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Publication date

2018

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Citation for published version (APA):

Diao, M. (2018). *Interactions between microorganisms and oxic-anoxic transitions*. [Thesis, fully internal, Universiteit van Amsterdam].

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References

- Aben RCH, Barros N, van Donk E, Frenken T, Hilt S, Kazanjian G *et al.* (2017). Cross continental increase in methane ebullition under climate change. *Nat Commun* **8**: 1682.
- Adamski JM, Villard SP. (1975). Application of the methylthymol blue sulfate method to water and wastewater analysis. *Anal Chem* **47**: 1191-1194.
- Anantharaman K, Hausmann B, Jungbluth SP, Kantor RS, Lavy A, Warren LA *et al.* (2018). Expanded diversity of microbial groups that shape the dissimilatory sulfur cycle. *ISME J* **12**: 1715-1728.
- Arvola L, George G, Livingstone DM, Järvinen M, Blenckner T, Dokulil MT *et al.* (2010). The impact of the changing climate on the thermal characteristics of lakes. In: George, G (ed). *The Impact of Climate Change on European Lakes*. Springer, Berlin, pp 85-101.
- Auguet JC, Nomokonova N, Camarero L, Casamayor EO. (2011). Seasonal changes of freshwater ammonia-oxidizing archaeal assemblages and nitrogen species in oligotrophic alpine lakes. *Appl Environ Microbiol* **77**: 1937-1945.
- Auguet JC, Triadó-Margarit X, Nomokonova N, Camarero L, Casamayor EO. (2012). Vertical segregation and phylogenetic characterization of ammonia-oxidizing archaea in a deep oligotrophic lake. *ISME J* **6**: 1786-1797.
- Azam F, Worden AZ. (2004). Microbes, molecules, and marine ecosystems. *Science* **303**: 1622-1624.
- Bader FG (1978). Analysis of double-substrate limited growth. *Biotechnol Bioeng* **20**: 183-202.
- Bae HS, Morrison E, Chanton JP, Ogram A. (2018). Methanogens are major contributors to nitrogen fixation in soils of the Florida Everglades. *Appl Environ Microbiol* **84**: e02222-17.
- Bañeras L, Ros-Ponsatí M, Cristina XP, Garcia-Gil JL, Borrego CM. Phosphorus deficiency and kinetics of alkaline phosphatase in isolates and natural populations of phototrophic sulphur bacteria. *FEMS Microbiol Ecol* **73**: 243-253.
- Bastviken D, Tranvik LJ, Downing JA, Crill PM, Enrich-Prast A. (2011). Freshwater methane emissions offset the continental carbon sink. *Science* **331**: 50.
- Beal EJ, House CH, Orphan VJ. (2009). Manganese- and iron-dependent marine methane oxidation. *Science* **325**: 184-187.
- Beisner BE, Haydon DT, Cuddington K. (2003). Alternative stable states in ecology. *Front Ecol Environ* **1**: 376-382.
- Benjamini Y, Hochberg Y. (1995). Controlling the false discovery rate: a practical and

- powerful approach to multiple testing. *J R Stat Soc Ser B Methodol* **57**: 289-300.
- Bentzon-Tilia M, Traving SJ, Mantikci M, Knudsen-Leerbeck H, Hansen JLS, Markager S *et al.* (2015). Significant N₂ fixation by heterotrophs, photoheterotrophs and heterocystous cyanobacteria in two temperate estuaries. *ISME J* **9**: 273-285.
- Best EPH, Blaauboer MCI, Cappenberg TE, Gons HJ, Gulati RD, De Kloet WA *et al.* (1978). Towards an integrated study of the ecosystem of Lake Vechten. *Hydrobiol Bull* **12**: 107-118.
- Berg C, Vandieken V, Thamdrup B, Jürgens K. 2015. Significance of archaeal nitrification in hypoxic waters of the Baltic Sea. *ISME J* **9**: 1319-1332.
- Bidre-Petit C, Boucher D, Kuever J, Alberic P, Jézéquel D, Chebance B *et al.* (2011). Identification of sulfur-cycle prokaryotes in a low-sulfate lake (Lake Pavin) using *aprA* and 16S rRNA gene markers. *Microb Ecol* **61**: 313-327.
- Biebl H, Pfennig N. (1978). Growth yields of green sulfur bacteria in mixed cultures with sulfur and sulfate reducing bacteria. *Arch Microbiol* **117**: 9-16.
- Biggs R, Carpenter SR, Brock WA. (2009). Turning back from the brink: detecting an impending regime shift in time to avert it. *Proc Natl Acad Sci USA* **106**: 826-831.
- Blaauboer MCI. (1982). The phytoplankton species composition and the seasonal periodicity in Lake Vechten from 1956 to 1979. *Hydrobiologia* **95**: 25-36.
- Blackwood JC, Hastings A, Mumby PJ. (2012). The effect of fishing on hysteresis in Caribbean coral reefs. *Theor Ecol* **5**: 105-114.
- Blodau C, Knorr KH. (2006). Experimental inflow of groundwater induces a "biogeochemical regime shift" in iron-rich and acidic sediments. *J Geophys Res* **111**: G02026.
- Boetius A, Ravensschlag K, Schubert CJ, Rickert D, Widdel F, Gieseke A *et al.* (2000). A marine microbial consortium apparently mediating anaerobic oxidation of methane. *Nature* **407**: 623-626.
- Bokulich NA, Rideout JR, Kopylova E, Bolyen E, Patnode J, Ellett Z *et al.* (2015). A standardized, extensible framework for optimizing classification improves marker-gene taxonomic assignments. *Peer J PrePrints* **3**: e934v2.
- Bollmann A, Bullerjahn GS, McKay RM. (2014). Abundance and diversity of ammonia-oxidizing archaea and bacteria in sediments of trophic end members of the Laurentian Great Lakes, Erie and Superior. *PLoS One* **9**: e97068.
- Breitburg D, Levin LA, Oschlies A, Grégoire M, Chavez FP, Conley DJ *et al.* (2018). Declining oxygen in the global ocean and coastal waters. *Science* **359**: eaam7240.
- Brown CT, Hug LA, Thomas BC, Sharon I, Castelle CJ, Singh A *et al.* (2015). Unusual biology across a group comprising more than 15% of domain Bacteria. *Nature* **523**: 208-211.
- Brunet RC, Garcia-Gil LJ. (1996). Sulfide-induced dissimilatory nitrate reduction to

References

- ammonia in anaerobic freshwater sediments. *FEMS Microbiol Ecol* **21**: 131-138.
- Bürgmann H, Jenni S, Vazquez F, Udert KM. (2011). Regime shift and microbial dynamics in a sequencing batch reactor for nitrification and anammox treatment of urine. *Appl Environ Microb* **77**: 5897-5907.
- Bush T, Butler IB, Free A, Allen RJ. (2015). Redox regime shifts in microbially mediated biogeochemical cycles. *Biogeosciences* **12**: 3713-3724.
- Bush T, Diao M, Allen RJ, Sinnige R, Muyzer G, Huisman J. (2017). Oxic-anoxic regime shifts mediated by feedbacks between biogeochemical processes and microbial community dynamics. *Nat Commun* **8**: 789.
- Camacho A, Vicente E, Miracle MR. (2000). Spatio-temporal distribution and growth dynamics of phototrophic sulfur bacteria populations in the sulfide-rich Lake Arcas. *Aquat Sci* **62**: 334-349.
- Campbell BJ, Engel AS, Porter ML, Takai K. (2006). The versatile ϵ -proteobacteria: key players in sulphidic habitats. *Nat Rev Microbiol* **4**: 458-468.
- Canfield DE, Raiswell R. (1999). The evolution of the sulfur cycle. *Am J Sci* **299**: 697-723.
- Cappenberg TE. (1974). Interrelations between sulfate-reducing and methane-producing bacteria in bottom deposits of a fresh-water lake. I. Field observations. *Antonie van Leeuwenhoek* **40**: 285-295.
- Cappenberg TE. (1975). Relationships between sulfate-reducing and methane-producing bacteria. *Plant Soil* **43**: 125-139.
- Casamayor EO, Schäfer H, Bañeras L, Pedrós-Alió C, Muyzer G. (2000). Identification of and spatio-temporal differences between microbial assemblages from two neighboring sulfurous lakes: comparison by microscopy and denaturing gradient gel electrophoresis. *Appl Environ Microb* **66**: 499-508.
- Casamayor EO, García-Cantizano J, Pedrós-Alió C. (2008). Carbon dioxide fixation in the dark by photosynthetic bacteria in sulfide-rich stratified lakes with oxic-anoxic interfaces. *Limnol Oceanogr* **53**: 1193-1203.
- Chase JM. (2010). Stochastic community assembly causes higher biodiversity in more productive environments. *Science* **328**: 1388-1391.
- Chavez FP, Ryan J, Lluch-Cota SE, Ñiquen CM. (2003). From anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* **299**: 217-221.
- Chislock MF, Doster E, Zitomer RA, Wilson AE. (2013). Eutrophication: causes, consequences, and controls in aquatic ecosystems. *Nature Education Knowledge* **4**:10.
- Christensen PB, Sørensen J. (1986). Temporal variation of denitrification activity in plant-covered, littoral sediment from Lake Hampen, Denmark. *Appl Environ Microbiol* **51**: 1174-1179.

- Ciglonečki I, Carić M, Kršinić F, Viličić D, Čosović B. (2005). The extinction by sulfide-turnover and recovery of a naturally eutrophic, meromictic seawater lake. *J Mar Syst* **56**: 29-44.
- Clements FE. (1916). *Plant Succession: An Analysis of the Development of Vegetation*. Carnegie Institution of Washington.
- Coban O, Kuschik P, Kappelmeyer U, Spott O, Martienssen M, Jetten MSM *et al.* (2015). Nitrogen transforming community in a horizontal subsurface-flow constructed wetland. *Water Res* **74**: 203-212.
- Cohen-Bazire G, Kunisawa R, Pfennig N. (1969). Comparative study of the structure of gas vacuoles. *J Bacteriol* **100**: 1049-1061.
- Conley DJ, Carstensen J, Vaquer-Sunyer R, Duarte CM. (2009). Ecosystem thresholds with hypoxia. *Hydrobiologia* **629**: 21-29.
- Conley DJ, Paerl HW, Howarth RW, Boesch DF, Seitzinger SP, Havens KE *et al.* (2009). Controlling eutrophication: nitrogen and phosphorus. *Science* **323**: 1014-1015.
- Conroy JD, Boegman L, Zhang H, Edwards WJ, Culver DA. (2011). "Dead Zone" dynamics in Lake Erie: the importance of weather and sampling intensity for calculated hypolimnetic oxygen depletion rates. *Aquat Sci* **73**: 289-304.
- Coolen MJL, Abbas B, van Bleijswijk J, Hopmans EC, Kuypers MMM, Wakeham SG *et al.* (2007). Putative ammonia-oxidizing Crenarchaeota in suboxic waters of the Black Sea: a basin-wide ecological study using 16S ribosomal and functional genes and membrane lipids. *Environ Microbiol* **9**: 1001-1016.
- Costa E, Pérez J, Kreft JU. (2006). Why is metabolic labour divided in nitrification? *Trends Microbiol* **14**: 213-219.
- Costello AM, Lidstrom ME. (1999). Molecular characterization of functional and phylogenetic genes from natural populations of methanotrophs in lake sediments. *Appl Environ Microbiol* **65**: 5066-5074.
- Cypionka H, Widdel F, Pfennig N. (1985). Survival of sulfate-reducing bacteria after oxygen stress, and growth in sulfate-free oxygen-sulfide gradients. *FEMS Microbiol Ecol* **31**: 39-45.
- Dai Y, Yang Y, Wu Z, Feng Q, Xie S, Liu Y. (2016). Spatiotemporal variation of planktonic and sediment bacterial assemblages in two plateau freshwater lakes at different trophic status. *Appl Microbiol Biot* **100**: 4161-4175.
- Daims H, Lebedeva EV, Pjevac P, Han P, Herbold C, Albertsen M *et al.* (2015). Complete nitrification by *Nitrospira* bacteria. *Nature* **528**: 504-509.
- Dang H, Chen R, Wang L, Guo L, Chen P, Tang Z *et al.* 2010. Environmental factors shape sediment anammox bacterial communities in hypernutrified Jiaozhou Bay, China. *Appl Environ Microbiol* **76**: 7036-7047.

References

- De Graaf W, Cappenberg TE. (1996). Evidence for isotopic exchange during metabolism of stable-isotope-labeled formate in a methanogenic sediment. *Appl Environ Microbiol* **62**: 3535-3537.
- De Wit R, van den Ende FP, van Gemerden H. (1995). Mathematical simulation of the interactions among cyanobacteria, purple sulfur bacteria and chemotrophic sulfur bacteria in microbial mat communities. *FEMS Microbiol Ecol* **17**: 117-136.
- Decristophoris PMA, Peduzzi S, Ruggeri-Bernardi N, Hahn D, Tonolla M (2009). Fine scale analysis of shifts in bacterial community structure in the chemocline of meromictic Lake Cadagno, Switzerland. *J Limnol* **68**: 16-24.
- Denman KL, Gargett AE. (1983). Time and space scales of vertical mixing and advection of phytoplankton in the upper ocean. *Limnol Oceanogr* **28**: 801-815.
- Dethlefsen L, Relman DA. (2011). Incomplete recovery and individualized responses of the human distal gut microbiota to repeated antibiotic perturbation. *Proc Natl Acad Sci* **108**: 4554-4561.
- Deutsch C, Brix H, Ito T, Frenzel H, Thompson L. (2011). Climate-forced variability of ocean hypoxia. *Science* **333**: 336-339.
- Deutzmann JS, Stief P, Brandes J, Schink B. (2014). Anaerobic methane oxidation coupled to denitrification is the dominant methane sink in a deep lake. *Proc Natl Acad Sci USA* **111**: 18273-18278.
- Dev S, Roy S, Bhattacharya J. (2016). Understanding the performance of sulfate reducing bacteria based packed bed reactor by growth kinetics study and microbial profiling. *J Environ Manag* **177**: 101-110.
- Diao M, Sinnige R, Kalbitz K, Kalbitz K, Huisman J, Muyzer G. (2017). Succession of bacterial communities in a seasonally stratified lake with an anoxic and sulfidic hypolimnion. *Front Microbiol* **8**: 2511.
- Diaz RJ, Rosenberg R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology: An Annual Review* **33**: 245-303.
- Diaz RJ, Rosenberg R. (2008). Spreading dead zones and consequences for marine ecosystems. *Science* **321**: 926-929.
- Ding X, Peng XJ, Jin BS, Xiao M, Chen JK, Li B *et al.* (2015). Spatial distribution of bacterial communities driven by multiple environmental factors in a beach wetland of the largest freshwater lake in China. *Front Microbiol* **6**: 129.
- Dokulil, MT, Teubner K. (2000). Cyanobacterial dominance in lakes. *Hydrobiologia* **438**: 1-12.
- Edgar RC. (2010). Search and clustering orders of magnitude faster than BLAST. *Bioinformatics* **26**: 2460-2461.

- Edgar RC, Haas BJ, Clemente JC, Quince C, Knight R. (2011). UCHIME improves sensitivity and speed of chimera detection. *Bioinformatics* **27**: 2194-2200.
- Edgar RC. (2013). UPARSE: highly accurate OTU sequences from microbial amplicon reads. *Nat Methods* **10**: 996-998.
- Edwardson CF, Hollibaugh JT. (2017). Metatranscriptomic analysis of prokaryotic communities active in sulfur and arsenic cycling in Mono Lake, California, USA. *ISME J* **11**: 2195-2208.
- Edwardson CF, Hollibaugh JT. (2017). Metatranscriptomic analysis of prokaryotic communities active in sulfur and arsenic cycling in Mono Lake, California, USA. *ISME J* **11**: 2195-2208.
- Eiler A, Bertilsson S. (2004). Composition of freshwater bacterial communities associated with cyanobacterial blooms in four Swedish lakes. *Environ Microbiol* **6**: 1228-1243.
- Eiler A, Heinrich F, Bertilsson S. (2012). Coherent dynamics and association networks among lake bacterioplankton taxa. *ISME J* **6**: 330-342.
- Eisenmann E, Beuerle J, Sulger K, Kroneck PMH, Schumacher W. (1995). Lithotrophic growth of *Sulfurospirillum deleyianum* with sulfide as electron donor coupled to respiratory reduction of nitrate to ammonia. *Arch Microbiol* **164**: 180-185.
- Elser JJ, Bracken MES, Cleland EE, Gruner DS, Harpole WS, Hillebrand H *et al.* (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* **10**: 1135-1142.
- Erbacher J, Huber BT, Norris RD, Markey M. (2001). Increased thermohaline stratification as a possible cause for an ocean anoxic event in the Cretaceous period. *Nature* **409**: 325-327.
- Erguder TH, Boon N, Wittebolle L, Marzorati M, Verstraete W. (2009). Environmental factors shaping the ecological niches of ammonia-oxidizing archaea. *FEMS Microbiol Rev* **33**: 855-869.
- Erisman JW, Sutton MA, Galloway J, Klimont Z, Winiwarter W. (2008). How a century of ammonia synthesis changed the world. *Nat Geosci* **1**: 636-639.
- Falkowski PG, Fenchel T, DeLong EF. (2008). The microbial engines that drive Earth's biogeochemical cycles. *Science* **320**: 1034-1039.
- Faust K, Raes J. (2012). Microbial interactions: from networks to models. *Nat Rev Microbiol* **10**: 538-550.
- Faust K, Sathirapongsasuti JF, Izard J, Segata N, Gevers D, Raes J *et al.* (2012). Microbial co-occurrence relationships in the human microbiome. *PLoS Comp Biol* **8**: e1002606.
- Faust K, Raes J. (2016). CoNet app: inference of biological association networks using Cytoscape [version 2]. *F1000 Res* **5**: 1519.
- Finlay JC, Small GE, Sterner RW. (2013). Human influences on nitrogen removal in lakes.

References

- Science* **342**: 247-250.
- Fortunato CS, Eiler A, Herfort L, Needoba JA, Peterson TD, Crump BC. (2013). Determining indicator taxa across spatial and seasonal gradients in the Columbia River coastal margin. *ISME J* **7**: 1899-1911.
- Fox J, Weisberg S. (2011). *An R Companion to Applied Regression*. SAGE Publications, Inc.
- Francis CA, Roberts KJ, Beman JM, Santoro AE, Oakley BB. (2005). Ubiquity and diversity of ammonia-oxidizing archaea in water columns and sediments of the ocean. *Proc Natl Acad Sci USA* **102**: 14683-14688.
- French E, Kozłowski JA, Mukherjee M, Bullerjahn G, Bollmann A. (2012). Ecophysiological characterization of ammonia-oxidizing archaea and bacteria from freshwater. *Appl Environ Microbiol* **78**: 5773-5780.
- Friedrich CG. (1998). Physiology and genetics of sulfur-oxidizing bacteria. *Adv Microb Physiol* **39**: 235-289.
- Frigaard NU, Dahl C. (2009). Sulfur metabolism in phototrophic sulfur bacteria. *Adv Microb Physiol* **54**: 103-200.
- Fuhrman JA. (2009). Microbial community structure and its functional implications. *Nature* **459**: 193-199.
- Gaby JC, Buckley DH. (2012). A comprehensive evaluation of PCR primers to amplify the *nifH* gene of nitrogenase. *PLoS One* **7**: e42149.
- Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP *et al.* (2004). Nitrogen cycles: past, present, and future. *Biogeochemistry* **70**: 153-226.
- Gao J, Luo X, Wu G, Li T, Peng Y. (2014). Abundance and diversity based on *amoA* genes of ammonia-oxidizing archaea and bacteria in ten wastewater treatment systems. *Appl Microbiol Biotechnol* **98**: 3339-3354.
- Garcia SL, Salka I, Grossart HP, Warnecke F. (2013). Depth-discrete profiles of bacterial communities reveal pronounced spatio-temporal dynamics related to lake stratification. *Environ Microbiol Rep* **5**: 549-555.
- Gerla DJ, Mooij WM, Huisman J. (2011). Photoinhibition and the assembly of light-limited phytoplankton communities. *Oikos* **120**: 359-368.
- Gerritse J, Schut F, Gottschal JC. (1992). Modelling of mixed chemostat cultures of an aerobic bacterium, *Comamonas testosteroni*, and an anaerobic bacterium, *Veillonella alcalescens*: comparison with experimental data. *Appl Environ Microbiol* **58**: 1466-1476.
- Gevertz D, Telang AJ, Voordouw G, Jenneman GE. (2000). Isolation and characterization of strains CVO and FWKOB, two novel nitrate-reducing, sulfide-oxidizing bacteria isolated from oil field brine. *Appl Environ Microbiol* **66**: 2491-2501.
- Ghosh W, Dam B. (2009). Biochemistry and molecular biology of lithotrophic sulfur

- oxidation by taxonomically and ecologically diverse bacteria and archaea. *FEMS Microbiol Rev* **33**: 999-1043.
- Giblin AE, Tobias CR, Song B, Weston N, Banta GT, Rivera-Monroy VH. (2013). The importance of dissimilatory nitrate reduction to ammonium (DNRA) in the nitrogen cycle of coastal ecosystems. *Oceanography* **26**: 124-131.
- Gieseke A, Bjerrum L, Wagner M, Amann R. (2003). Structure and activity of multiple nitrifying bacterial populations co-existing in a biofilm. *Environ Microbiol* **5**: 355-369.
- Gleason HA. (1926). The individualistic concept of the plant association. *Bulletin of the Torrey Botanical Club* **53**: 7-26.
- Goldhaber MB. (2003). Sulfur-rich sediments. *Treatise on Geochemistry* **7**: 257-288.
- Gons HJ, Rijkeboer M. (1992). The 'true' growth efficiency of phytoplankton as influenced by light attenuation and insolation: implications of the photosynthesis-irradiance relationship. *Hydrobiol* **238**: 169-176.
- Gonzalez-Martinez A, Rodriguez-Sanchez A, van Loosdrecht MCM, Gonzalez-Lopez J, Vahala R. (2016). Detection of comammox bacteria in full-scale wastewater treatment bioreactors using *tag*-454-pyrosequencing. *Environ Sci Pollut R* **23**: 25501-25511.
- Gregersen LH, Bryant DA, Frigaard NU. (2011). Mechanisms and evolution of oxidative sulfur metabolism in green sulfur bacteria. *Front Microbiol* **2**: 116.
- Grote J, Jost G, Labrenz M, Herndl GJ, Jürgens K. (2008). *Epsilonproteobacteria* represent the major portion of chemoautotrophic bacteria in sulfidic waters of pelagic redoxclines of the Baltic and Black Seas. *Appl Environ Microbiol* **74**: 7546-7551.
- Guerrero R, Montesinos E, Pedrós-Alió C, Esteve I, Mas J. (1985). Phototrophic sulfur bacteria in two Spanish lakes: vertical distribution and limiting factors. *Limnol Oceanogr* **30**: 919-931.
- Guyoneaud R, Caumette P, Imhoff JF. (2015). *Thiorhodococcus*. In: Whitman WB *et al.* (eds). *Bergey's Manual of Systematics of Archaea and Bacteria*.
- Halm H, Musat N, Lam P, Langlois R, Musat F, Peduzzi S *et al.* (2009). Co-occurrence of denitrification and nitrogen fixation in a meromictic lake, Lake Cadagno (Switzerland). *Environ Microbiol* **11**: 1945-1958.
- Hamersley MR, Woebken D, Boehrer B, Schultze M, Lavik G, Kuypers MMM. (2009). Water column anammox and denitrification in a temperate permanently stratified lake (Lake Rassnitzer, Germany). *Syst Appl Microbiol* **32**: 571-582.
- Hamilton TL, Bovee RJ, Thiel V, Sattin SR, Mohr W, Schaperdoth I *et al.* (2014). Coupled reductive and oxidative sulfur cycling in the phototrophic plate of a meromictic lake. *Geobiology* **12**: 451-468.

References

- Hammer Ø, Harper DAT, Ryan PD. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontol Electron* **4**: art .4.
- Hansel CM, Lentini CJ, Tang YZ, Johnston DT, Wankel SD, Jardine PM. (2015). Dominance of sulfur-fueled iron oxide reduction in low-sulfate freshwater sediments. *ISME J* **9**: 2400-2412.
- Hanson RS, Hanson TE. (1996). Methanotrophic bacteria. *Microbiol Rev* **60**: 439-471.
- Harhangi HR, Le Roy M, van Alen T, Hu BL, Groen J, Kartal B, Tringe SG *et al.* (2012). Hydrazine synthase, a unique phylomarker with which to study the presence and Biodiversity of anammox bacteria. *Appl Environ Microbiol* **78**: 752-758.
- Harke MJ, Davis TW, Watson SB, Gobler CJ. (2016). Nutrient-controlled niche differentiation of western Lake Erie cyanobacterial populations revealed via metatranscriptomic surveys. *Environ Sci Technol* **50**: 604-615.
- Haroon MF, Hu S, Shi Y, Imelfort M, Keller J, Hugenholtz P *et al.* (2013). Anaerobic oxidation of methane coupled to nitrate reduction in a novel archaeal lineage. *Nature* **500**: 567-570.
- Harter J, Krause HM, Schuettler S, Ruser R, Fromme M, Scholten T *et al.* (2014). Linking N₂O emissions from biochar-amended soil to the structure and function of the N-cycling microbial community. *ISME J* **8**: 660-674.
- Hastings RC, Saunders JR, Hall GH, Pickup RW, McCarthy AJ. (1998). Application of molecular biological techniques to a seasonal study of ammonia oxidation in a eutrophic freshwater lake. *Appl Environ Microbiol* **64**: 3674-3682.
- Hausmann B, Knorr KH, Schreck K, Tringe SG, del Rio TG, Loy A *et al.* (2016). Consortia of low-abundance bacteria drive sulfate reduction-dependent degradation of fermentation products in peat soil microcosms. *ISME J* **10**: 2365-2375.
- Hausmann B, Pelikan C, Herbold CW, Köstlbacher S, Albertsen M, Eichorst SA *et al.* (2018). Peatland *Acidobacteria* with a dissimilatory sulfur metabolism. *ISME J* **12**: 1729-1742.
- He R, Wooller MJ, Pohlman JW, Tiedje JM, Leigh MB. (2015). Methane-derived carbon flow through microbial communities in arctic lake sediments. *Environ Microbiol* **17**: 3233-3250.
- He S, Stevens SLR, Chan LK, Bertilsson S, del Rio TG, Tringe SG *et al.* (2017). Ecophysiology of freshwater verrucomicrobia inferred from metagenome-assembled genomes. *mSphere* **2**: e00277-17.
- Hemp J, Lückner S, Schott J, Pace LA, Johnson JE, Schink B *et al.* (2016). Genomics of a phototrophic nitrite oxidizer: insights into the evolution of photosynthesis and nitrification. *ISME J* **10**: 2669-2678.
- Hendzel L, Hecky R, Findlay D. (1994). Recent changes of N₂-fixation in Lake 227 in

- response to reduction of the N: P loading ratio. *Can J Fish Aquat Sci* **51**: 2247-2253.
- Herlemann DPR, Labrenz M, Jürgens K, Bertilsson S, Waniek JJ, Andersson AF. (2011). Transitions in bacterial communities along the 2000 km salinity gradient of the Baltic Sea. *ISME J* **5**: 1571-1579.
- Herrmann M, Saunders AM, Schramm A. (2009). Effect of lake trophic status and rooted macrophytes on community composition and abundance of ammonia-oxidizing prokaryotes in freshwater sediments. *Appl Environ Microbiol* **75**: 3127-3136.
- Hou J, Song C, Cao X, Zhou Y. (2013). Shifts between ammonia-oxidizing bacteria and archaea in relation to nitrification potential across trophic gradients in two large Chinese lakes (Lake Taihu and Lake Chaohu). *Water Res* **47**: 2285-2296.
- Hu B, Shen L, Lian X, Zhu Q, Liu S, Huang Q *et al.* (2014). Evidence for nitrite-dependent anaerobic methane oxidation as a previously overlooked microbial methane sink in wetlands. *Proc Natl Acad Sci USA* **111**: 4495-4500.
- Huisman J, Sharples J, Stroom JM, Visser PM, Kardinaal WEA, Verspagen JMH *et al.* (2004). Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology* **85**: 2960-2970.
- Huisman J, Matthijs HCP, Visser PM. (2005). *Harmful Cyanobacteria*. Springer Aquatic Ecology Series 3. Springer, Dordrecht.
- Imberger J. (1985). The diurnal mixed layer. *Limnol Oceanogr* **30**: 737-770.
- Imboden DM, Wüest A. (1995). Mixing mechanisms in lakes. In: Lerman A *et al.* (eds) *Physics and chemistry of lakes*. Springer, Berlin, pp 83-138.
- Imhoff JF. (2001). Transfer of *Pfennigia purpurea* Tindall 1999 (*Amoebobacter purpureus* Eichler and Pfennig 1988) to the genus *Lamprocystis* as *Lamprocystis purpurea* comb. nov.. *Int J Syst Evol Microbiol* **51**: 1699-1701.
- Imhoff, JF. (2004). Taxonomy and physiology of phototrophic purple bacteria and green sulfur bacteria. In Blankenship RE *et al.* (eds). *Anoxygenic photosynthetic bacteria*. Kluwer academic publishers, London, pp 1-15.
- Ingvorsen K, Zehnder AJB, Jørgensen BB. (1984). Kinetics of sulfate and acetate uptake by *Desulfobacter postgatei*. *Appl Environ Microbiol* **47**: 403-408.
- Inouye RS, Tilman D. (1995). Convergence and divergence of old-field vegetation after 11 yr of nitrogen addition. *Ecology* **76**: 1872-1887.
- IPCC. (2013). Climate change 2013: the physical science basis. in Stocker TF *et al.* (eds). *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, pp 1-1535.
- Jenkyns HC. (2010). Geochemistry of oceanic anoxic events. *Geochem Geophys Geosyst* **11**: Q03004.

References

- Jenny, JP, Normandeau A, Francus P, Taranu ZE, Gregory-Eaves I, Lapointe F *et al.* (2016). Urban point sources of nutrients were the leading cause for the historical spread of hypoxia across European lakes. *Proc Natl Acad Sci USA* **113**: 12655-12660.
- Jenny JP, Francus P, Normandeau A, Lapointe F, Perga ME, Ojala A *et al.* (2016). Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. *Glob Change Biol* **22**: 1481-1489.
- Jin Q, Bethke CM. (2007). The thermodynamics and kinetics of microbial metabolism. *Am J Sci* **307**: 643-677.
- Jones CM, Hallin S. (2010). Ecological and evolutionary factors underlying global and local assembly of denitrifier communities. *ISME J* **4**: 633-641.
- Jones DT, Taylor WR, Thornton JM. (1992). The rapid generation of mutation data matrices from protein sequences. *Comput Appl Biosci* **8**: 275-282.
- Jones ZL, Jasper JT, Sedlak DL, Sharp JO. (2017). Sulfide-induced dissimilatory nitrate reduction to ammonium supports anaerobic ammonium oxidation (Anammox) in an open-water unit process wetland. *Appl Environ Microbiol* **83**: e00782-17.
- Jørgensen BB. (1982). Mineralization of organic matter in the sea bed: the role of sulphate reduction. *Nature* **296**: 643-645.
- Joye SB, Hollibaugh JT. (1995). Influence of sulfide inhibition of nitrification on nitrogen regeneration in sediments. *Science* **270**: 623-625.
- Kalyuzhnyi S, Fedorovich V, Lens P, Hulshoff Pol L, Lettinga G. (1998). Mathematical modelling as a tool to study population dynamics between sulfate reducing and methanogenic bacteria. *Biodegradation* **9**: 187-199.
- Kämpf C, Pfennig N. (1980). Capacity of Chromatiaceae for chemotrophic growth. Specific respiration rates of *Thiocystis violacea* and *Chromatium vinosum*. *Arch Microbiol* **127**: 125-135.
- Kandeler E, Deiglmayr K, Tschirko D, Bru D, Philippot L. (2006). Abundance of *narG*, *nirS*, *nirK*, and *nosZ* genes of denitrifying bacteria during primary successions of a glacier foreland. *Appl Environ Microbiol* **72**: 5957-5962.
- Kanehisa M, Sato Y, Morishima K. (2016). BlastKOALA and GhostKOALA: KEGG tools for functional characterization of genome and metagenome sequences. *J Mol Biol* **428**: 726-731.
- Kang DD, Froula J, Egan R, Wang Z. (2015). MetaBAT, an efficient tool for accurately reconstructing single genomes from complex microbial communities. *Peer J* **3**: e1165.
- Kara EL, Hanson PC, Hu YH, Winslow L, McMahon KD. (2013). A decade of seasonal dynamics and co-occurrences within freshwater bacterioplankton communities from eutrophic Lake Mendota, WI, USA. *ISME J* **7**: 680-684.

- Karhunen J, Arvola L, Peura S, Tiirola M. (2013). Green sulphur bacteria as a component of the photosynthetic plankton community in small dimictic humic lakes with an anoxic hypolimnion. *Aquat Microb Ecol* **68**: 267-272.
- Karl D, Letelier R, Tupas L, Dore J, Christian J, Hebel D. (1997). The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* **388**: 533-538.
- Karlson K, Rosenberg R, Bonsdorff E. (2002). Temporal and spatial large-scale effects of eutrophication and oxygen deficiency on benthic fauna in Scandinavian and Baltic Waters - a review. *Oceanography and Marine Biology: an Annual Review* **40**: 427-489.
- Kent AD, Yannarell AC, Rusak JA, Triplett EW, McMahon KD. (2007). Synchrony in aquatic microbial community dynamics. *ISME J* **1**: 38-47.
- Kits KD, Sedlacek CJ, Lebedeva EV, Han P, Bulaev A, Pjevac P *et al.* (2017). Kinetic analysis of a complete nitrifier reveals an oligotrophic lifestyle. *Nature* **549**: 269-272.
- Koch H, Galushko A, Albertsen M, Schintlmeister A, Gruber-Dorninger C, Lückner S *et al.* (2014). Growth of nitrite-oxidizing bacteria by aerobic hydrogen oxidation. *Science* **345**: 1052-1054.
- Kondo R, Osawa K, Mochizuki L, Fujioka Y, Butani J. (2006). Abundance and diversity of sulphate-reducing bacterioplankton in Lake Suigetsu, a meromictic lake in Fukui, Japan. *Plankton Benthos Res* **1**: 165-177.
- Könneke M, Bernhard AE, de la Torre JR, Walker CB, Waterbury JB, Stahl DA. (2005). Isolation of an autotrophic ammonia-oxidizing marine archaeon. *Nature* **437**: 543-546.
- Kraft B, Tegetmeyer HE, Sharma R, Klotz MG, Ferdelman TG, Hettich RL *et al.* (2014). The environmental controls that govern the end product of bacterial nitrate respiration. *Science* **345**: 676-679.
- Kreyling J, Jentsch A, Beierkuhnlein C. (2011). Stochastic trajectories of succession initiated by extreme climatic events. *Ecol Lett* **14**: 758-764.
- Kromkamp J, van den Heuvel A, Mur LR. (1989). Phosphorus uptake and photosynthesis by phosphate-limited cultures of the cyanobacterium *Microcystis aeruginosa*. *Br Phycol J* **24**: 347-355.
- Kubo K, Kojima H, Fukui M. (2014). Vertical distribution of major sulfate-reducing bacteria in a shallow eutrophic meromictic lake. *Syst Appl Microbiol* **37**: 510-519.
- Kumar S, Stecher G, Tamura K. (2016). MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol Biol Evol* **33**: 1870-1874.
- Kump LR, Pavlov A, Arthur MA. (2005). Massive release of hydrogen sulfide to the surface ocean and atmosphere during intervals of oceanic anoxia. *Geology* **33**: 397-400.
- Kuypers MMM, Pancost RD, Nijenhuis IA, Sinninghe Damsté JS. (2002). Enhanced

References

- productivity led to increased organic carbon burial in the euxinic North Atlantic basin during the late Cenomanian oceanic anoxic event. *Paleoceanography* **17**: 1051.
- Kuypers MMM, Sliekers AO, Lavik G, Schmid M, Jørgensen BB, Kuenen JG *et al.* (2003). Anaerobic ammonium oxidation by anammox bacteria in the Black Sea. *Nature* **422**: 608-611.
- Lagostina L, Goldhammer T, Røy H, Evans TW, Lever MA, Jørgensen BB *et al.* (2015). Ammonia-oxidizing bacteria of the *Nitrosospira* cluster 1 dominate over ammonia-oxidizing archaea in oligotrophic surface sediments near the South Atlantic Gyre. *Environ Microbiol Rep* **7**: 404-413.
- Lahti L, Salojärvi J, Salonen A, Scheffer M, de Vos WM. (2014). Tipping elements in the human intestinal ecosystem. *Nat Commun* **5**: 4344.
- Lauro FM, DeMaere MZ, Yau S, Brown MV, Ng C, Wilkins D *et al.* (2011). An integrative study of a meromictic lake ecosystem in Antarctica. *ISME J* **5**: 879-895.
- Lavik G, Stührmann T, Brüchert V, Van der Plas A, Mohrholz V, Lam P *et al.* (2009). Detoxification of sulphidic African shelf waters by blooming chemolithotrophs. *Nature* **457**: 581-584.
- Lee JA, Francis CA. (2017). Spatiotemporal characterization of San Francisco Bay denitrifying communities: a comparison of *nirK* and *nirS* diversity and abundance. *Microb Ecol* **73**: 271-284.
- Lehtimäki J, Moisander P, Sivonen K, Kononen K. (1997). Growth, nitrogen fixation, and nodularin production by two Baltic Sea cyanobacteria. *Appl Environ Microbiol* **63**: 1647-1656.
- Leininger S, Urich T, Schloter M, Schwark L, Qi J, Nicol GW *et al.* (2006). Archaea predominate among ammonia-oxidizing prokaryotes in soils. *Nature* **442**: 806-809.
- Lennon JT, Jones SE. (2011). Microbial seed banks: the ecological and evolutionary implications of dormancy. *Nat Rev Microbiol* **9**: 119-130.
- Levipan HA, Molina V, Fernandez C. (2014). *Nitrospina*-like bacteria are the main drivers of nitrite oxidation in the seasonal upwelling area of the Eastern South Pacific (Central Chile ~ 36°S). *Environ Microbiol Rep* **6**: 565-573.
- Li D, Liu CM, Luo R, Sadakane K, Lam TW. (2014). MEGAHIT: an ultra-fast single-node solution for large and complex metagenomics assembly via succinct *de Bruijn* graph. *Bioinformatics* **31**: 1674-1676.
- Li J, Nedwell DB, Beddow J, Dumbrell AJ, McKew BA, Thorpe EL *et al.* (2015). *amoA* gene abundances and nitrification potential rates suggest that benthic ammonia-oxidizing bacteria and not archaea dominate N cycling in the Colne Estuary, United Kingdom. *Appl Environ Microbiol* **81**: 159-165.

- Li M, Hong Y, Cao H, Klotz MG, Gu JD. (2013). Diversity, abundance, and distribution of NO-forming nitrite reductase-encoding genes in deep-sea subsurface sediments of the South China Sea. *Geobiology* **11**: 170-179.
- Li JH, Purdy KJ, Takii S, Hayashi H. (1999). Seasonal changes in ribosomal RNA of sulfate-reducing bacteria and sulfate reducing activity in a freshwater lake sediment. *FEMS Microbiol Ecol* **28**: 31-39.
- Lima-Mendez G, Faust K, Henry N, Decelle J, Colin S, Carcillo F *et al.* (2015). Determinants of community structure in the global plankton interactome. *Science* **348**: 1262073.
- Lindström ES, Kamst-Van Agterveld MP, Zwart G. (2005). Distribution of typical freshwater bacterial groups is associated with pH, temperature, and lake water retention time. *Appl Environ Microbiol* **71**: 8201-8206.
- Lipsewers YA, Bale NJ, Hopmans EC, Schouten S, Sinnighe Damsté JS, Villanueva L. (2014). Seasonality and depth distribution of the abundance and activity of ammonia oxidizing microorganisms in marine coastal sediments (North Sea). *Front Microbiol* **5**: 472.
- Livingstone DM. (2003). Impact of secular climate change on the thermal structure of a large temperate central European lake. *Clim Change* **57**: 205-225.
- Llirós M, Casamayor EO, Borrego C. (2008). High archaeal richness in the water column of a freshwater sulfurous karstic lake along an interannual study. *FEMS Microbiol Ecol* **66**: 331-342.
- Llorens-Marès T, Yooseph S, Goll J, Hoffman J, Vila-Costa M, Borrego CM *et al.* (2015). Connecting biodiversity and potential functional role in modern euxinic environments by microbial metagenomics. *ISME J* **9**: 1648-1661.
- Llorens-Marès T, Liu Z, Allen LZ, Rusch DB, Craig MT, Dupont CL *et al.* (2017). Speciation and ecological success in dimly lit waters: horizontal gene transfer in a green sulfur bacteria bloom unveiled by metagenomic assembly. *ISME J* **11**: 201-211.
- Lu S, Liao M, Xie C, He X, Li D, He L *et al.* (2015). Seasonal dynamics of ammonia-oxidizing microorganisms in freshwater aquaculture ponds. *Ann Microbiol* **65**: 651-657.
- Lu S, Liu X, Ma Z, Liu Q, Wu Z, Zeng X *et al.* (2016). Vertical segregation and phylogenetic characterization of ammonia-oxidizing bacteria and archaea in the sediment of a freshwater aquaculture pond. *Front Microbiol* **6**: 1539.
- Luther GW, Findlay AJ, MacDonald DJ, Owings SM, Hanson TE, Beinart RA *et al.* (2011). Thermodynamics and kinetics of sulfide oxidation by oxygen: a look at inorganically controlled reactions and biologically mediated processes in the environment. *Front Microbiol* **2**: 62.

References

- MacIntyre S. (1993). Vertical mixing in a shallow, eutrophic lake: possible consequences for the light climate of phytoplankton. *Limnol Oceanogr* **38**: 798-817.
- MacIntyre S, Flynn KM, Jellison R, Romero JR. (1999). Boundary mixing and nutrient fluxes in Mono Lake, California. *Limnol Oceanogr* **44**: 512-529.
- Madigan MT. (1995). Microbiology of nitrogen fixation by anoxygenic photosynthetic bacteria. In: Blankenship RE *et al.* (eds). *Anoxygenic Photosynthetic Bacteria*. Springer, Dordrecht, pp 915-928.
- Manske AK, Glaeser J, Kuypers MMM, Overmann. (2005). Physiology and phylogeny of green sulfur bacteria forming a monospecific phototrophic assemblage at a depth of 100 meters in the Black Sea. *Appl Environ Microbiol* **71**: 8049-8060.
- Marchant HK, Ahmerkamp S, Lavik G, Tegetmeyer HE, Graf J, Klatt JM *et al.* (2017). Denitrifying community in coastal sediments performs aerobic and anaerobic respiration simultaneously. *ISME J* **11**: 1799-1812.
- Marietou A. (2016). Nitrate reduction in sulfate-reducing bacteria. *FEMS Microbiol Lett* **363**: fnw155.
- Martens-Habben W, Berube PM, Urakawa H, de la Torre JR, Stahl DA. (2009). Ammonia oxidation kinetics determine niche separation of nitrifying archaea and bacteria. *Nature* **461**: 976-979.
- Matsumoto S, Katoku M, Saeki G, Terada A, Aoi Y, Tsuneda S *et al.* (2010). Microbial community structure in autotrophic nitrifying granules characterized by experimental and simulation analyses. *Environ Microbiol* **12**: 192-206.
- McCutcheon SC, Martin JL, Barnwell TO. (1993). Water quality. In: Maidment DR (ed). *Handbook of Hydrology*. McGraw-Hill, pp 11.1-11.6.
- Meire L, Soetaert, KER, Meysman FJR. (2013). Impact of global change on coastal oxygen dynamics and risk of hypoxia. *Biogeosciences* **10**: 2633-2653.
- Meyer F, Paarmann D, D'Souza M, Olson R, Glass EM, Kubal M *et al.* (2008). The metagenomics RAST server - a public resource for the automatic phylogenetic and functional analysis of metagenomes. *BMC Bioinformatics* **9**: 386.
- Michalak AM, Anderson EJ, Beletsky D, Boland S, Bosch NS, Bridgeman TB *et al.* (2013). Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proc Natl Acad Sci USA* **110**: 6448-6452.
- Middelburg JJ, Levin LA. (2009). Coastal hypoxia and sediment biogeochemistry. *Biogeosciences* **6**: 1273-1293.
- Miller SR, Bebout BM. (2004). Variation in sulfide tolerance of photosystem II in phylogenetically diverse cyanobacteria from sulfidic habitats. *Appl Environ Microbiol* **70**: 736-744.

- Millero FJ, Hubinger S, Fernandez M, Garnett S. (1987). Oxidation of H₂S in seawater as a function of temperature, pH, and ionic strength. *Environ Sci Technol* **21**, 439-443.
- Montesinos E. (1987). Change in size of *Chromatium minus* cells in relation to growth rate, sulfur content, and photosynthetic activity: a comparison of pure cultures and field populations. *Appl Environ Microbiol* **53**: 864-871.
- Mori Y, Kataoka T, Okamura T, Kondo R. (2013). Dominance of green sulfur bacteria in the chemocline of the meromictic Lake Suigetsu, Japan, as revealed by dissimilatory sulfite reductase gene analysis. *Arch Microbiol* **195**: 303-312.
- Mosier AC, Francis CA. (2010). Denitrifier abundance and activity across the San Francisco Bay estuary. *Environ Microbiol Rep* **2**: 667-676.
- Mur LR, Skulberg OM, Utkilen H. (1999). Cyanobacteria in the environment. In: Chorus I *et al.* (eds). *Toxic Cyanobacteria in Water: A Guide to Their Public Health Consequences, Monitoring and Management*. London: E & FN Spon, pp 15-40.
- Muyzer G, Stams AJM. (2008). The ecology and biotechnology of sulphate-reducing bacteria. *Nat Rev Microbiol* **6**: 441-454.
- Muyzer G, Kuenen JG, Robertson LA. (2013). Colorless sulfur bacteria. In: Rosenberg E *et al.* (eds). *The Prokaryotes: Prokaryotic physiology and biochemistry*. Springer, Berlin, pp 555-588.
- Nelson CE. (2009). Phenology of high-elevation pelagic bacteria: the roles of meteorologic variability, catchment inputs and thermal stratification in structuring communities. *ISME J* **3**: 13-30.
- Nelson MB, Martiny AC, Martiny JBH. (2016). Global biogeography of microbial nitrogen-cycling traits in soil. *Proc Natl Acad Sci USA* **113**: 8033-8040.
- Neubacher EC, Parker RE, Trimmer M. (2011). Short-term hypoxia alters the balance of the nitrogen cycle in coastal sediments. *Limnol Oceanogr* **56**: 651-665.
- Newton RJ, Jones SE, Eiler A, McMahon KD, Bertilsson S. (2011). A guide to the natural history of freshwater lake bacteria. *Microbiol Mol Biol Rev* **75**: 14-49.
- Noguerola I, Picazo A, Llirós M, Camacho A, Borrego CM. (2015). Diversity of freshwater *Epsilonproteobacteria* and dark inorganic carbon fixation in the sulphidic redoxcline of a meromictic karstic lake. *FEMS Microbiol Ecol* **91**: fiv086.
- North RP, North RL, Livingstone DM, Köster O, Kipfer R. (2014). Long-term changes in hypoxia and soluble reactive phosphorus in the hypolimnion of a large temperate lake: consequences of a climate regime shift. *Glob Change Biol* **20**: 811-823.
- Nürnberg GK. (1995). Quantifying anoxia in lakes. *Limnol Oceanogr* **40**: 1100-1111.
- Ohkouchi N, Nakajima Y, Okada H, Ogawa NO, Suga H, Oguri K *et al.* (2005). Biogeochemical processes in the saline meromictic Lake Kaiike, Japan: implications from molecular isotopic evidences of photosynthetic pigments. *Environ Microbiol* **7**:

References

- 1009-1016.
- Okazaki Y, Nakano SI. (2016). Vertical partitioning of freshwater bacterioplankton community in a deep mesotrophic lake with a fully oxygenated hypolimnion (Lake Biwa, Japan). *Environ Microbiol Rep* **8**: 780-788.
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB *et al.* (2013). Vegan: community ecology package. R package version 2.0-10.
- Osborn TR. (1980). Estimates of the local rate of vertical diffusion from dissipation measurements. *J Phys Oceanogr* **10**: 83-89.
- Ouyang Y, Norton JM, Stark JM. (2017). Ammonium availability and temperature control contributions of ammonia oxidizing bacteria and archaea to nitrification in an agricultural soil. *Soil Biol Biochem* **113**: 161-172.
- Overmann J, Cypionka H, Pfennig N. (1992). An extremely low-light-adapted phototrophic sulfur bacterium from the Black Sea. *Limnol Oceanogr* **37**: 150-155.
- Paerl HW, Huisman J. (2008). Blooms like it hot. *Science* **320**: 57-58.
- Paerl HW, Huisman J. (2009). Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Env Microb Rep* **1**: 27-37.
- Pachiadaki MG, Sintés E, Bergauer K, Brown JM, Record NR, Swan BK *et al.* (2017). Major role of nitrite-oxidizing bacteria in dark ocean carbon fixation. *Science* **358**: 1046-1051.
- Paganin P, Chiarini L, Bevivino A, Dalmastrì C, Farcomeni A, Izzo G *et al.* (2013). Vertical distribution of bacterioplankton in Lake Averno in relation to water chemistry. *FEMS Microbiol Ecol* **84**: 176-188.
- Pancost RD, Crawford N, Magness S, Turner A, Jenkyns HC, Maxwell JR. (2004). Further evidence for the development of photic-zone euxinic conditions during Mesozoic oceanic anoxic events. *J Geol Soc* **161**: 353-364.
- Park BJ, Park SJ, Yoon DN, Schouten S, Sinninghe Damsté JS, Rhee SK. (2010). Cultivation of autotrophic ammonia-oxidizing archaea from marine sediments in coculture with sulfur-oxidizing bacteria. *Appl Environ Microbiol* **76**: 7575-7587.
- Parks DH, Imelfort M, Skennerton CT, Hugenholtz P, Tyson GW. (2015). CheckM: assessing the quality of microbial genomes recovered from isolates, single cells, and metagenomes. *Genome Res* **25**: 1043-1055.
- Pauer JJ, Auer MT. (2000). Nitrification in the water column and sediment of a hypereutrophic lake and adjoining river system. *Water Res* **34**: 1247-1254.
- Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC *et al.* (2017). Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. *Science* **355**: eaai9214.
- Peduzzi S, Welsh A, Demarta A, Decristophoris P, Peduzzi R, Hahn D *et al.* (2011).

- Thiocystis chemoclinalis* sp. nov. and *Thiocystis cadagnonensis* sp. nov., motile purple sulfur bacteria isolated from the chemocline of a meromictic lake. *Int J Syst Evol Microbiol* **61**: 1682-1687.
- Peeters F, Livingstone DM, Goudsmit GH, Kipfer R, Forster R. (2002). Modeling 50 years of historical temperature profiles in a large central European lake. *Limnol Oceanogr* **47**: 186-197.
- Pester M, Rattei T, Flechl S, Gröngroft A, Richter A, Overmann J *et al.* (2012). *amoA*-based consensus phylogeny of ammonia-oxidizing archaea and deep sequencing of *amoA* genes from soils of four different geographic regions. *Environ Microbiol* **14**: 525-539.
- Pfennig N, Trüper HG. (1989). Anoxygenic phototrophic bacteria. In: Staley JT *et al.* (eds). *Bergey's manual of systematic bacteriology*. Williams & Wilkins, Baltimore, pp 1635-1709.
- Pinto AJ, Marcus DN, Zeeshan Ijaz U, Santos QMB, Dick GJ, Raskin L. (2016). Metagenomic evidence for the presence of comammox *Nitrospira*-like bacteria in a drinking water system. *mSphere* **1**: e00054-15.
- Pjevac P, Korlević M, Berg JS, Bura-Nakić E, Ciglencčki I, Amann R *et al.* (2015). Community shift from phototrophic to chemotrophic sulfide oxidation following anoxic holomixis in a stratified seawater lake. *Appl Environ Microbiol* **81**: 298-308.
- Rabalais NN, Turner RE, Wiseman WJ. (2002). Gulf of Mexico hypoxia, A.K.A. "The Dead Zone". *Annu Rev Ecol Syst* **33**: 253-263.
- Rabalais NN, Turner RE, Sen Gupta BK, Boesch DF, Chapman P, Murrell MC. (2007). Hypoxia in the northern Gulf of Mexico: does the science support the plan to reduce, mitigate, and control hypoxia? *Estuaries Coast* **30**: 753-772.
- Rappé MS, Giovannoni SJ. (2003). The uncultured microbial majority. *Annu Rev Microbiol* **57**: 369-394.
- Raymond J, Siefert JL, Staples CR, Blankenship RE. (2004). The natural history of nitrogen fixation. *Mol Biol Evol* **21**: 541-554.
- Ravishankara AR, Daniel JS, Portmann RW. (2009). Nitrous oxide (N₂O): the dominant ozone-depleting substance emitted in the 21st century. *Science* **326**: 123-125.
- Riera XG, Garcia-Gil LJ, Abella A. (1988). Lake Vechten, Schleinsee and Buchensee as examples of west central european holomictic lakes containing phototrophic bacteria. *Sci Gerundensis* **14**: 57-69.
- Rogozin DY, Zykov VV, Degermendzhi AG. (2012). Ecology of purple sulfur bacteria in the highly stratified meromictic Lake Shunet (Siberia, Khakassia) in 2002-2009. *Microbiology* **81**: 727-735.
- Rotthauwe JH, Witzel KP, Liesack W. (1997). The ammonia monooxygenase structural gene *amoA* as a functional marker: molecular fine-scale analysis of natural ammonia-

References

- oxidizing populations. *Appl Environ Microbiol* **63**: 4704-4712.
- Rush D, Sinninghe Damsté JS. (2017). Lipids as paleomarkers to constrain the marine nitrogen cycle. *Environ Microbiol* **19**: 2119-2132.
- Ruttenberg KC. (2003). The global phosphorus cycle. *Treatise on Geochemistry* **8**: 585-643.
- Saarenheimo J, Aalto SL, Syväranta J, Devlin SP, Tirola M, Jones RI. (2016). Bacterial community response to changes in a tri-trophic cascade during a whole-lake fish manipulation. *Ecology* **97**: 684-693.
- Salcher MM, Pernthaler J, Zeder M, Psenner R, Posch T. (2008). Spatio-temporal niche separation of planktonic *Betaproteobacteria* in an oligo-mesotrophic lake. *Environ Microbiol* **10**: 2074-2086.
- Samad MS, Bertilsson S. (2017). Seasonal variation in abundance and diversity of bacterial methanotrophs in five temperate lakes. *Front Microbiol* **8**: 142.
- Santos HF, Carmo FL, Duarte G, Dini-Andreote F, Castro CB, Rosado AS *et al.* (2014). Climate change affects key nitrogen-fixing bacterial populations on coral reefs. *ISME J* **8**: 2272-2279.
- Sañudo-Wilhelmy SA, Kustka AB, Gobler CJ, Hutchins DA, Yang M, Lwiza K *et al.* (2001). Phosphorus limitation of nitrogen fixation by *Trichodesmium* in the central Atlantic Ocean. *Nature* **411**: 66-69.
- Satinsky BM, Smith CB, Sharma S, Landa M, Medeiros PM, Coles VJ *et al.* (2017). Expression patterns of elemental cycling genes in the Amazon River Plume. *ISME J* **11**: 1852-1864.
- Saxton MA, Arnold RJ, Bourbonniere RA, McKay RML, Wilhelm SW. (2012). Plasticity of total and intracellular phosphorus quotas in *Microcystis aeruginosa* cultures and Lake Erie algal assemblages. *Front Microbiol* **3**: 3.
- Schaub BEM, van Gemerden H. (1994). Simultaneous phototrophic and chemotrophic growth in the purple sulfur bacterium *Thiocapsa roseopersicina* M1. *FEMS Microbiol Ecol* **13**: 185-196.
- Scheffer M, Carpenter SR. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol Evol* **18**: 648-656.
- Scheffer M, Szabó S, Gragnani A, van Nes EH, Rinaldi S, Kautsky N *et al.* (2003). Floating plant dominance as a stable state. *Proc Natl Acad Sci USA* **100**: 4040-4045.
- Schlesinger WH. (2009). On the fate of anthropogenic nitrogen. *Proc Natl Acad Sci USA* **106**: 203-208.
- Schlitzer R. (2002). Interactive analysis and visualization of geoscience data with Ocean Data View. *Comput Geosci* **28**: 1211-1218.
- Schmidt ML, White JD, Deneff VJ. (2016). Phylogenetic conservation of freshwater lake habitat preference varies between abundant bacterioplankton phyla. *Environ*

- Microbiol* **18**: 1212-1226.
- Schröder A, Persson L, De Roos AM. (2005). Direct experimental evidence for alternative stable states: a review. *Oikos* **110**: 3-19.
- Schubert CJ, Durisch-Kaiser E, Wehrli B, Thamdrup B, Lam P, Kuypers MMM. (2006). Anaerobic ammonium oxidation in a tropical freshwater system (Lake Tanganyika). *Environ Microbiol* **8**: 1857-1863.
- Sela-Adler M, Ronen Z, Herut B, Antler G, Vigderovich H, Eckert W *et al.* (2017). Co-existence of methanogenesis and sulfate reduction with common substrates in sulfate-rich estuarine sediments. *Front Microbiol* **8**: 766.
- Shade A, Jones SE, McMahon KD. (2008). The influence of habitat heterogeneity on freshwater bacterial community composition and dynamics. *Environ Microbiol* **10**: 1057-1067.
- Shade A, Peter H, Allison SD, Baho DL, Berga M, Bürgmann H *et al.* (2012). Fundamentals of microbial community resistance and resilience. *Front Microbiol* **3**: 417.
- Shade A, Read JS, Youngblut ND, Fierer N, Knight R, Kratz TK *et al.* (2012). Lake microbial communities are resilient after a whole-ecosystem disturbance. *ISME J* **6**: 2153-2167.
- Shaffer G, Olsen SM, Pedersen JOP. (2009). Long-term ocean oxygen depletion in response to carbon dioxide emissions from fossil fuels. *Nat Geosci* **2**: 105-109.
- Shapleigh J. (2013). Denitrifying prokaryotes. In: Rosenbers E (ed). *The Prokaryotes*, Fourth edn. Springer-Verlag, Berlin, pp 405-425.
- Sievert SM, Kiene R, Schulz H. The sulfur cycle. *Oceanography* **20**:117-123.
- Sievert SM, Wieringa EBA, Wirsén CO, Taylor CD. (2007). Growth and mechanism of filamentous-sulfur formation by *Candidatus Arcobacter sulfidicus* in opposing oxygen-sulfide gradients. *Environ Microbiol* **9**: 271-276.
- Šimek K, Nedoma J, Znachor P, Kasalický V, Jezbera J, Horňák K *et al.* (2014). A finely tuned symphony of factors modulates the microbial food web of a freshwater reservoir in spring. *Limnol Oceanogr* **59**: 1477-1492.
- Sinninghe Damsté JS, Köster J. (1998). A euxinic southern North Atlantic Ocean during the Cenomanian/Turonian oceanic anoxic event. *Earth Planet Sci Lett* **158**: 165-173.
- Smith JM, Mosier AC, Francis CA. 2015. Spatiotemporal relationships between the abundance, distribution, and potential activities of ammonia-oxidizing and denitrifying microorganisms in intertidal sediments. *Microb Ecol* **69**: 13-24.
- Sorokin DY, Lüscher S, Vejmelkova D, Kostrikina NA, Kleerebezem R, Rijpstra WIC *et al.* (2012). Nitrification expanded: discovery, physiology and genomics of a nitrite-oxidizing bacterium from the phylum *Chloroflexi*. *ISME J* **6**: 2245-2256.
- Sorokin DY, Tourova TP, Muyzer G. (2013). Isolation and characterization of two novel

References

- alkalitolerant sulfidogens from a Thiopaq bioreactor, *Desulfonatronum alkalitolerans* sp. nov., and *Sulfurospirillum alkalitolerans* sp. nov. *Extremophiles* **17**: 535-543.
- Stahl DA, de la Torre JR. (2012). Physiology and diversity of ammonia-oxidizing archaea. *Annu Rev Microbiol* **66**: 83-101.
- Steenbergen CLM. (1982). Contribution of photosynthetic sulphur bacteria to primary production in Lake Vechten. *Hydrobiologia* **95**: 59-64.
- Steenbergen CLM, Korthals HJ. (1982). Distribution of phototrophic microorganisms in the anaerobic and microaerophilic strata of Lake Vechten (The Netherlands). Pigment analysis and role in primary production. *Limnol Oceanogr* **27**: 883-895.
- Steenbergen CLM, Verdouw H. (1982). Lake Vechten: aspects of its morphometry, climate, hydrology and physico-chemical characteristics. *Hydrobiologia* **95**: 11-23.
- Stefan HG, Fang X, Hondzo M. (1998). Simulated climate change effects on year-round water temperatures in temperate zone lakes. *Clim Change* **40**: 547-576.
- Steffen MM, Belisle BS, Watson SB, Boyer GL, Bourbonniere RA, Wilhelm SW. (2015). Metatranscriptomic evidence for co-occurring top-down and bottom-up controls on toxic cyanobacterial communities. *Appl Environ Microbiol* **81**: 3268-3276.
- Sterngren AE, Hallin S, Bengtson P. (2015). Archaeal ammonia oxidizers dominate in numbers, but bacteria drive gross nitrification in N-amended grassland soil. *Front Microbiol* **6**: 1350.
- Storelli N, Peduzzi S, Saad MM, Frigaard NU, Perret X, Tonolla M. (2013). CO₂ assimilation in the chemocline of Lake Cadagno is dominated by a few types of phototrophic purple sulfur bacteria. *FEMS Microbiol Ecol* **84**: 421-432.
- Strous M, Fuerst JA, Kramer EHM, Logemann S, Muyzer G, van de Pas-Schoonen KT *et al.* (1999). Missing lithotroph identified as new planctomycete. *Nature* **400**: 446-449.
- Sweerts JRA, De Beer D, Nielsen LP, Verdouw H, Van den Heuvel JC, Cohen Y *et al.* (1990). Denitrification by sulphur oxidizing *Beggiatoa* spp. mats on freshwater sediments. *Nature* **344**: 762-763.
- Sweerts JRA, Bär-Gilissen MJ, Cornelese AA, Cappenberg TE. (1991). Oxygen-consuming processes at the profundal and littoral sediment-water interface of a small meso-eutrophic lake (Lake Vechten, The Netherlands). *Limnol Oceanogr* **36**: 1124-1133.
- Takahashi M, Ichimura S. (1968). Vertical distribution and organic matter production of photosynthetic sulfur bacteria in Japanese lakes. *Limnol Oceanogr* **13**: 644-655.
- Tedford EW, MacIntyre S, Miller SD, Czikowsky MJ. (2014). Similarity scaling of turbulence in a temperate lake during fall cooling. *J Geophys Res Oceans* **119**: 4689-4713.
- Thackeray SJ, Jones ID, Maberly SC. (2008). Long-term change in the phenology of spring phytoplankton: species-specific responses to nutrient enrichment and climatic change. *J Ecol* **96**: 523-535.

- Third KA, Sliemers AO, Kuenen JG, Jetten MSM. (2001). The CANON system (completely autotrophic nitrogen-removal over nitrite) under ammonium limitation: interaction and competition between three groups of bacteria. *Syst Appl Microbiol* **24**: 588-596.
- Tonolla M, Peduzzi S, Hahn D, Peduzzi R. (2003). Spatio-temporal distribution of phototrophic sulfur bacteria in the chemocline of meromictic Lake Cadagno (Switzerland). *FEMS Microbiol Ecol* **43**: 89-98.
- Tonolla M, Peduzzi R, Hahn D. (2005). Long-term population dynamics of phototrophic sulfur bacteria in the chemocline of Lake Cadagno, Switzerland. *Appl Environ Microbiol* **71**: 3544-3550.
- Trüper HG, Schlegel HG. (1964). Sulphur metabolism in Thiorhodaceae I. quantitative measurements on growing cells of *Chromatium okenii*. *Antonie van Leeuwenhoek* **30**: 225-238.
- Turk KA, Rees AP, Zehr JP, Pereira N, Swift P, Shelley R *et al.* (2011). Nitrogen fixation and nitrogenase (*nifH*) expression in tropical waters of the eastern North Atlantic. *ISME J* **5**: 1201-1212.
- Ulloa O, Canfield DE, DeLong EF, Letelier RM, Stewart FJ. (2012). Microbial oceanography of anoxic oxygen minimum zones. *Proc Natl Acad Sci USA* **109**: 15996-16003.
- Vaquier-Sunyer R, Duarte CM. (2008). Thresholds of hypoxia for marine biodiversity. *Proc Natl Acad Sci USA* **105**: 15452-15457.
- van den Berg EM, van Dongen U, Abbas B, van Loosdrecht MCM. (2015). Enrichment of DNRA bacteria in a continuous culture. *ISME J* **9**: 2153-2161.
- Van Gemerden H. (1984). The sulfide affinity of phototrophic bacteria in relation to the location of elemental sulfur. *Arch Microbiol* **139**: 289-294.
- van Kessel MAHJ, Speth DR, Albertsen M, Nielsen PH, Op den Camp HJM, Kartal B *et al.* (2015). Complete nitrification by a single microorganism. *Nature* **528**: 555-559.
- Veraart AJ, Faassen EJ, Dakos V, van Nes EH, Lürling M, Scheffer M. (2012). Recovery rates reflect distance to a tipping point in a living system. *Nature* **481**: 357-359.
- Verdouw H, Dekkers EMJ. (1982). Nitrogen cycle of Lake Vechten: concentration patterns and internal mass-balance. *Hydrobiologia* **95**: 191-197.
- Verspagen JMH, Van de Waal DB, Finke JF, Visser PM, Van Donk E, Huisman J. (2014). Rising CO₂ levels will intensify phytoplankton blooms in eutrophic and hypertrophic lakes. *PLoS One* **9**: e104325.
- Vila X, Abella CA. (1994). Effects of light quality on the physiology and the ecology of planktonic green sulfur bacteria in lakes. *Photosynth Res* **41**: 53-65.
- Vissers EW, Blaga CI, Bodelier PLE, Muyzer G, Schleper C, Sinnighe Damsté JS *et al.* (2013). Seasonal and vertical distribution of putative ammonia-oxidizing thaumarchaeotal communities in an oligotrophic lake. *FEMS Microbiol Ecol* **83**: 515-

References

- 526.
- Visser PM, Verspagen JMH, Sandrini G, Stal LJ, Matthijs HCP, Davis TW *et al.* (2016). How rising CO₂ and global warming may stimulate harmful cyanobacterial blooms. *Harmful Algae* **54**: 145-159.
- Walker LR, Moral RD. (2003). *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge.
- Walsby AE. Gas vesicles. (1994). *Microbiol Rev* **58**: 94-144.
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC *et al.* (2002). Ecological responses to recent climate change. *Nature* **416**: 389-395.
- Wenk CB, Zopfi J, Gardner WS, McCarthy MJ, Niemann H, Veronesi M *et al.* (2014). Partitioning between benthic and pelagic nitrate reduction in the Lake Lugano south basin. *Limnol Oceanogr* **59**: 1421-1433.
- Widder S, Allen RJ, Pfeiffer T, Curtis TP, Wiuf C, Sloan WT *et al.* (2016). Challenges in microbial ecology: building predictive understanding of community function and dynamics. *ISME J* **10**: 2557-2568.
- Winogradsky S. (1890). Recherches sur les organismes de la nitrification. Annales de l'Inst. Pasteur: Paris, pp 213-231.
- Wu Y, Ke X, Hernández M, Wang B, Dumont MG, Jia Z *et al.* (2013). Autotrophic growth of bacterial and archaeal ammonia oxidizers in freshwater sediment microcosms incubated at different temperatures. *Appl Environ Microbiol* **79**: 3076-3084.
- Yang J, Jiang H, Dong H, Wu G, Hou W, Zhao W *et al.* (2013). Abundance and diversity of sulfur-oxidizing bacteria along a salinity gradient in four Qinghai-Tibetan lakes, China. *Geomicrobiol J* **30**: 851-860.
- Yang Y, Li N, Zhao Q, Yang M, Wu Z, Xie S *et al.* (2016). Ammonia-oxidizing archaea and bacteria in water columns and sediments of a highly eutrophic plateau freshwater lake. *Environ Sci Pollut Res* **23**: 15358-15369.
- Yang Y, Zhao Q, Cui Y, Wang Y, Xie S, Liu Y. (2016). Spatio-temporal variation of sediment methanotrophic microorganisms in a large eutrophic lake. *Microb Ecol* **71**: 9-17.
- Yang Y, Dai Y, Li N, Li B, Xie S, Liu Y. (2017). Temporal and spatial dynamics of sediment anaerobic ammonium oxidation (Anammox) bacteria in freshwater lakes. *Microb Ecol* **73**: 285-295.
- Yool A, Martin AP, Fernández C, Clark DR. (2007). The significance of nitrification for oceanic new production. *Nature* **447**: 999-1002.
- Yu Z, Yang J, Amalfitano S, Yu X, Liu L. (2014). Effects of water stratification and mixing on microbial community structure in a subtropical deep reservoir. *Sci Rep* **4**: 5821.
- Zani S, Mellon MT, Collier JL, Zehr JP. (2000). Expression of *nifH* genes in natural microbial assemblages in Lake George, New York, detected by reverse transcriptase

- PCR. *Appl Environ Microbiol* **66**: 3119-3124.
- Zehr JP, Carpenter EJ, Villareal TA. (2000). New perspectives on nitrogen-fixing microorganisms in tropical and subtropical oceans. *Trends Microbiol* **8**: 68-73.
- Zeng J, Zhao D, Li H, Huang R, Wang J, Wu QL. (2016). A monotonically declining elevational pattern of bacterial diversity in freshwater lake sediments. *Environ Microbiol* **18**: 5175-5186.
- Zhang J, Gilbert D, Gooday AJ, Levin L, Naqvi SWA, Middelburg JJ *et al.* (2010). Natural and human-induced hypoxia and consequences for coastal areas: synthesis and future development. *Biogeosciences* **7**: 1443-1467.
- Zhang J, Kobert K, Flouri T, Stamatakis A. (2014). PEAR: a fast and accurate Illumina Paired-End reAd mergeR. *Bioinformatics* **30**: 614-620.
- Zhang J, Yang Y, Zhao L, Li Y, Xie S, Liu Y. (2015). Distribution of sediment bacterial and archaeal communities in plateau freshwater lakes. *Appl Microbiol Biot* **99**: 3291-3302.
- Zumft WG. (1997). Cell biology and molecular basis of denitrification. *Microbiol Mol Biol Rev* **61**: 533-616.
- Zuur A, Ieno EN, Walker N, Saveliev AA, Smith GM. (2009). *Mixed Effects Models and Extensions in Ecology with R*. Berlin: Springer

Summary

Oxygen depletion in waters may lead to hypoxia and anoxia, which are detrimental for most aerobic organisms. Although hypoxia and anoxia have occurred throughout geological time, the frequency, intensity and duration of hypoxia and anoxia in lakes, coastal waters and open oceans have increased during the past decades, most likely due to eutrophication and global warming. Oxygen consumption by microorganisms plays an important role in the development of hypoxia and anoxia and, vice versa, microbial activity is also strongly affected by changes in oxygen availability. In particular, many of the biogeochemical transformations mediated by microorganisms involve oxidation-reduction reactions. Hence, as hypoxia and anoxia are increasingly threatening aquatic ecosystems, it is imperative to understand the interactions between microorganisms and oxic-anoxic transitions. Therefore, this thesis investigates the diversity and dynamics of microbial communities during oxic-anoxic transitions in a seasonally stratified lake (Lake Vechten) in the Netherlands. The following research questions have been addressed:

- (1) How do oxic-anoxic transitions affect bacterial community dynamics?
- (2) How are microbial and chemical feedbacks involved in oxic-anoxic transitions?
- (3) How do oxic-anoxic transitions affect the microbial sulfur and nitrogen cycle?

The influences of oxic-anoxic transitions on bacterial community dynamics in Lake Vechten were investigated in Chapter 2. *Cyanobacteria* and *Planktomyces* were abundant throughout the water column in early spring. During summer stratification, heterotrophic *Alphaproteobacteria*, *Bacteroidetes* and *Actinobacteria* became abundant in the aerobic epilimnion, *Gammaproteobacteria* (mainly *Chromatiaceae*) dominated in the metalimnion, and *Chlorobi*, *Betaproteobacteria*, *Deltaproteobacteria* and *Firmicutes* were abundant in the anoxic sulfidic hypolimnion. After fall turnover, the entire water column became hypoxic, *Polynucleobacter* (*Betaproteobacteria*) and *Methylobacter* (*Gammaproteobacteria*) spread out from the former meta- and hypolimnion to the surface layer, and *Epsilonproteobacteria* dominated in the bottom water layer. When the lake became fully mixed and oxic during the winter and early spring, *Cyanobacteria* and *Planktomyces* dominated the bacterial community again. Overall, the bacterial community composition at

different depths in the water column diverged during summer stratification and converged when the lake was mixed, indicating large spatio-temporal changes during oxic-anoxic transitions.

The interactions between microbial community composition, biogeochemical oxidation-reduction reactions and oxic-anoxic transitions were studied by a mathematical model in Chapter 3. The model predicts that gradual changes in oxygen influx can induce major regime shifts, in which the ecosystem shifts abruptly between an oxic state dominated by *Cyanobacteria* and an anoxic state with phototrophic sulfur bacteria and sulfate-reducing bacteria (SRB). Observations from Lake Vechten supported the model predictions, and showed hysteresis in the transition between oxic and anoxic states with similar changes in microbial community composition as predicted by the model. The hysteresis loops and tipping points associated with these regime shifts are likely a common feature of oxic-anoxic transitions in aquatic environments, causing rapid drops in oxygen levels that are not easily reversed. These results reveal and emphasize the vital roles of microorganisms in mediating oxic-anoxic transitions.

The dynamics of SRB and sulfur-oxidizing bacteria (SOB) during oxic-anoxic transitions were studied in detail in Chapter 4. SRB, green sulfur bacteria (GSB), purple sulfur bacteria (PSB), and colorless sulfur bacteria (CSB) inhabited the sediment during the winter and early spring when the water column was mixed. Once the water column stratified in late spring and summer, various SRB species expanded into the anoxic hypolimnion, and PSB and GSB bloomed in the metalimnion and hypolimnion during summer. When hypoxia spread throughout the water column during fall turnover, SRB and GSB vanished from the water column, whereas CSB (mainly *Arcobacter*) and PSB (*Lamprocystis*) became dominant. They oxidized the sulfide that had accumulated in the hypolimnion during summer stratification. These results support the view that, once ecosystems have become anoxic and sulfidic, a large oxygen influx is needed to overcome this state and bring the ecosystem back into the oxic state.

In Chapter 5, the seasonal succession of microorganisms involved in the nitrogen cycle during oxic-anoxic transitions was investigated. Ammonia-oxidizing archaea (AOA), ammonia-oxidizing bacteria (AOB), and anaerobic ammonium-oxidizing (anammox) bacteria were abundantly present in the sediment during the winter period. Nitrogen-fixing bacteria and denitrifying bacteria increased in the water

Summary

column in spring, when nitrate was gradually depleted and the hypolimnion became anoxic. Denitrifying bacteria containing *nirS* genes were exclusively present in the anoxic hypolimnion. During summer stratification, abundances of AOA, AOB and anammox bacteria decreased in the sediment. After the lake was mixed during fall turnover, AOA, AOB and anammox bacteria increased to high abundances again. In general, nitrogen microorganisms in the water column and sediment displayed a pronounced seasonal succession, which was closely linked to the oxic-anoxic transitions.

Remaining questions on the diversity and functioning of microbial communities that are likely of interest for future research were discussed in Chapter 6. For instance, further efforts need to be made to assess links between the microbial sulfur and nitrogen cycle. Activity and diversity of microorganisms involved in the sulfur and nitrogen cycle and other important biogeochemical cycles (e.g., the carbon cycle) should be explored in further detail. Furthermore, accurate prediction of tipping points during oxic-anoxic transitions in lakes and coastal water will require refined quantification of microbially-mediated oxidation-reduction reactions in biogeochemical cycles. Preliminary results from metagenomics and metatranscriptomics analysis of samples collected from different water layers and the sediment of Lake Vechten indicate that these approaches can expand our understanding of microbial diversity and activity. For instance, the metatranscriptome revealed high activities of *Euryarchaeota* and *Chloroflexi* in the anoxic hypolimnion, whereas our earlier 16S rRNA gene analysis had not detected *Euryarchaeota* and only indicated a very low relative abundance of *Chloroflexi*.

Overall, this thesis advances our knowledge of dynamic changes in microbial community composition (especially of microorganisms involved in the sulfur and nitrogen cycle) in seasonally stratified lakes. In particular, our results show that the composition of microbial communities does not only track seasonal changes in environmental conditions, but also affects and modifies the environment through the involvement of microorganisms in biogeochemical oxidation-reduction processes. This interplay between biogeochemical processes and microbial community composition causes pronounced 'oxic-anoxic regime shifts', with drastic changes in the structure and functioning of lake microbial communities during oxic-anoxic transitions. Hence, the information in this thesis may contribute to an improved understanding and prediction of the major impact of microorganisms on the sulfur

and nitrogen cycle and the development of hypoxia and anoxia in aquatic ecosystems.

Samenvatting

Zuurstofdepletie in wateren kan leiden tot hypoxie (zuurstofarm water) en anoxie (zuurstofloos water), wat massale sterfte van aërobe organismen tot gevolg kan hebben. Hoewel hypoxie en anoxie vaker voorkwamen in de geologische geschiedenis van de aarde, zijn de frequentie, intensiteit en duur van hypoxie en anoxie in meren, kustwateren en open oceanen de afgelopen decennia toegenomen, hoogstwaarschijnlijk als gevolg van eutrofiëring en het broeikas-effect. Zuurstofverbruik door micro-organismen speelt een belangrijke rol bij de ontwikkeling van hypoxie en anoxie en, vice versa, microbiële activiteit wordt ook sterk beïnvloed door veranderingen in zuurstofbeschikbaarheid. Veel van de biogeochemische transformaties waar micro-organismen bij betrokken zijn bestaan immers uit oxidatie-reductie reacties. Aangezien hypoxie en anoxie in toenemende mate een bedreiging vormen voor aquatische ecosystemen, is het noodzakelijk om de interacties tussen micro-organismen en de omslag van zuurstofrijk naar zuurstofloos water beter te begrijpen. Daarom onderzoekt dit proefschrift de diversiteit en dynamiek van microbiële gemeenschappen tijdens de seizoensveranderingen in zuurstofconcentraties in een gestratificeerd voedselrijk meer (het meertje Vechten) in Nederland. De volgende vragen zijn onderzocht:

- (1) Hoe beïnvloedt de omslag van zuurstofrijk naar zuurstofarm water de dynamiek van bacteriën in de gemeenschap?
- (2) Hoe zijn microbiologische en biogeochemische terugkoppelingen betrokken bij deze omslag van zuurstofrijk naar zuurstofarm water?
- (3) Hoe beïnvloeden de seizoensveranderingen in zuurstofconcentraties de microbiële zwavel- en stikstofkringloop?

De invloed van veranderingen in zuurstofbeschikbaarheid op de seizoensdynamiek van bacteriële gemeenschappen in het meertje Vechten werd onderzocht in Hoofdstuk 2. *Cyanobacteria* en *Planktomycetes* waren in de vroege lente overvloedig aanwezig in de waterkolom. Tijdens de zomerstratificatie waren heterotrofe *Alphaproteobacteria*, *Bacteroidetes* en *Actinobacteria* abundant in het

zuurstofrijke epilimnion, *Gammaproteobacteria* (voornamelijk *Chromatiaceae*) domineerden in het metalimnion, en *Chlorobi*, *Betaproteobacteria*, *Deltaproteobacteria* en *Firmicutes* waren overvloedig aanwezig in het zuurstofloze en sulfidische hypolimnion. Na menging van de waterkolom in de herfst verspreidden *Polynucleobacter* (*Betaproteobacteria*) en *Methylobacter* (*Gammaproteobacteria*) zich van het eerdere meta- en hypolimnion naar de oppervlaktelaag en domineerden *Epsilonproteobacteria* in de onderste waterlaag. Toen het meer volledig gemengd en zuurstofrijk werd tijdens de winter en het vroege voorjaar, domineerden *Cyanobacteria* en *Planktomycetes* de bacteriële gemeenschap opnieuw. Over het algemeen liep de samenstelling van de bacteriële gemeenschap op verschillende dieptes in de waterkolom uiteen tijdens de zomerstratificatie en om vervolgens weer te convergeren toen het meer werd gemengd, wat wijst op grote spatio-temporele veranderingen tijdens de omslag tussen zuurstofrijk en zuurstofarm water.

De interacties tussen de samenstelling van de microbiële gemeenschap, biogeochemische oxidatie-reductie reacties en veranderingen in zuurstofconcentraties werden bestudeerd met behulp van een wiskundig model in hoofdstuk 3. Het model voorspelt dat geleidelijke veranderingen in de zuurstofaanvoer belangrijke *regime shifts* kunnen veroorzaken, waarbij het ecosysteem abrupt verschuift van een zuurstofrijke toestand gedomineerd door cyanobacteriën naar een zuurstofloze toestand met fototrofe zwavelbacteriën en sulfaat-reducerende bacteriën (SRB). Waarnemingen van het meertje Vechten ondersteunden deze modelvoorspellingen en toonden aan dat er sprake is van hysteresis in de overgang tussen de zuurstofrijke en zuurstofloze toestand met veranderingen in de microbiële gemeenschap die goed overeenkomen met de modelvoorspellingen. Het optreden van hysteresis en kantelpunten die samenhangen met deze regime shifts is waarschijnlijk een wijdverbreid kenmerk van de omslag van zuurstofrijk naar zuurstofarm water in aquatische ecosystemen, waardoor een plotselinge afname van de zuurstofconcentratie niet gemakkelijk kan worden teruggedraaid. Deze resultaten benadrukken de belangrijke rol die micro-organismen spelen bij het optreden van verschuivingen tussen zuurstofrijk en zuurstofarm water.

De dynamica van SRB en zwaveloxiderende bacteriën (SOB) tijdens de omslag van zuurstofrijk naar zuurstofarm water werd in hoofdstuk 4 in detail bestudeerd. SRB, groene zwavelbacteriën (GSB), paarse zwavelbacteriën (PSB) en kleurloze

zwavelbacteriën (CSB) waren wijdverbreid in het sediment tijdens de winter en vroege voorjaar toen de waterkolom gemengd was. Na stratificatie van de waterkolom in de late lente en zomer verspreiden verschillende SRB-soorten zich uit over het zuurstofloze hypolimnion, terwijl PSB en GSB bloeiden in het metalimnion en hypolimnion tijdens de zomer. Toen zuurstofarm water zich tijdens de menging van deze waterlagen in de herfst door de gehele waterkolom verspreidde, verdwenen SRB en GSB uit de waterkolom, terwijl CSB (voornamelijk *Arcobacter*) en PSB (*Lamprocystis*) dominant werden. Deze bacteriën oxideerden het sulfide dat zich tijdens de zomerstratificatie in het hypolimnion had opgehoopt. Deze resultaten ondersteunen de voorspelling van het eerdere model dat, zodra ecosystemen zuurstofloos en sulfidisch zijn geworden, er een grote zuurstofaanvoer nodig is om deze zuurstofloze toestand te overwinnen en het ecosysteem weer terug te brengen in een zuurstofrijke toestand.

In hoofdstuk 5 werd de seizoensgebonden successie van micro-organismen die betrokken zijn bij de stikstofkringloop onderzocht tijdens de verschuivingen van zuurstofrijk naar zuurstofarm water. Ammonia-oxiderende archaea (AOA), ammonia-oxiderende bacteriën (AOB) en anaërobe ammonium-oxiderende (anammox) bacteriën waren in de winterperiode overvloedig aanwezig in het sediment. Stikstof-fixerende bacteriën en denitrificerende bacteriën namen in het voorjaar in de waterkolom toe, toen nitraat geleidelijk uitgeput raakte en het hypolimnion zuurstofloos werd. Denitrificerende bacteriën die *nirS*-genen bevatten, waren uitsluitend aanwezig in het zuurstofloze hypolimnion. Tijdens de stratificatie in de zomer daalden de abundanties van AOA-, AOB- en anammox-bacteriën in het sediment. Nadat het meer tijdens de herfst was gemengd, namen de AOA-, AOB- en anammox-bacteriën opnieuw toe tot hoge abundanties. De micro-organismen betrokken bij de stikstofcyclus in de waterkolom en sediment vertoonden dus een uitgesproken successie, die nauw verbonden was met de overgangen tussen zuurstofrijke en zuurstofloze condities.

Resterende vragen over de diversiteit en het functioneren van microbiële gemeenschappen die interessant zouden kunnen zijn voor toekomstig onderzoek werden besproken in hoofdstuk 6. Er zou nader onderzoek gedaan kunnen worden naar de samenhang tussen de microbiële zwavel- en stikstofcyclus. Verder is meer onderzoek wenselijk naar met name de activiteit en diversiteit van micro-organismen die betrokken zijn bij de zwavel- en stikstofkringloop en andere belangrijke

biogeochemische cycli (bijvoorbeeld de koolstofcyclus). De voorspelbaarheid van de kantelpunten tussen zuurstofrijk en zuurstofarm water in meren en kustwateren zal bovendien profiteren van een betere kwantificering van de door micro-organismen veroorzaakte oxidatie-reductie reacties in biogeochemische cycli. Voorlopige resultaten van metagenomics en metatranscriptomics-analyse van monsters verzameld uit verschillende waterlagen en het sediment van het meertje Vechten geven aan dat deze benaderingen ons begrip van microbiële diversiteit en activiteit kunnen vergroten. Het metatranscriptoom onthulde bijvoorbeeld hoge activiteiten van *Euryarchaeota* en *Chloroflexi* in het zuurstofloze hypolimnion, terwijl onze eerdere analyse op basis van 16S rRNA sequenties de *Euryarchaeota* niet had ontdekt en slechts een zeer lage relatieve hoeveelheid *Chloroflexi* aangaf.

Samenvattend bevordert dit proefschrift onze kennis van dynamische veranderingen in de samenstelling van microbiële gemeenschappen in gestratificeerde meren. Onze resultaten laten met name zien dat microbiële gemeenschappen niet alleen seizoensveranderingen in hun omgeving volgen, maar ook actief de omgeving beïnvloeden en veranderen door de belangrijke rol van micro-organismen in biogeochemische oxidatie-reductie processen. Dit samenspel tussen biogeochemische processen en de microbiële samenstelling veroorzaakt drastische omslagen tussen zuurstofrijk en zuurstofarm water, die gepaard gaan met grote veranderingen in de structuur en het functioneren van microbiële gemeenschappen. Hiermee kan de informatie in dit proefschrift bijdragen aan een beter begrip en voorspelling van de grote impact van micro-organismen op de zwavel- en stikstofcyclus en de ontwikkeling van zuurstofloosheid in aquatische ecosystemen.

摘要

水体中氧气耗竭会导致低氧区和无氧区的形成，严重危害大多数好氧生物的生存。低氧区和无氧区存在于整个地质时期，但是受水体富营养化和全球变暖的影响，低氧区和无氧区在湖泊、近海以及远洋的发生频率、发生强度和持续时间在过去几十年里显著增加。微生物消耗氧气会加速低氧区和无氧区的形成，而氧气浓度的变化也会显著影响微生物的活性。在微生物调控的生物地球化学转化过程中，包含很多氧化-还原反应。鉴于低氧区和无氧区对水体生态系统的威胁不断加剧，探究微生物与好氧-厌氧转化过程的相互作用是十分紧急且必要的。因此，本论文研究了荷兰一个季节性分层湖泊 (Lake Veichten) 中，微生物在湖水好氧-厌氧转化过程中的群落多样性以及动态变化。本论文主要研究了如下问题：

- (1) 湖泊中好氧-厌氧转化过程如何影响细菌群落动态变化？
- (2) 微生物以及化学反馈是如何影响湖泊中好氧-厌氧转化过程的？
- (3) 湖泊中好氧-厌氧转化过程如何影响微生物硫以及氮循环？

论文第二章研究了湖泊中好氧-厌氧转化过程对细菌群落动态的影响。早春，蓝藻和浮霉菌门大量分布在不同水层。夏季湖水开始分层，异养的 α -变形菌纲，拟杆菌门和放线菌门大量存在于富氧的表水层， γ -变形菌纲（多为着色菌科）成为变温层的主要细菌群落，而绿菌门、 β -变形菌纲、 δ -变形菌纲以及厚壁菌门分布在厌氧含硫的深水层。秋季，湖水被混匀后，整个水层变为缺氧状态，多核杆菌属（ β -变形菌纲）和甲基杆状菌属（ γ -变形菌纲）从先前的变温层和深水层扩散到湖泊表层，同时 ϵ -变形菌纲成为湖泊底层的主要细菌群落。冬季和早春，当湖水完全混合并变为富氧状态后，蓝藻和浮霉菌门重新占据细菌群落的主体。概括来说，不同水层的细菌群落结构在夏季湖水分层时分化，而在湖水混合时趋同。这些实验结果显示细菌群落在湖水好氧-厌氧转化过程中发生很大的空间和时间尺度上的变化。

第三章通过数学模型拟合研究了微生物群落结构，生物地球化学氧化-还原反应以及湖水好氧-厌氧转化过程之间的相互作用。数学模型显示氧气的缓慢变化会引起急剧的稳态转换，即生态系统从以蓝细菌为主导的好氧状态骤变为光合硫细菌和硫酸盐还原菌（SRB）主导的厌氧状态。湖泊中监测到的数据印证了数学模型的预测，证实了

在湖水好氧-厌氧转化过程中存在迟滞现象，而且微生物群落结构发生了如模型所预测的变化。稳态转换中的迟滞现象和临界点现象很可能是水体好氧-厌氧转化过程中的普遍特征，而这会造成氧气浓度发生难以逆转的大幅度下降。以上实验结果揭示并凸显了微生物在调控水体好氧-厌氧转化过程中的重要作用。

论文的第四章详细研究了硫酸盐还原菌和硫氧化细菌（**SOB**）在湖水好氧-厌氧转化过程中的动态变化。冬季和早春，当湖水完全混合时，硫酸盐还原菌、绿硫菌（**GSB**）、紫硫菌（**PSB**）以及无色硫细菌（**CSB**）主要分布在湖泊的底泥中。晚春和夏季，当湖水开始分层，各类硫酸盐还原菌开始迁移到厌氧的深水层。与此同时，紫硫菌和绿硫菌在变温层和深水层大量增殖。秋季，深水层在湖水混匀过程中扩散到整个水体，紫硫菌和绿硫菌从水体中消失，而无色硫细菌（主要是弓形菌属）和紫硫菌（俊囊菌属）开始主导细菌群落，并氧化湖泊中夏季分层时期积累的还原性硫化物。这些实验结果显示一旦水体生态系统进入厌氧硫化状态，需要大量的氧气才能改变这种稳态并把整个生态系统转化到好氧状态。

论文第五章研究了湖水好氧-厌氧过程中参与氮循环的微生物的季节动态变化。冬季，氨氧化古菌（**AOA**）、氨氧化细菌（**AOB**）、厌氧氨氧化细菌（**anammox**）大量分布于湖泊底泥中。春季，当硝酸盐被逐渐消耗以及深水层变为厌氧后，水层中固氮菌和反硝化细菌的数量开始增加。含有**nirS**基因的反硝化细菌仅分布于厌氧的深水层中。夏季湖水分层后，湖泊底泥中氨氧化古菌、氨氧化细菌、厌氧氨氧化细菌的量锐减。秋季，当湖泊被混匀后，这些细菌的量又开始增多。总的来说，参与氮循环的微生物在湖水和底泥都发生了明显的季节动态变化，而这些变化与好氧-厌氧转化过程紧密相关。

第六章讨论并展望了未来有待开展的关于微生物多样性及功能的研究。比如，探索微生物硫循环和微生物氮循环之间的相互关联，以及深入研究参与硫循环、氮循环以及其它重要的生物地球化学循环（如碳循环）的微生物的种类及活性。此外，精准预测湖泊和近海中好氧-厌氧转化过程中的临界点还需要精确地量化出微生物调节的生物地球化学过程中的氧化-还原反应。不同水层和底泥中的微生物的宏基因组和宏转录组的初步分析结果显示这些分析方法可以扩展我们对微生物多样性和活性的认识。例如，宏转录组分析结果显示广古菌门和绿弯菌门在厌氧深水层有很高的活性，而**16S rRNA**基因分析并未探测到广古菌门，同时仅显示了极少量的绿弯菌门。

摘要

综上所述，本论文提升了我们对季节性分层湖泊中微生物，尤其是参与硫循环和氮循环的微生物的空间和时间动态变化的认识。值得注意的是，本论文的研究结果揭示微生物群落并不是完全被动接受环境因素的影响，微生物也可以通过参与生物地球化学中的氧化-还原反应来影响和改变周边环境。这种生物地球化学反应和微生物群落结构之间的相互作用引发了水体中明显的“好氧-厌氧稳态变化”，并伴随着湖泊中微生物群落结构和功能的急剧变化。因此，本论文中的信息有助于我们更精准地理解和预测微生物对硫循环和氮循环的重要影响，以及水体生态系统中低氧区和厌氧区的形成。

Author Contributions

Chapter 2: JH and GM designed the study. MD, RS, KK and GM performed the sampling and data analysis. MD, JH and GM wrote the manuscript.

Chapter 3: GM and JH conceived the idea, and TB and RJA added further suggestions. TB, RS, and JH designed the model. TB and JH performed the model simulations and analysis. MD, RS, and GM sampled the lake. MD performed the nutrient analysis. MD and GM performed the 16S rRNA gene sequence and network analysis. TB, MD, GM, and JH wrote the manuscript, and all authors commented on the final version.

Chapter 4: MD, JH and GM designed the study. MD performed the fieldwork and lab experiments. MD, JH and GM analyzed the data and wrote the manuscript.

Chapter 5: MD, JH and GM designed the study. MD, CB and MSM performed the fieldwork and lab experiments. MD, JH and GM analyzed the data and wrote the manuscript.

Curriculum Vitae

Muhe Diao was born on the 31st of October 1987, in Shandong, China. After 4-years bachelor studies in biology at Shandong Agricultural University, he became interested in environmental science. Therefore, he followed a master program in Environmental Science and Engineering at Shandong University in 2009. During the master study, he performed research in biological wastewater treatment, in specific on rapid formation of aerobic nitrifying granule and its stability. Since then, he was fascinated by the interactions between microorganisms and the surrounding environment.



In July 2012 he got a PhD scholarship from Chinese government, which can support a 4-years study over the world. Hence, he moved to the Netherlands and started his PhD study at the Department of Freshwater and Marine Ecology (FAME), University of Amsterdam in January 2013. His research is on 'Interactions between microorganisms and oxic-anoxic transitions', and supervised by Prof. Gerard Muyzer and Prof. Jef Huisman. He has presented and discussed the research results in national and international conferences. The results from his PhD are described in this thesis and also in several peer-reviewed publications.

Publications

- Diao M**, Huisman J, Muyzer G. (2018). Spatio-temporal dynamics of sulfur bacteria during oxic-anoxic regime shifts in a seasonally stratified lake. *FEMS Microbiology Ecology* **94**: fiy040.
- Wang S, Zhang B, **Diao M**, Shi J, Jiang Y, Cheng Y *et al.* (2018). Enhancement of synchronous bio-reductions of vanadium (V) and chromium (VI) by mixed anaerobic culture. *Environmental Pollution* **242**: 249-526.
- Bush T, **Diao M**, Allen RJ, Sinnige R, Muyzer G, Huisman J. (2017). Oxic-anoxic regime shifts mediated by feedbacks between biogeochemical processes and microbial community dynamics. *Nature Communications* **8**: 789.
- Diao M**, Sinnige R, Kalbitz K, Huisman J, Muyzer G. (2017). Succession of bacterial communities in a seasonally stratified lake with an anoxic and sulfidic hypolimnion. *Frontiers in Microbiology* **8**: 2511.
- Cao X, **Diao M**, Zhang B, Liu H, Wang S, Yang M. (2017). Spatial distribution of vanadium and microbial community responses in surface soil of Panzhihua mining and smelting area, China. *Chemosphere* **183**: 9-17.
- Gao M, **Diao M**, Yuan S, Wang Y, Xu H, Wang X. (2017). Effects of phenol on physicochemical properties and treatment performances of partial nitrifying granules in sequencing batch reactors. *Biotechnology Reports* **13**: 13-18.
- Wang X, **Diao M**, Yang Y, Shi Y, Gao M, Wang S. (2012). Enhanced aerobic nitrifying granulation by static magnetic field. *Bioresource Technology* **110**: 105-110.
- Shi Y, Wang X, Qi Z, **Diao M**, Gao M, Xing S *et al.* (2011). Sorption and biodegradation of tetracycline by nitrifying granules and the toxicity of tetracycline on granules. *Journal of Hazardous Materials* **191**: 103-109.

Manuscript

- Diao M**, Balkema C, Muñoz MS, Huisman J, Muyzer G. Seasonal succession of bacteria and archaea involved in the nitrogen cycle of a seasonally stratified lake. (*submitted*)

Acknowledgements

Doing a PhD is like running a marathon, requiring enormous time and effort. Finally, I am crossing the finish line! Looking back, I would like to thank all the people who helped me during the past 5 years. Without their guidance and help, I would not be able to get here.

Gerard and Jef, many thanks for offering me the opportunity to start a PhD study at the University of Amsterdam. Thereby I can explore science and life in Europe, which greatly expands my knowledge and experiences! Gerard, you picked me up from Schiphol Airport in a cold winter evening, which made me feel warmer and the start of my Dutch life much easier. In the following 5 years, you guided me in fieldwork, lab work, experimental design, data analysis and scientific writing. It is impossible for me to finish my PhD without your great effort, thank you so much! Jef, your amazing memory, keen insight, fast thinking, great passion and especially pursuing perfection impress me all the time. You instructed me how to ask and answer scientific questions, and how to tell the story in a logical and graceful manner, which are the prerequisites to do good research. Working together with you has always been very productive and promising, inspiring me to go further in my career. Just like 5 years ago, you and Gerard helped me to get another great opportunity to continue my research at the Leibniz Institute DSMZ in Germany! All in all, it is a great pleasure to be supervised by both of you, and I really appreciate the knowledge and the honor you have offered!

Ruben and Tim, working together and hanging out with you guys are really pleasant, thanks so much for all the cooperations and good times! I would like to thank my other collaborators, Prof. Karsten Kalbitz and Prof. Rosalind Allen, for their contributions to the project. To my student, María and Bart, thanks for the good work you have done.

During these years, we have visited Lake Vechten 22 times. Thanks to all the great 'science drivers': Cherel, Pieter, Bas, Jolanda, and Maud. Emily, thanks for joining the field work with Cherel and me again and again, having McDonald's burgers and ice cream after intensive fieldwork was awesome! Anca and Estelle, you are always ready to help me whenever I need, thanks so much for your assistance in the fieldwork, lab work and data analysis! Tom, how about another swim in Lake

Vechten and some more drinks? Peter and Leo, thanks for analyzing all the samples from Lake Vechten, and all the delightful conversations we had.

Amanda, everyone knows how hard it is to plan two PhD defenses on the same day. So glad we made it! Thanks for all the smart jokes and massive Thanksgiving dinners! David, wanna try early music together?

Catarina and Tim, I feel so happy to see you guys getting together and having a happy family! Tim, I run a half marathon with a name 'Wolfgang' last year, and now I am in Wolfgang's country, coincidence or destiny?

Charlotte, thanks for your unique perspectives, creative ideas and great music, very special and very nice!

Erik, thanks for the conversations after work, thereby I do not feel so lonely in the office.

Hey Gio, StarCraft? Honor guide us!

Hongjie, we had boat trip, horse riding, jägermeister, schweinshaxe and summer festival together, what is the next?

Joost, it is so great to meet you and be your paranymp for your PhD defense. Buddy, now your paranymp is going to have his PhD defense!

Lex, doing research and (especially) sports with you has so much fun ☺

Qian and Quanxing, thanks for all the good times we shared together.

Veerle, you have been my closest neighbor for 4 years (or maybe even longer?). Thanks for being there, helping and encouraging me all the time! I can easily write a single page to anyone of you guys to express my gratitude. Anyway, long story short, I really appreciate the drinks, dinners, parties, running, football, bowling, Karting, and all the happy moments we shared together. These beautiful memories make my Amsterdam life so unforgettable.

I would like to thank Hans and Maayke, for encouraging me to 'pursue a career' and 'keep the spirit'! Thanks to Petra, Susanne, Merijn, Pascale, Mariël, Elisa, Fleur, Anouk, Corrien, Maria, and other colleagues from the FAME department for all the academic and non-academic activities.

Thanks to Alex, Bart, Ke, Lin, Songyu, Huasheng, Marian, Milo, Paula, Seyed, Natasha, Niko, Tom and other friends from IBED for the drinks, BBQ, football and parties.

Acknowledgements

Jason, Xia, Xiaoning, Stefano and Simon, I cannot imagine how my Amsterdam life would be without you guys. All the drinks, dinners, parties and trips we had together were fulfilled with countless laughs! Thanks guys!

To my powerful and amazing gym buddies: Dongdong, Wei, Yansong, Shan, Yanni, Hui, Dechao and Anna, it is so nice to have you guys around! Becoming stronger and happier together is wonderful! Wish we always have the strength!

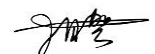
I have lived in the east, north and west of Amsterdam. As Kenan described, I moved like a Mongolian in the last year of my PhD. I was really lucky that my roommates were all very nice to me. Xiang, Jiajia, Lovro and Joser, it was really nice to share the apartments and happiness with you. Mika, Kenan, Yixuan, Leigo, Nancy, Henry and Angela, thanks for all the good times we shared together!

I have made many Chinese friends in Amsterdam. Zepeng, Yang Liu, Que, Hui Xiong, Xiaotang, Wei Du, Qianqian, Jie, Yanfang, Xiaolong, Yongqiang, Yuan Gao, Zhaochun, Shaosong, Ninghang, Hao Zhu, Wei Quan, Lingxue, Zhou Tang, Zhongyu, Zhongcheng, Yadan, Jiesen, Wenyang, Chang Li, Shuai Liao, Beibei, Nan Jiang, Sijia, Xiaojing, Bangchi, Benchi, Liang Zhao, Junchao, Jason Liu, Chuan Wu, Xiaoxin, Lilly and Jiayi, thanks for sharing the good times with me in Amsterdam.

Thanks to my master supervisors, who introduced me to science, Prof. Shuguang Wang, Dr. Nan Bao and Dr. Xinhua Wang. Thanks to Jessie, for all the support in these years, I wish you all the best in the future. Thanks to my friends in China, England and Australia: Suqing, Jinlin, Pengyu, Guohui, Chao Song, Pengpeng, Fenglong, Kang and Lin Jing for their support and help.

Xinyu, thanks for designing the cover for this thesis. 欣遇异国，诗画半夏。

At last, I would like to thank all the support from my family. I always feel so lucky to have my grandparents, parents, uncles, aunts, brothers, sisters, and my nieces and nephews in my life. It is impossible for me to finish this long study without your countless encouragements and endless support. 感谢姥姥、姥爷和父母三十年来的无私关怀和言传身教，深恩此生难报！感激爷爷奶奶、舅姨叔叔和兄弟姐妹们一直以来给予我的理解、包容、支持和关爱。有幸做你们的家人，真好！



2018.08.18

Braunschweig, Deutschland