governs growth rate and colony formation of *Phaeocystis* (Prymnesiophyceae). J Plankton Res 15:809–821
- 40/Popovich CA, Gayoso AM (1999) Effect of irradiance and temperature on the growth rate of *Thalassiosira curviseriata* Takano (Bacillariophyceae), a bloom diatom in Bahia Blanca estuary (Argentina). J Plankton Res 21:1101-1110
- 41/Post AF, Dubinsky Z, Wyman K, Falkowski PG (1985) Physiological responses of a marine planktonic diatom to transitions in growth irradiance. Mar Ecol Prog Ser 25:141-149
- 42/Quigg A, Irwin AJ, Finkel ZV (2003) The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. Nature 425:291–294

- 43/Rey C Harris R, Irigoien X, Head R, Carlotti F (2001) Influence of algal diet on growth and ingestion of *Calanus helgolandicus* nauplii. Mar Ecol Prog Ser 216:151–165
- 44/Ríos AF, Fraga F, Figueira FG, Pérez FF (1998) A modelling approach to the Redfield ratio deviations in the ocean. Cienc Mar 62:169-176
- 45/Rodríguez J, Blanco JM, Jiménez-Gómez F, Echevarría F, Gil J, Rodríguez V, Ruiz J, Bautista B, Guerrero F (1998) Patterns in the size structure of the phytoplankton community in the deep fluorescence maximum of the Alboran Sea (southwestern Mediterranean). Deep-Sea Res Pt I 45:1577–1593
- 46/Sakshaug E, Andresen K, Myklestad S, Olsen Y (1983) Nutrient status of phytoplankton communities in Norwegian waters (marine, brackish, and fresh) as revealed by their chemical composition. J Plankton Res 5:175-196
- 47/Seixas P, Coutinho P, Ferreira M, Otero A (2009) Nutritional value of the cryptophyte *Rhodomonas lens* for *Artemia* sp.. J Exp Mar Biol Ecol 381:1–9 http://www.sciencedirect.com/science/article/pii/S0022098109003724 - cor1
- 48/Seixas P, Rey-Méndez M, Valente LMP, Otero A (2008) Producing juvenile *Artemia* as prey for *Octopus vulgaris* paralarvae with different microalgal species of controlled biochemical composition. Aquaculture 283:83–91
- 49/Sharpe SC, Koester JA, Loebl M, Cockshutt AM, Campbell DA, Irwin AJ, Finkel ZV (2012) Influence of Cell Size and DNA Content on Growth Rate and Photosystem II Function in Cryptic Species of *Ditylum brightwellii*. PLoS ONE 7:e52916
- 50/Strom SL, Buskey EJ (1993) Feeding, growth, and behavior of the thecate heterotrophic dinoflagellate *Oblea rotunda*. Limnol Oceanogr 38:965–977
- 51/Strzepek RF, Harrison PJ (2004) Photosynthetic architecture differs in coastal and oceanic diatoms. Nature 431:689–692
- 52/Strzepek RF, Price NM (2000) Influence of irradiance and temperature on the iron content of the marine diatom *Thalassiosira weissflogii* (Bacillariophyceae). Mar Ecol Prog Ser 206:107–117
- 53/Timmermans KR, van der Wagt B, Veldhuis MJW, Maatman A, de Baar HJW (2005) Physiological responses of three species of marine pico-phytoplankton to ammonium, phosphate, iron and light limitation. J Sea Res 53:109–120
- 54/Verity PG (1982) Effect of temperature, irradiance, and daylength on the marine diatom *Leptocylindrus Danicus* Cleve. IV. Growth. J Exp Mar Biol Ecol 60:209-222
- 55/Verity PG, Robertson CY, Tronzo CR, Andrews MG, Nelson JR, Sieracki ME (1992) Relationships between cell volume and the carbon and nitrogen content of marine photosynthetic nanoplankton. Limnol Oceanogr 37:1434-1446
- 56/Verity PG, Smayda TJ, Sakshaug E (1991) Photosynthesis, excretion, and growth rates of *Phaeocystis* colonies and solitary cells. Polar Res 10:117–128

### Supplement 3. Other traits (Nitrate scaled affinity, temperature dependent growth, and morphology)

The Nitrate scaled affinity ( $N_{saff}$ , L µmol<sup>-1</sup> day<sup>-1</sup>) was calculated according to the allometric equation established by Edwards et al. (2012), based on the compilation of literature data for 64 marine species cultivated at or near 20°C with sufficient light:

$$LogN_{saff}$$
= -0.63 logV+2.9

where V ( $\mu$ m<sup>3</sup>) corresponds to the mean cell biovolume of each species /functional group.

Growth rate for *Phaeocystis* (Schoemann et al. 2005) and the coccolithophore *Emiliania huxleyii* (Fielding 2013) were calculated from growth-temperature equations. Maximal growth rate calculated for *E. huxleyii* was compared with data from laboratory experiments with six other species of coccolithophores (Buitenhuis et al. 2008). For diatoms, we applied the equation established by Bissinger et al. (2008). Finally, maximal growth rates of *Synechococcus* spp. and picoeukaryotes were assessed from a worldwide field database compiled by Chen et al. (2014), using data where media was nutrient-enriched, complemented by data from Stawiarski (2014) and Pittera et al (2014). No value was found in the literature concerning marine cryptophytes.

Biovolume (V,  $\mu m^3$ ) and surface area (S,  $\mu m^2$ ) of each phytoplankton group were calculated using the geometrical formula given by Hillebrand et al. (1999), based on measurements by cytometry for *Synechococcus* spp., picoeukaryotes, *Phaeocystis* haploid cells, and coccolithophores; and by inverted microscopy according to the Utermohl method for *Phaeocystis* colonies, diatoms species, and cryptophytes. For microscopy, 20 specimens of each diatom species, 20 of each size category of cryptophytes, and all healthy *Phaeocystis* colonies were measured at each sampling date in a settled volume of 10 ml. The resulting V and surface to volume ratio (S/V ratio) of the diatoms and cryptophytes communities were obtained by weighting each of them to the abundance proportion of each species, and each size category, respectively. For cytometry, cell size was estimated using calibration beads according to the following equations:

(Correction Factor) = (Real beads size / Measured beads size) (1)

[Estimated Particles size  $(\mu m)$ ] = (Measured Particles size \* Correction Factor) (2)

Finally, the V and S/V ratio of each phytoplankton group used in this study corresponds to their median over the entire period. Presence or absence of flagella was based on the taxonomy of pico- and nanophytoplankters described in the EEC (Not et al. 2004, Genitsaris et al. 2015).

### References

- Bissinger JE, Montagnes DJS, Harples J, Atkinson D (2008) Predicting marine phytoplankton maximum growth rates from temperature: Improving on the Eppley curve using quantile regression. Limnol Oceanogr 53:487–493
- Brand LE, Guillard RRL (1981) The effects of continuous light and light intensity on the reproduction rates of twenty-two species of marine phytoplankton J Exp Mar Biol Ecol 50:119–132.
- Buitenhuis ET, Pangerc T, Franklin DJ, Le Quéré C, Malin G (2008) Growth rates of six coccolithophorid strains as a function of temperature. Limnol Oceanogr 53:1181–1185
- Chen B, Hongbin L, Bangqin H, Jing W (2014). Temperature effects on the growth rate of marine picoplankton. Mar Ecol Prog Ser 505:37-47
- Edwards KF, Litchman E, Thomas M, Klausmeier CA 2012. Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. Limnol Oceanogr 57:554-566
- Fielding SR (2013) *Emiliania huxleyi* specific growth rate dependence on temperature Limnol Oceanogr 58:663–666
- Genitsaris S, Monchy S, Viscogliosi E, Sime-Ngando T, Ferreira S, Christaki U (2015) Seasonal variations of marine protist community structure based on taxon-specific traits using the eastern English Channel as a model coastal system. FEMS Microbiol Ecol 91: fiv034

- Hillebrand H, Dürselen CD, Kirschtel D, Pollingher U, Zohary T (1999) Biovolume calculation for pelagic and benthic microalgae. J Phycol 35: 403–424
- Not F, Latasa M, Marie D, Cariou T, Vaulot D, Simon N (2004) A single species, *Micromonas pusilla* (Prasinophyceae), dominates the eukaryotic picoplankton in the Western English Channel. Appl Environ Microb 70:4064-4072
- Paasche E (1967) Marine plankton algae grown with light-dark cycles. I. Coccolithus huxleyi. Physio Plantarum 20:946–956
- Pittera J, Humily F, Thorel M, Grulois D, Garczarek L', Six C (2014) Connecting thermal physiology and latitudinal niche partitioning in marine *Synechococcus*. The ISME Journal 1–16
- Platt T, Gallegos CL, <u>Harrison</u> WG (1980) Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. J Mar Res 38:687-701
- Rasband WS (2006) ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, (http://imagej.nih.gov/ij/)
- Raven JA 1997 The vacuole: a cost-benefit analysis. Adv Bot Res 25:59-86
- Schoemann V, Becquevort S, Stefels J, Rousseau W, Lancelot C (2005) *Phaeocystis* blooms in the global ocean and their controlling mechanisms: a review. J Sea Res 53:43-66
- Schwaderer AS, Yoshiyama K, de Tezanos Pinto P, Swenson NG, Klausmeier CA, Litchman E (2011). Ecoevolutionary differences in light utilization traits and distributions of freshwater phytoplankton. Limnol Oceanogr 56:589–598
- Stawiarski B 2014 The physiological response of picophytoplankton to light, temperature and nutrients including climate change model simulations. Doctoral Thesis. University of East Anglia 157 pp.

### Supplement 4

Fig. S1. Relation between CWM-S/Vbis for each diatom species value (see Supplement 1) and CWM-S/V considering the median (see Table 1 in the main article). CWM-S/V: Phytoplankton community- weighted mean of the Surface area to cell Volume ratio.



### **Supplement 5**

Fig. S2. Position of the observed (black circles) functional diversity values (A: functional evenness, FEve; B: functional divergence, RaoQ) in 999 null distributions along the resource gradient (RLQ axis). The grey zone and grey circles represent the range of the 999 randomized values and the individual mean, respectively. N: nutrient concentrations, L: light intensity for phytoplankton growth, +: high, -: low.

