



UvA-DARE (Digital Academic Repository)

Out of balance: implications of climate change for the ecological stoichiometry of harmful cyanobacteria

van de Waal, D.B.

[Link to publication](#)

Citation for published version (APA):

van de Waal, D. B. (2010). *Out of balance: implications of climate change for the ecological stoichiometry of harmful cyanobacteria*.

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

References

- Agawin NSR, Rabouille S, Veldhuis MJW, Servatius L, Hol S, Van Overzee HMJ, and Huisman J. 2007. Competition and facilitation between unicellular nitrogen-fixing cyanobacteria and non-nitrogen-fixing phytoplankton species. *Limnol. Oceanogr.* 52: 2233-2248.
- Allen MM, and Hutchison F. 1980. Nitrogen limitation and recovery in the cyanobacterium *Aphanocapsa* 6308. *Arch. Microbiol.* 128: 1-7.
- Allen MM. 1984. Cyanobacterial cell inclusions. *Ann. Rev. Microbiol.* 38: 1-25.
- Allen MM. 1988. Inclusions: Cyanophycin. *Methods Enzymol.* 167: 207-213.
- Anderson NJ, Jeppesen E, and Søndergaard M. 2005. Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. *Freshw. Biol.* 50: 1589-1593.
- Atkinson A, Siegel V, Pakhomov E, and Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432: 100-103.
- Babica P, Bláha L, and Maršálek B. 2006. Exploring the natural role of microcystins: a review of effects on photoautotrophic organisms. *J. Phycol.* 42: 9-20.
- Badger MR, Price GD, Long BM, and Woodger FJ. 2006. The environmental plasticity and ecological genomics of the cyanobacterial CO₂ concentrating mechanism. *J. Exp. Bot.* 57: 249-265.
- Bañares-España E, López-Rodas V, Salgado C, Costas E, and Flores-Moya A. 2006. Inter-strain variability in the photosynthetic use of inorganic carbon, exemplified by the pH compensation point, in the cyanobacterium *Microcystis aeruginosa*. *Aquat. Bot.* 85: 159-162.
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, Feldman GC, Milligan AJ, Falkowski PG, Letelier RM, and Boss ES. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444: 752-755.
- Bellerby RGJ, Schulz KG, Riebesell U, Neill C, Nondal G, Johannessen T, and Brown KR. 2007. Marine ecosystem community carbon and nutrient uptake stoichiometry under varying ocean acidification during the PeECE III experiment. *Biogeosciences Discuss* 4: 4631-4652.
- Benincà E, Huisman J, Heerkloss R, Jöhnk KD, Branco P, Van Nes EH, Scheffer M, and Ellner SP. 2008. Chaos in a long-term experiment with a plankton community. *Nature* 451: 822-825.
- Berger SA, Diehl S, Stibor H, Trommer G, Ruhlenstroth M, Wild A, Weigert A, Jäger CG, and Striebel M. 2007. Water temperature and mixing depth affect timing and magnitude of events during spring succession of the plankton. *Oecologia* 150: 643-654.
- Betts RA, Boucher O, Collins M, Cox PM, Falloon PD, Gedney N, Hemming DL, Huntingford C, Jones CD, Sexton DMH, and Webb MJ. 2007. Projected increase in continental runoff due to plant responses to increasing carbon dioxide. *Nature* 448: 1037-1041.
- Bezemer TM, and Jones TH. 1998. Plant-insect herbivore interactions in elevated atmospheric CO₂: quantitative analyses and guild effects. *Oikos* 82: 212-222.

- Börner T, and Dittmann E. 2005 Molecular biology of cyanobacterial toxins: genetic basis of microcystin production. *Harmful Cyanobacteria* (Huisman J, Matthijs HCP, and Visser PM, eds), pp. 25-40. Springer, Dordrecht, The Netherlands.
- Brewer PG, and Goldman JC. 1976. Alkalinity changes generated by phytoplankton growth. *Limnol. Oceanogr.* 21: 108-117.
- Briand JF, Robillot C, Quiblier-Lloberas C, and Bernard C. 2002. A perennial bloom of *Planktothrix agardhii* (Cyanobacteria) in a shallow eutrophic French lake: limnological and microcystin production studies. *Arch. Hydrobiol.* 153: 605-622.
- Briand E, Escoffier N, Straub C, Sabart M, Quiblier C, and Humbert JF. 2009. Spatiotemporal changes in the genetic diversity of a bloom-forming *Microcystis aeruginosa* (cyanobacteria) population. *ISME J.* 3: 419-429.
- Briand E, Gugger M, François JC, Bernard C, Humbert JF, and Quiblier C. 2008. Temporal variations in the dynamics of potentially microcystin-producing strains in a bloom-forming *Planktothrix agardhii* (Cyanobacterium) population. *Appl. Environ. Microb.* 74: 3839-3848.
- Bryant JP, Chapin FS III, and Klein DR. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* 40: 357-368.
- Caldeira K, and Wickett ME. 2003. Anthropogenic carbon and ocean pH. *Nature* 425: 365.
- Caraco NF, and Miller R. 1998. Effects of CO₂ on competition between a cyanobacterium and eukaryotic phytoplankton. *Can. J. Fish. Aquat. Sci.* 55: 54-62.
- Carmichael WW. 2001. Health effects of toxin-producing cyanobacteria: 'the cyanoHABs'. *Hum. Ecol. Risk Assess.* 7: 1393-1407.
- Carpenter SR, Caraco NF, Correll DL, Howarth RW, Sharpley AN, and Smith VH. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* 8: 559-568.
- Chen YM, Lee TH, Lee SJ, Huang HB, Huang R, and Chou HN. 2006. Comparison of protein phosphatase inhibition activities and mouse toxicities of microcystins. *Toxicon* 47: 742-746.
- Chorus I, and Bartram J. 1999. Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management. WHO, E & FN Spon, London, UK.
- Christiansen G, Fastner J, Erhard M, Börner T, and Dittmann E. 2003. Microcystin biosynthesis in *Planktothrix*: genes, evolution and manipulation. *J. Bacteriol.* 185: 564-572.
- Cloern JE. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210: 223-253.
- Codd GA, Lindsay J, Young FM, Morrison LF, and Metcalf JS. 2005. Harmful cyanobacteria: from mass mortalities to management measures. In: *Harmful Cyanobacteria* (Huisman J, Matthijs HCP, and Visser PM, eds.), pp. 1-23. Springer, Dordrecht, The Netherlands.
- Cole JJ, Prairie YT, Caraco NF, McDowell WH, Tranvik LJ, Striegl RG, Duarte CM, Kortelainen P, Downing JA, Middelburg JJ, and Melack J. 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosystems* 10: 171-184.
- Commichau FM, Forchhammer K, and Stülke J. 2006. Regulatory links between carbon and nitrogen metabolism. *Curr. Opin. Microbiol.* 9: 167-172.
- DeMott WR, Zhang QX, and Carmichael WW. 1991. Effects of toxic cyanobacteria and purified toxins on the survival and feeding of a copepod and three species of *Daphnia*. *Limnol. Oceanogr.* 36: 1346-1357.

- Diehl S, Berger S, Ptacnik R, and Wild A. 2002. Phytoplankton, light, and nutrients in a gradient of mixing depths: field experiments. *Ecology* 83: 399-411.
- Dittmann E, Neilan BA, and Börner T. 2001. Molecular biology of peptide and polyketide biosynthesis in cyanobacteria. *Appl. Microbiol. Biotechnol.* 57: 467-473.
- Dittmann E, Neilan BA, Erhard M, Von Döhren H, and Börner T. 1997. Insertional mutagenesis of a peptide synthetase gene which is responsible for hepatotoxin production in the cyanobacterium *Microcystis* PCC 7806. *Mol. Microbiol.* 26: 779-787.
- Doblin MA, Coyne KJ, Rinta-Kanto JM, Wilhelm SW, and Dobbs FC. 2007. Dynamics and short-term survival of toxic cyanobacteria species in ballast water from NOBOB vessels transiting the Great Lakes: implications for HAB invasions. *Harmful Algae* 6: 519-530.
- Dokulil MT, and Teubner K. 2000. Cyanobacterial dominance in lakes. *Hydrobiologia* 438: 1-12.
- Doney SC. 2006. Plankton in a warmer world. *Nature* 444: 695-696.
- Doney SC, Fabry VJ, Feely RA, and Kleypas JA. 2009. Ocean acidification: the other CO₂ problem. *Annu. Rev. Mar. Sci.* 1: 169-192.
- Downing TG, Meyer C, Gehringer MM, and Van de Venter M. 2005. Microcystin content of *Microcystis aeruginosa* is modulated by nitrogen uptake rate relative to specific growth rate or carbon fixation rate. *Environ. Toxicol.* 20: 257-262.
- Droop MR. 1973. Some thoughts on nutrient limitation in algae. *J. Phycol.* 9: 264-272.
- Ducobu H, Huisman J, Jonker RR, and Mur LR. 1998. Competition between a prochlorophyte and a cyanobacterium under various phosphorus regimes: comparison with the Droop model. *J. Phycol.* 34: 467-476.
- Elser JJ, and Urabe J. 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology* 80: 735-751.
- Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H, Ngai JT, Seabloom EW, Shurin JB, and Smith JE. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10: 1135-1142.
- Elzenga JTM, Prins HBA, and Stefels J. 2000. The role of extracellular carbonic anhydrase activity in inorganic carbon utilization of *Phaeocystis globosa* (Prymnesiophyceae): a comparison with other marine algae using the isotopic disequilibrium technique. *Limnol. Oceanogr.* 45: 372-380.
- Engel A, Zondervan I, Aerts K, Beaufort L, Benthien A, Chou L, Delille B, Gattuso JP, Harlay J, Heemann C, Hoffmann L, Jacquet S, Nejstgaard J, Pizay MD, Rochelle-Newall E, Schneider U, Terbrueggen A, and Riebesell U. 2005. Testing the direct effect of CO₂ concentration on a bloom of the coccolithophorid *Emiliania huxleyi* in mesocosm experiments. *Limnol. Oceanogr.* 50: 493-507.
- Falkowski PG, and Davis CS. 2004. Natural proportions. *Nature* 431: 131.
- Fastner J, Fliieger I, and Neumann U. 1998. Optimised extraction of microcystins from field samples: a comparison of different solvents and procedures. *Wat. Res.* 32: 3177-3181.
- Feng Y, Hare CE, Leblanc K, Rose JM, Zhang Y, DiTullio GR, Lee PA, Wilhelm SW, Rowe JM, Sun J, Nemcek N, Gueguen C, Passow U, Benner I, Brown C, and Hutchins DA. 2009. Effects of increased pCO₂ and temperature on the North Atlantic spring bloom. I. The phytoplankton community and biogeochemical response. *Mar. Ecol. Prog. Ser.* 388: 13-25.

- Fenner N, Ostle N, McNamara N, Sparks T, Harmens H, Reynolds B, and Freeman C. 2007. Elevated CO₂ effects on peatland plant community carbon dynamics and DOC production. *Ecosystems* 10: 635-647.
- Field CB, Behrenfeld MJ, Randerson JT, and Falkowski P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281: 237-240.
- Fitznar HP, Lobbes JM, and Kattner G. 1999. Determination of enantiomeric amino acids with high-performance liquid chromatography and pre-column derivatisation with *o*-phthalaldehyde and *N*-isobutyrylcysteine in seawater and fossil samples (mollusks). *J. Chromatogr. A* 832: 123-132.
- Flores E, and Herrero A. 2005. Nitrogen assimilation and nitrogen control in cyanobacteria. *Biochem. Soc. Trans.* 33: 164-167.
- Flores E, Frías JE, Rubio LM, and Herrero A. 2005. Photosynthetic nitrate assimilation in cyanobacteria. *Photosynth. Res.* 83: 117-133.
- Forchhammer K. 2004. Global carbon/nitrogen control by P_{II} signal transduction in cyanobacteria: from signals to targets. *FEMS Microbiol. Rev.* 28: 319-333.
- Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, and Vörösmarty CJ. 2004. Nitrogen cycles: past, present, and future. *Biogeochem.* 70: 153-226.
- Glibert PM, Seitzinger S, Heil CA, Burkholder JM, Parrow MW, Codispoti LA, and Kelly V. 2005. The role of eutrophication in the global proliferation of harmful algal blooms: new perspectives and new approaches. *Oceanography* 18: 198-209.
- Goldman JC, Riley CB, and Dennett MR. 1982. The effect of pH in intensive microalgal cultures. II. Species competition. *J. Exp. Mar. Biol. Ecol.* 57: 15-24.
- Gross EM. 2003. Allelopathy of aquatic autotrophs. *Crit. Rev. Plant. Sci.* 22: 313-339.
- Grover JP. 1991. Resource competition in a variable environment: phytoplankton growing according to the variable-internal-stores model. *Am. Nat.* 138: 811-835.
- Grover JP. 1997. Resource Competition. Chapman & Hall, London, UK.
- Hamilton JG, Zangerl AR, DeLucia EH, and Berenbaum MR. 2001. The carbon-nutrient balance hypothesis: its rise and fall. *Ecol. Lett.* 4: 86-95.
- Hansen PJ, Lundholm N, and Rost B. 2007. Growth limitation in marine red-tide dinoflagellates: effects of pH versus inorganic carbon availability. *Mar. Ecol. Prog. Ser.* 334: 63-71.
- Hansen PJ. 2002. Effect of high pH on the growth and survival of marine phytoplankton: implications for species succession. *Aquat. Microb. Ecol.* 28: 279-288.
- Harada KI. 1996. Chemistry and detection of microcystins. In: *Toxic microcystins* (Watanabe MF, Harada KI, Carmichael WW, and Fujiki H, eds.), pp. 103-148. CRC Press, New York, USA.
- Harper D. 1992. Eutrophication of freshwaters: principles, problems and restoration. Chapman & Hall, London, UK.
- Hays GC, Richardson AJ, and Robinson C. 2005. Climate change and marine plankton. *Trends Ecol. Evol.* 20: 337-344.
- Hein M. 1997. Inorganic carbon limitation of photosynthesis in lake phytoplankton. *Freshw. Biol.* 37: 545-552.
- Herrero A, and Flores E. 1990. Transport of basic amino acids by the dinitrogen-fixing cyanobacterium *Anabaena* PCC 7120. *J. Biol. Chemistry* 265: 3931-3935.
- Hesse K, and Kohl JG. 2001. Effects of light and nutrient supply on growth and microcystin content of different strains of *Microcystis aeruginosa*. In:

- Cyanotoxins: occurrence, causes, consequences* (Chorus I, ed.), pp. 104-114. Springer, Berlin, Germany.
- Hessen DO, and Anderson TR. 2008. Excess carbon in aquatic organisms and ecosystems: physiological, ecological, and evolutionary implications. *Limnol. Oceanogr.* 53: 1685-1696.
- Hinga KR. 2002. Effects of pH on coastal marine phytoplankton. *Mar. Ecol. Prog. Ser.* 238: 281-300.
- Hinton MJ, Schiff SL, and English MC. 1997. The significance of storms for the concentration and export of dissolved organic carbon from two Precambrian Shield catchments. *Biogeochem.* 36: 67-88.
- Hoeger SJ, Schmid D, Blom JF, Ernst B, and Dietrich DR. 2007. Analytical and functional characterization of microcystins [Asp³]MC-RR and [Asp³,Dhb⁷]MC-RR: consequences for risk assessment? *Environ. Sci. Technol.* 41: 2609-2616.
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, and Hatziolos ME. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318: 1737-1742.
- Hood JM, Vanni MJ, and Flecker AS. 2005. Nutrient recycling by two phosphorus-rich grazing catfish: the potential for phosphorus-limitation of fish growth. *Oecologia* 146: 247-257.
- Howarth RW, Billen G, Swaney D, Townsend A, Jaworski N, Lajtha K, Downing JA, Elmgren R, Caraco N, Jordan T, Berendse F, Freney J, Kudeyarov V, Murdoch P, and Zhao-Liang Y. 1996. Regional nitrogen budgets and riverine N & P fluxes for the drainages to the North Atlantic Ocean: natural and human influences. *Biogeochem.* 35: 75-139.
- Huisman J, Matthijs HCP, and Visser PM. 2005. Harmful cyanobacteria. Springer, Dordrecht, The Netherlands.
- Huisman J, Pham Thi NN, Karl DM, and Sommeijer B. 2006. Reduced mixing generates oscillations and chaos in the oceanic deep chlorophyll maximum. *Nature* 439: 322-325.
- Huisman J, Sharples J, Stroom JM, Visser PM, Kardinaal WEA, Verspagen JMH, and Sommeijer B. 2004. Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology* 85: 2960-2970.
- Huisman J, van Oostveen P, and Weissing FJ. 1999. Critical depth and critical turbulence: two different mechanisms for the development of phytoplankton blooms. *Limnol. Oceanogr.* 44: 1781-1787.
- Huisman J. 1999. Population dynamics of light-limited phytoplankton: microcosm experiments. *Ecology* 80: 202-210.
- Huisman J, and Weissing FJ. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. *Ecology* 75: 507-520.
- Huisman J, Matthijs HCP, Visser PM, Balke H, Sigon CAM, Passarge J, Weissing FJ, and Mur LR. 2002. Principles of the light-limited chemostat: theory and ecological applications. *Antonie Van Leeuwenhoek Int. J. Gen. Mol. Microbiol.* 81: 117-133.
- Huisman J, Jonker RR, Zonneveld C, and Weissing FJ. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. *Ecology* 80: 211-222.
- Hutchins DA, Fu FX, Zhang Y, Warner ME, Feng Y, Portune K, Bernhardt PW, and Mulholland MR. 2007. CO₂ control of *Trichodesmium* N₂ fixation, photosynthesis,

- growth rates, and elemental ratios: implications for past, present, and future ocean biogeochemistry. *Limnol. Oceanogr.* 52: 1293-1304.
- Ibelings BW, and Maberly SC. 1998. Photoinhibition and the availability of inorganic carbon restrict photosynthesis by surface blooms of cyanobacteria. *Limnol. Oceanogr.* 43: 408-419.
- Iglesias-Rodriguez MD, Halloran PR, Rickaby REM, Hall IR, Colmenero-Hidalgo E, Gittins JR, Green DRH, Tyrrell T, Gibbs SJ, Von Dassow P, Rehm E, Armbrust EV, and Boessenkool KP. 2008. Phytoplankton calcification in a high-CO₂ world. *Science* 320: 336-340.
- Ikeda T, and Mitchell AW. 1982. Oxygen uptake, ammonia excretion and phosphate excretion by krill and other Antarctic zooplankton in relation to their body size and chemical composition. *Mar. Biol.* 71: 283-298.
- Jang MH, Ha K, Joo GJ, and Takamura N. 2003. Toxin production of cyanobacteria is increased by exposure to zooplankton. *Freshw. Biol.* 48: 1540-1550.
- Janse I, Kardinaal WEA, Kamst-Van Agterveld M, Meima M, Visser PM, and Zwart G. 2005. Contrasting microcystin production and cyanobacterial population dynamics in two *Planktothrix*-dominated freshwater lakes. *Environ. Microb.* 7: 1514-1524.
- Jensen TC, and Verschoor AM. 2004. Effects of food quality on life history of the rotifer *Brachionus calyciflorus* Pallas. *Freshw. Biol.* 49: 1138-1151.
- Jöhnk KD, Huisman J, Sharples J, Sommeijer B, Visser PM, and Stroom JM. 2008. Summer heatwaves promote blooms of harmful cyanobacteria. *Glob. Change Biol.* 14: 495-512.
- Johnson KJ. 1982. Carbon dioxide hydration and dehydration kinetics in seawater. *Limnol. Oceanogr.* 27: 849-855.
- Kamjunke N, and Jähnichen S. 2000. Leucine incorporation by *Microcystis aeruginosa*. *Limnol. Oceanogr.* 45: 741-743.
- Kaplan A, and Reinhold L. 1999. CO₂ concentrating mechanisms in photosynthetic microorganisms. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 50: 539-570.
- Kardinaal WEA, and Visser PM. 2005a. Cyanotoxines drijven tot overlast: inventarisatie van microcystine concentraties 2000-2004 in Nederlandse oppervlaktewateren. RIZA werkdocument 2005-057x.
- Kardinaal WEA, and Visser PM. 2005b. Dynamics of cyanobacterial toxins: sources of variability in microcystin concentrations. *Harmful Cyanobacteria* (Huisman J, Matthijs HCP, and Visser PM, eds.), pp. 41-63. Springer, Dordrecht, The Netherlands.
- Kardinaal WEA, Janse I, Kamst-Van Agterveld M, Meima M, Snoek J, Mur LR, Huisman J, Zwart G, and Visser PM. 2007a. *Microcystis* genotype succession in relation to microcystin concentrations in freshwater lakes. *Aquat. Microb. Ecol.* 48: 1-12.
- Kardinaal WEA, Tonk L, Janse I, Hol S, Slot P, Huisman J, and Visser PM. 2007b. Competition for light between toxic and nontoxic strains of the harmful cyanobacterium *Microcystis*. *Appl. Environ. Microbiol.* 73: 2939-2946.
- Karl DM, Letelier R, Tupas L, Dore J, Christian J, and Hebel D. 1997. The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388: 533-538.
- Keating KI. 1977. Allelopathic influence on blue-green bloom sequence in a eutrophic lake. *Science* 296: 885-887.

- Kim BR, Nakano S, Kim BH, and Han MS. 2006. Grazing and growth of the heterotrophic flagellate *Diphyllaea rotans* on the cyanobacterium *Microcystis aeruginosa*. *Aquat. Microb. Ecol.* 45: 163-170.
- Klausmeier CA, Litchman E, and Levin SA. 2004. Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnol. Oceanogr.* 49: 1463-1470.
- Koricheva J. 2002. The carbon-nutrient balance hypothesis is dead: long live the carbon-nutrient balance hypothesis? *Oikos* 98: 537-539.
- Koski M, Engström J, and Viitasalo M. 1999. Reproduction and survival of the calanoid copepod *Eurytemora affinis* fed with toxic and non-toxic cyanobacteria. *Mar. Ecol. Prog. Ser.* 186: 187-197.
- Kotak BG, Lam AKY, Prepas EE, Kenefick SL, and Hrudey SE. 1995. Variability of the hepatotoxin microcystin-LR in hypereutrophic drinking water lakes. *J. Phycol.* 31: 248-263.
- Kuiper-Goodman T, Falconer I, and Fitzgerald J. 1999. Human health aspects. In: *Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management* (Chorus I, and Bartram J, eds.), pp. 113-153. E & FN Spon, London, UK.
- Kurmayer R, and Kutzenberger T. 2003. Application of real-time PCR for quantification of microcystin genotypes in a population of the toxic cyanobacterium *Microcystis* sp. *Appl. Environ. Microbiol.* 69: 6723-6730.
- Langer G, Geisen M, Baumann KH, Kläs J, Riebesell U, Thoms S, and Young JR. 2006. Species-specific responses of calcifying algae to changing seawater carbonate chemistry. *Geochem. Geophys. Geosyst.* 7: Q09006. doi: 10.1029/2005GC001227.
- Lawton LA, Edwards C, and Codd GA. 1994. Extraction and high-performance liquid chromatographic method for the determination of microcystins in raw and treated waters. *Analyst* 119: 1525-1530.
- Levitan O, Rosenberg G, Setlik I, Setlikova E, Grigel J, Klepetar J, Prasil O, and Berman-Frank I. 2007. Elevated CO₂ enhances nitrogen fixation and growth in the marine cyanobacterium *Trichodesmium*. *Glob. Change Biol.* 13: 531-538.
- Long BM, Jones GJ, and Orr PT. 2001. Cellular microcystin content in N-limited *Microcystis aeruginosa* can be predicted from growth rate. *Appl. Environ. Microbiol.* 67: 278-283.
- Lu CD. 2006. Pathways and regulation of bacterial arginine metabolism and perspectives for obtaining arginine overproducing strains. *Appl. Microbiol. Biotechnol.* 70: 261-272.
- Lüring M. 2003. Effects of microcystin-free and microcystin-containing strains of the cyanobacterium *Microcystis aeruginosa* on growth of the grazer *Daphnia magna*. *Environ. Toxicol.* 18: 202-210.
- Maberly SC. 1996. Diel, episodic and seasonal changes in pH and concentrations of inorganic carbon in a productive lake. *Freshw. Biol.* 35: 579-598.
- Macedo MF, Duarte P, Mendes P, and Ferreira JG. 2001. Annual variation of environmental variables, phytoplankton species composition and photosynthetic parameters in a coastal lagoon. *J. Plankton Res.* 23: 719-732.
- Mackerras AH, De Chazal NM, and Smith GD. 1990. Transient accumulations of cyanophycin in *Anabaena cylindrica* and *Synechocystis* 6308. *J. Gen. Microbiol.* 136: 2057-2065.

- Maheswaran M, Ziegler K, Lockau W, Hagemann M, and Forchhammer K. 2006. P_{II}-Regulated arginine synthesis controls accumulation of cyanophycin in *Synechocystis* sp. strain PCC 6803. *J. Bacteriol.* 188: 2730-2734.
- Malej A, Faganeli J, and Pezdič J. 1993. Stable isotope and biochemical fractionation in the marine pelagic food chain: the jellyfish *Pelagia noctiluca* and net zooplankton. *Mar. Biol.* 116: 565-570.
- Marahiel MA, Stachelhaus T, and Mootz HD. 1997. Modular peptide synthetases involved in non-ribosomal peptide synthesis. *Chem. Rev.* 97: 2651-2673.
- Martin CL, and Tortell PD. 2008. Bicarbonate transport and extracellular carbonic anhydrase in marine diatoms. *Physiol. Plantarum* 133: 106-116.
- Matthijs HCP, Balke H, Van Hes UM, Kroon BMA, Mur LR, and Binot RA. 1996. Application of light-emitting diodes in bioreactors: flashing light effects and energy economy in algal culture (*Chlorella pyrenoidosa*). *Biotechnol. Bioeng.* 50: 98-107.
- McCarthy MJ, Lavrentyev PJ, Yang L, Zhang L, Chen Y, Qin B, and Gardner WS. 2007. Nitrogen dynamics and microbial food web structure during a summer cyanobacterial bloom in a subtropical, shallow, well-mixed, eutrophic lake (Lake Taihu, China). *Hydrobiologia* 581: 195-207.
- Moe SJ, Stelzer RS, Forman MR, Harpole WS, Daufresne T, and Yoshida T. 2005. Recent advances in ecological stoichiometry: insights for population and community ecology. *Oikos* 109: 29-39.
- Møgelhøj MK, Hansen PJ, Henriksen P, and Lundholm N. 2006. High pH and not allelopathy may be responsible for negative effects of *Nodularia spumigena* on other algae. *Aquat. Microb. Biol.* 43: 43-54.
- Monteith DT, Stoddard JL, Evans CD, De Wit HA, Forsius M, Høgåsen T, Wilander A, Skjelkvåle BL, Jeffries DS, Vuorenmaa J, Keller B, Kopáček, and Vesely J. 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* 450: 537-540.
- Montesinos ML, Herrero A, and Flores E. 1997. Amino acid transport in taxonomically diverse cyanobacteria and identification of two genes encoding elements of a neutral amino acid permease putatively involved in recapture of leaked hydrophobic amino acids. *J. Bacteriol.* 179: 853-862.
- Morel FMM. 1987. Kinetics of nutrient uptake and growth in phytoplankton. *J. Phycol.* 23: 137-150.
- Moroney JV, and Nyalvez RA. 2007. Proposed carbon dioxide concentrating mechanism in *Chlamydomonas reinhardtii*. *Eukaryot. Cell* 6: 1251-1259.
- Nishizawa T, Ueda A, Asayama M, Fujii K, Harada KI, Ochi K, and Shirai M. 2000. Polyketide synthase gene coupled to the peptide synthetase module involved in the biosynthesis of the cyclic heptapeptide microcystin. *J. Biochem.* 127: 779-789.
- Nishizawa T, Asayama M, Fujii K, Harada KI, and Shirai M. 1999. Genetic analysis of the peptide synthetase genes for a cyclic heptapeptide microcystin in *Microcystis* spp. *J. Biochem.* 126: 520-529.
- Nixon SW. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199-219.
- Oh HM, Lee SJ, Jang MH, and Yoon BD. 2000. Microcystin production by *Microcystis aeruginosa* in a phosphorus-limited chemostat. *Appl. Environ. Microbiol.* 66: 176-179.

- Oppermann-Sanio FB, and Steinbüchel A. 2002. Occurrence, functions and biosynthesis of polyamides in microorganisms and biotechnological production. *Naturwissenschaften* 89: 11-22.
- Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner GK, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig MF, Yamanaka Y, and Yool A. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681-686.
- Orr PT, and Jones GJ. 1998. Relationship between microcystin production and cell division rates in nitrogen-limited *Microcystis aeruginosa* cultures. *Limnol. Oceanogr.* 43: 1604-1614.
- Paerl HW, and Huisman J. 2008. Blooms like it hot. *Science* 320: 57-58.
- Passarge J, Hol S, Escher M, and Huisman J. 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? *Ecol. Monogr.* 76: 57-72.
- Pauly D, Watson R, and Alder J. 2005. Global trends in world fisheries: impacts on marine ecosystems and food security. *Philos. Trans. R. Soc. B* 360: 5-12.
- Pedersen MF, and Hansen PJ. 2003. Effects of high pH on the growth and survival of six marine heterotrophic protists. *Mar. Ecol. Prog. Ser.* 260: 33-41.
- Peeters F, Straile D, Lorke A, and Livingstone DM. 2008. Earlier onset of the spring phytoplankton bloom in lakes of the temperate zone in a warmer climate. *Glob. Change Biol.* 13: 1898-1909.
- Phlips EJ, Cichra M, Havens K, Hanlon C, Badylak S, Rueter B, Randall M, and Hansen P. 1997. Relationships between phytoplankton dynamics and the availability of light and nutrients in a shallow sub-tropical lake. *J. Plankton Res.* 19: 319-342.
- Pilati A, and Vanni MJ. 2007. Ontogeny, diet shifts, and nutrient stoichiometry in fish. *Oikos* 116: 1663-1674.
- Polovina JJ, Howell EA, and Abecassis M. 2008. Ocean's least productive waters are expanding. *Geophys. Res. Lett.* 35: L03618. doi:10.1029/2007GL031745.
- Portielje R, and Lijklema L. 1995. Carbon dioxide fluxes across the air-water interface and its impact on carbon availability in aquatic systems. *Limnol. Oceanogr.* 40: 690-699.
- Price GD, Badger MR, Woodger FJ, and Long BM. 2008. Advances in understanding the cyanobacterial CO₂-concentrating-mechanism (CCM): functional components, Ci transporters, diversity, genetic regulation and prospects for engineering into plants. *J. Exp. Bot.* 59: 1441-1461.
- Purcell JE. 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. *J. Mar. Biol. Assoc. UK* 85: 461-476.
- Rabalais NN, Turner RE, and Scavia D. 2002. Beyond science into policy: Gulf of Mexico hypoxia and the Mississippi River. *BioScience* 52: 129-142.
- Rantala A, Fewer DP, Hisbergues M, Rouhiainen L, Vaitomaa J, Börner T, and Sivonen K. 2004. Phylogenetic evidence for the early evolution of microcystin synthesis. *Proc. Natl. Acad. Sci. USA* 101: 568-573.
- Rapala J, Sivonen K, Lyra C, and Niemelä SI. 1997. Variation of microcystins, cyanobacterial hepatotoxins, in *Anabaena* spp. as a function of growth stimuli. *Appl. Environ. Microbiol.* 63: 2206-2212.

- Redfield AC. 1934. On the proportions of organic derivatives in sea water and their relation to the composition of plankton. In: *James Johnstone memorial volume* (Daniel RJ, ed.), pp. 176-192. Liverpool University Press, Liverpool, UK.
- Reich PB, Hungate BA, and Luo Y. 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annu. Rev. Ecol. Evol. Syst.* 37: 611-636.
- Reynolds CS. 1987. Cyanobacterial water blooms. *Adv. Bot. Res.* 13: 67-143.
- Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, and Morel FMM. 2000. Reduced calcification of marine plankton in response to increased atmospheric CO₂. *Nature* 407: 364-367.
- Riebesell U, Schulz KG, Bellerby RGJ, Botros M, Fritsche P, Meyerhöfer M, Neill C, Nondal G, Oschlies A, Wohlers J, and Zöllner E. 2007. Enhanced biological carbon consumption in a high CO₂ ocean. *Nature* 450: 545-549.
- Riley MA, and Gordon DM. 1999. The ecological role of bacteriocins in bacterial competition. *Trends Microbiol.* 7: 129-133.
- Rohrlack T, and Utkilen H. 2007. Effects of nutrients and light availability on production of bioactive anabaenopeptins and microviridin by the cyanobacterium *Planktothrix agardhii*. *Hydrobiologia* 583: 231-240.
- Rohrlack T, Dittmann E, Börner T, and Christoffersen K. 2001. Effects of cell-bound microcystins on survival and feeding of *Daphnia* spp. *Appl. Environ. Microbiol.* 67: 3523-3529.
- Rohrlack T, Dittmann E, Henning M, Börner T, and Kohl JG. 1999. Role of microcystins in poisoning and food ingestion inhibition of *Daphnia galeata* caused by the cyanobacterium *Microcystis aeruginosa*. *Appl. Environ. Microbiol.* 65: 737-739.
- Rost B, Riebesell U, Burkhardt S, and Sültemeyer D. 2003. Carbon acquisition of bloom-forming marine phytoplankton. *Limnol. Oceanogr.* 48: 55-67.
- Rost B, Zondervan I, and Wolf-Gladrow D. 2008. Sensitivity of phytoplankton to future changes in ocean carbonate chemistry: current knowledge, contradictions and research directions. *Mar. Ecol. Prog. Ser.* 373: 227-237.
- Sabine CL, Feely RA, Gruber N, Key RM, Lee K, Bullister JL, Wanninkhof R, Wong CS, Wallace DWR, Tilbrook B, Millero FJ, Peng TH, Kozyr A, Ono T, and Rios AF. 2004. The oceanic sink for anthropogenic CO₂. *Science* 305: 367-371.
- Sarmiento JL, Slater R, Barber R, Bopp L, Doney SC, Hirst AC, Kleypas J, Matear R, Mikolajewicz U, Monfray P, Soldatov V, Spall SA, and Stouffer R. 2004. Response of ocean ecosystems to climate warming. *Global Biogeochem. Cy.* 8: GB3003. doi:10.1029/2003GB002134.
- Scheffer M, Carpenter S, Foley JA, Folke C, and Walker B. 2001. Catastrophic shifts in ecosystems. *Nature* 413: 591-596.
- Schindler DW, Curtis PJ, Bayley SE, Parker BR, Beaty KG, and Stainton MP. 1997. Climate-induced changes in the dissolved organic carbon budgets of boreal lakes. *Biogeochem.* 36: 9-28.
- Schippers P, Lüring M, and Scheffer M. 2004. Increase of atmospheric CO₂ promotes phytoplankton productivity. *Ecol. Lett.* 7: 446-451.
- Schriek S, Rueckert C, Staiger D, Pistorius EK, and Michel KP. 2007. Bioinformatic evaluation of L-arginine catabolic pathways in 24 cyanobacteria and transcriptional analysis of genes encoding enzymes of L-arginine catabolism in the cyanobacterium *Synechocystis* sp. PCC 6803. *BMC Genomics* 8: 437.
- Schwarz G. 1978. Estimating the dimension of a model. *Ann. Statist.* 6: 461-464.

- Semyalo R, Rohrlack T, and Larsson P. 2009. Growth and survival responses of a tropical *Daphnia* (*Daphnia lumholzi*) to cell-bound microcystins. *J. Plankton Res.* 31: 827-835.
- Shapiro J. 1990. Current beliefs regarding dominance by blue-greens: the case for the importance of CO₂ and pH. *Verh. Int. Ver. Theor. Angew. Limnol.* 24: 38-54.
- Siegenthaler U, and Sarmiento JL. 1993. Atmospheric carbon dioxide and the ocean. *Nature* 365: 119-125.
- Sivonen K, and Jones G. 1999. Cyanobacterial toxins. In: *Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management* (Chorus I, and Bartram J, eds.), pp. 41-111. E & FN Spon, London, UK.
- Smith VH, Joye SB, and Howarth RW. 2006. Eutrophication of freshwater and marine ecosystems. *Limnol. Oceanogr.* 51: 351-355.
- Smith VH, Tilman GD, and Nekola JC. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* 100: 179-196.
- Sobek S, Tranvik L, and Cole JJ. 2005. Temperature independence of carbon dioxide supersaturation in global lakes. *Global Biogeochem. Cy.* 19: GB2003. doi:10.1029/2004GB002264.
- Sokal RR, and Rohlf FJ. 1995. Biometry. 3rd edn. Freeman, New York, USA.
- Solomon S, Qin D, Manning M, Marquis M, Averyt K, Tignor MMB, Miller Jr HL, and Zhenlin C. 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- Sommer U. 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. *Limnol. Oceanogr.* 30: 335-346.
- Stamp N. 2003. Out of the quagmire of plant defense hypotheses. *Quart. Rev. Biol.* 78: 23-55.
- Stephan DP, Ruppel HG, and Pistorius EK. 2000. Interrelation between cyanophycin synthesis, L-arginine catabolism and photosynthesis in the cyanobacterium *Synechocystis* sp. strain PCC 6803. *Zeitschrift f. Naturforsch. Section C* 55: 927-942.
- Sterner RW and Elser JJ. 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press, Princeton, NJ, USA.
- Stomp M, Huisman J, De Jongh F, Veraart AJ, Gerla D, Rijkeboer M, Ibelings BW, Wollenzien UIA, and Stal LJ. 2004. Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature* 432: 104-107.
- Stumm W, and Morgan JJ. 1996. Aquatic chemistry: Chemical equilibria and rates in natural waters. Wiley-Interscience, New York, USA.
- Talling JF. 1976. The depletion of carbon dioxide from lake water by phytoplankton. *J. Ecol.* 64: 79-121.
- Tandeau de Marsac N, Lee HM, Hisbergues M, Castets AM, and Bédu S. 2001. Control of nitrogen and carbon metabolism in cyanobacteria. *J. Appl. Phycol.* 13: 287-292.
- Tapia MI, Ochoa de Alda JAG, Llama MJ, and Serra JL. 1996. Changes in intracellular amino acids and organic acids induced by nitrogen starvation and nitrate or ammonium resupply in the cyanobacterium *Phormidium laminosum*. *Planta* 198: 526-531.
- Tillett D, Dittmann E, Erhard M, Von Döhren H, Börner T, and Neilan BA. 2000. Structural organization of microcystin biosynthesis in *Microcystis aeruginosa*

- PCC7806: an integrated peptide-polyketide synthetase system. *Chem. Biol.* 7: 753-764.
- Tilman D. 1981. Experimental tests of resource competition theory using four species of Lake Michigan algae. *Ecology* 62: 802-815.
- Tilman D. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ, USA.
- Tonk L, Van de Waal DB, Slot P, Huisman J, Matthijs HCP, and Visser PM. 2008. Amino acid availability determines the ratio of microcystin variants in the cyanobacterium *Planktothrix agardhii*. *FEMS Microbiol. Ecol.* 65: 383-390.
- Tonk L, Visser PM, Christiansen G, Dittmann E, Snelder EOFM, Wiedner C, Mur LR, and Huisman J. 2005. The microcystin composition of the cyanobacterium *Planktothrix agardhii* changes towards a more toxic variant with increasing light intensity. *Appl. Environ. Microbiol.* 71: 5177-5181.
- Tortell PD, DiTullio GR, Sigman DM, and Morel FMM. 2002. CO₂ effects on taxonomic composition and nutrient utilization in an Equatorial Pacific phytoplankton assemblage. *Mar. Ecol. Prog. Ser.* 236: 37-43.
- Trimborn S, Lundholm N, Thoms S, Richter KU, Krock B, Hansen PJ, and Rost B. 2008. Inorganic carbon acquisition in potentially toxic and non-toxic diatoms: the effect of pH-induced changes in seawater carbonate chemistry. *Physiol. Plantarum* 133: 92-105.
- Trubetskova IL, and Haney JF. 2006. Effects of differing concentrations of microcystin-producing *Microcystis aeruginosa* on growth, reproduction, survivorship and offspring of *Daphnia magna*. *Arch. Hydrobiol.* 167: 533-546.
- Urabe J, and Waki N. 2009. Mitigation of adverse effects of rising CO₂ on a planktonic herbivore by mixed algal diets. *Glob. Change Biol.* 15: 523-531.
- Urabe J, Kyle M, Makino W, Yoshida T, Andersen T, and Elser JJ. 2002. Reduced light increases herbivore production due to stoichiometric effects of light/nutrient balance. *Ecology* 83: 619-627.
- Urabe J, Togari J, and Elser JJ. 2003. Stoichiometric impacts of increased carbon dioxide on a planktonic herbivore. *Glob. Change Biol.* 9: 818-825.
- Urabe J, and Waki N. 2009. Mitigation of adverse effects of rising CO₂ on a planktonic herbivore by mixed algal diets. *Glob. Change Biol.* 15: 523-531.
- Utkilen H, and Gjørlme N. 1995. Iron-stimulated toxin production in *Microcystis aeruginosa*. *Appl. Environ. Microbiol.* 61: 797-800.
- Van de Waal DB, Verschoor AM, Verspagen JMH, Van Donk E, and Huisman J. 2010. Climate-driven changes in the ecological stoichiometry of aquatic ecosystems. *Front. Ecol. Environ.* 8: 145-152.
- Van de Waal DB, Verspagen JMH, Lürling M, Van Donk E, Visser PM, and Huisman J. 2009. The ecological stoichiometry of toxins produced by harmful cyanobacteria: an experimental test of the carbon-nutrient balance hypothesis. *Ecol. Lett.* 12: 1326-1335.
- Van Lieere L, and Mur LR. 1978. Light-limited cultures of the blue-green alga *Oscillatoria agardhii*. *Mitt. Int. Ver. Limnol.* 21: 158-167.
- Vázquez-Bermúdez MF, Herrero A, and Flores E. 2000. Uptake of 2-oxoglutarate in *Synechococcus* strains transformed with the *Escherichia coli kgtP* gene. *J. Bacteriol.* 182: 211-215.
- Verschoor AM, Vos M, and Van der Stap I. 2004. Inducible defences prevent strong population fluctuations in bi- and tritrophic food chains. *Ecol. Lett.* 7: 1143-1148.

- Verspagen JMH, Passarge J, Jöhnk KD, Visser PM, Peperzak L, Boers O, Laanbroek HJ, and Huisman J. 2006. Water management strategies against toxic *Microcystis* blooms in the Dutch delta. *Ecol. Appl.* 16: 313-327.
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, and Tilman DG. 1997. Human alteration of the global nitrogen cycle: sources and consequences. *Ecol. Appl.* 7: 737-750.
- Vrede T, Andersen T, and Hessen DO. 1999. Phosphorus distribution in three crustacean zooplankton species. *Limnol. Oceanogr.* 44: 225-229.
- Walsby AE, Hayes PK, Boje R, and Stal LJ. 1997. The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytol.* 136: 407-417.
- Watanabe MF, and Oishi S. 1985. Effects of environmental factors on toxicity of a cyanobacterium (*Microcystis aeruginosa*) under culture conditions. *Appl. Environ. Microbiol.* 49: 1342-1344.
- Welch MJ, Lifton JF, and Seck JA. 1969. Tracer studies with radioactive oxygen-15. Exchange between carbon dioxide and water. *J. Phys. Chem.* 73: 3351-3356.
- Welker M, and Von Döhren H. 2006. Cyanobacterial peptides: nature's own combinatorial biosynthesis. *FEMS Microbiol. Rev.* 30: 530-563.
- Weyhenmeyer GA, Jeppesen E, Adrian R, Arvola L, Blenckner T, Jankowski T, Jennings E, Nöges P, Nöges T, and Straile D. 2007. Nitrate-depleted conditions on the increase in shallow northern European lakes. *Limnol. Oceanogr.* 52: 1346-1353.
- Wiedner C, Visser PM, Fastner J, Metcalf JS, Codd GA, and Mur LR. 2003. Effects of light on the microcystin content of *Microcystis* strain PCC 7806. *Appl. Environ. Microbiol.* 69: 1475-1481.
- Wilken S, Wiezer S, Huisman J, and Van Donk E. 2010. Microcystins do not provide anti-herbivore defence against mixotrophic flagellates. *Aquat. Microb. Ecol.* (in press).
- Winder M, and Schindler DE. 2004. Climatic effects on the phenology of lake processes. *Glob. Change Biol.* 10: 1844-1856.
- Wolf-Gladrow DA, Zeebe RE, Klaas C, Körtzinger A, and Dickson AG. 2007. Total alkalinity: the explicit conservative expression and its application to biogeochemical processes. *Mar. Chem.* 106: 287-300.
- Zimov SA, Schuur EAG, and Chapin FS III. 2006. Permafrost and the global carbon budget. *Science* 312: 1612-1613.
- Zondervan I. 2007. The effects of light, macronutrients, trace metals and CO₂ on the production of calcium carbonate and organic carbon in coccolithophores: a review. *Deep-Sea Res. PT. II* 54: 521-537.